Identifying the spatial pattern of wood distribution in northeastern North American streams

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ABSTRACT

The spatial distribution of instream wood influences important ecological processes but has proven challenging to describe quantitatively. We present a modified version of a previously described metric used to quantify the spatial extent and pattern of instream wood distribution, then apply this approach in evaluating the distribution of wood habitat in forested northeastern North American streams. This revised metric, a 'binned neighbor-K analysis', provides greater resolution in evaluating the presence of aggregated, periodic, or segregated wood distributions in stream ecosystems. We employed this metric in evaluating the distribution of wood within 17 streams in two regions of northeastern North America. Our results indicate that the binned neighbor-K approach more accurately represents the spatial extent at which wood accumulates in streams by identifying recurring intervals in streams within which instream wood is not present and by more accurately quantifying the spatial extent of wood aggregations and periodically repeating occurrences of accumulated wood. We also used this metric to quantify the overall extent of wood 'organization' in streams, which revealed similarities and differences in instream wood distribution patterns in the two regions evaluated. Wood distribution patterns in both study regions were generally consistent with our expectations of increased organization at an intermediate stream size (up to 10 m bankfull width), then in larger streams (>10 m) wood was less organized. These observed patterns result from landscape and ecosystem influences upon wood accumulation and movement in streams.

1. Introduction

Despite the widely recognized importance of instream wood and organic debris dams in forested stream ecosystems, analytical approaches to quantify the spatial extent and pattern of instream wood distribution are rare and the usefulness of available metrics has been seldom evaluated. Wood influences stream geomorphology (Bilby, 1984; Montgomery et al., 1995; Buffington et al., 2002; Andreoli et al., 2007), biotic habitat (Elliot, 1986; Smock et al., 1989; Cederholm et al., 1997; Roni and Quinn, 2001), and biogeochemical cycling (Webster et al., 2000; Ensign and Doyle, 2005; Warren et al., 2007), therefore quantifying the spatial distribution of instream wood is important for understanding the corresponding distribution of key stream functions.

Although a small number of previous studies have quantified patterns in instream wood distribution and attempted to assess underlying factors that influence the regularity and spatial heteroge-neity of these key structural elements (Wing et al., 1999; Keim et al., 2000; Kraft and Warren, 2003; Young et al., 2006; Morris et al., 2007; Wohl and Jaeger, 2009), methods to quantify spatial pattern in wood or other stream features are not well enough established to be included in the standard toolbox for stream ecologists (Hauer and Lamberti, 2006). With this in mind, the current study has two components. First, we present a modified version of a previously described metric (Kraft and Warren, 2003) used to quantify the spatial extent and pattern of instream wood distribution. Second, we apply this new approach in evaluating the distribution of instream wood in forested northeastern North American streams.

The most commonly reported pattern of wood distribution in streams has been the accumulation of instream wood into wood jams, also commonly referred to as woody debris dams (Lienkaemper and Swanson, 1987; Nakamura and Swanson, 1994; Montgomery et al., 1995; Gurnell et al., 2002; Young et al., 2006; Manners and Doyle, 2008). Alternative spatial distribution patterns of instream wood have been quantified or described in only a few previous studies; these patterns include segregation (stream sections from which wood is absent) and periodicity (wood observed at regularly spaced intervals) (Wing et al., 1999; Keim et al., 2000; Kraft and Warren, 2003).

In a previous publication we described and used a neighbor-K analysis to quantify the spatial arrangement of instream wood in a

single dimension using a series of distance intervals (Kraft and Warren, 2003). For each piece of wood along a stream reach, this metric evaluated the number of other pieces occurring within increasing distance intervals extending upstream or downstream from the focal piece of instream wood. The aggregate number of instream wood pieces encountered within each interval was then compared to results from the same analysis conducted with 1000 randomized wood distributions to determine whether wood in the study stream was aggregated, segregated or demonstrated periodicity in spatial arrangement. Although wood segregation and wood periodicity were occasionally noted in the previously published neighbor-K analysis, these trends were rarely significant (Kraft and Warren, 2003).

In ongoing evaluations of instream wood conducted subsequent to that publication, we recognized a limitation inherent in the original analytical approach, in that aggregation of wood at smaller scales inappropriately influenced the metric used to assess wood distributions at subsequently larger spatial extents. Specifically, the previous metric included all wood within small distance intervals in the summed value for each larger distance interval. The use of overlapping rather than discrete distance intervals decreased the probability of the metric recognizing significant segregation. Similarly, the presence of substantial segregation at one or more distance intervals reduced the ability of the neighbor-K metric to identify periodicity at subsequent distance intervals. In response to this deficiency, we have revised the neighbor-K analysis by assessing the presence of wood at discreet distance intervals. This revised metric, which we refer to as the 'binned neighbor-K analysis', provides greater resolution in evaluating the regular occurrence or regular absence of wood along a stream channel relative to a random distribution.

A second component of this study uses the binned neighbor-K analysis to quantify trends of instream wood distribution across streams in central New Hampshire and northern New York State. Wood accumulation in streams has been reported to occur in association with particular geomorphic features, such as channel meanders and island point bars (Abbe and Montgomery, 1996; Gurnell et al., 2002; Parsons and Thoms, 2007). In large stream systems where the length of instream wood is generally less than the bankfull width of the stream, regular accumulations of wood often occur at predicable depositional locations along pool-riffle intervals (Braudrick and Grant, 2000; Gurnell et al., 2002; Wohl and Jaeger, 2009). Wood export is more restricted in mid-sized streams where some instream wood pieces are longer than the bankfull width. In these streams, the transport and subsequent accumulation of wood likely depends upon the interaction between stream width, stream energy, and the presence or absence of channel-spanning wood (Lienkaemper and Swanson, 1987; Young, 1994; Martin and Benda, 2001; Gurnell, 2003). In small streams with limited transport capacity, the spatial arrangement of wood is likely to be most influenced by input processes from the surrounding landscape rather than by transport and accumulation; and wood losses are dominated by decomposition processes (Gurnell, 2003; Wohl and Jaeger, 2009).

Bankfull width also influences the occurrence and absence of instream wood by constraining the movement of long pieces and by reflecting the discharge capacity at a particular location (Dunne and Leopold, 1978). In this study, we expected to find the least amount of instream wood organization — i.e., aggregation or segregation in wood distributions — in small streams. We expected to find segregated patterns of wood distribution in larger streams with greater transport potential, reflecting the occurrence of stream locations from which wood was absent and transported downstream. Finally, we expected to find the greatest amount of wood periodicity in the largest streams where wood transport and deposition were expected to occur in association with channel features.

2. Material and methods

2.1. Study sites

This study was conducted within 17 streams in two regions of northeastern North America: 11 streams within the Hubbard Brook Experimental Forest (NH, USA) and 6 streams in the Adirondack Mountains (NY, USA). Riparian zones were primarily dominated by mature, mixed hardwood-conifer forests. Stream bankfull width at the study sites ranged from 1.4 to 15.2 m; stream gradient ranged from ~1% to ~24%, and reach lengths were 150 to 1200 m long (from 22 to 139 times mean bankfull width) (Table 1). Additional detail regarding site characteristics can be found in Keeton et al. (2007) for the Adirondack locations and in Warren et al. (2007) for the Hubbard Brook streams.

2.2. Neighbor-K analysis

We recorded the linear location along the stream reach of all large instream wood within the bankfull channel of each stream by measuring the wood location from an upstream or downstream reference point using a 100-m tape placed through the center of the stream channel. Large instream wood was defined as dead wood within the bankfull channel with diameter >10 cm and length >1 m. Using the same criteria as our previous research in this region (Keeton et al., 2007; Warren et al., 2009), debris dams were defined as an accumulation of smaller wood (between 0.5 and 1 cm in diameter) against or around at least one key piece of instream wood >10 cm in diameter (with a minimum debris dam volume of ~0.5 m³). Stream study reaches were >150 m in length and did not include any anthropogenic features (e.g., roads or culverts).

To examine the distribution patterns of instream wood and debris dams within stream reaches, we modified a linear neighbor-K analysis (Kraft and Warren, 2003) that was originally conceived as a one-dimensional version of Ripley's K, a second-order statistic that evaluates the spatial pattern of points within a landscape (Ripley, 1977). A similar neighbor-K statistic has been used to evaluate the aggregation and segregation of events through time (Bhopal et al., 1992; Cressie, 1993; Diggle, 2006). In our application, single pieces of instream wood were characterized as points or 'events' distributed along a one-dimensional transect within each stream reach. The distributions of instream wood were considered one-dimensional because the widths of study streams were small by comparison with reach lengths.

The previously used neighbor-K statistic evaluates the number of points within a series of distances centered at each point (e.g., piece of instream wood) within a stream. Our previous estimates of $\hat{K}(t)$, the test statistic, were calculated as follows:

$$\hat{K}(t) = n^{-1} \sum_{i \neq j} \sum_{i \neq j} I_t \left(u_{ij} \right) \qquad (1)$$

where n is the number of points in the stream reach; u_{ij} is the distance between points i and j; $I_t(u)$, the counter variable, equals 1 if $u \leq t$ and equals 0 if $u > t$; and the summation is over all pairs of points not more than distance t apart.

For the binned neighbor-K analysis, the binned estimates of $\hat{K}(t)$ differ from the previous test statistic by evaluating the distribution of points (events) within specific distance 'bins' of length (b), rather than throughout an entire distance interval (t). The new test statistic is calculated over a distance range from $(t_m$ to $t_{m+1})$ that encompasses a distance increment (b), such that $t_m = b*m$ and $t_{m+1} = (b*m) + (b-1)$ where m ranges from 0 to an integer equal to 50% of the reach length divided by the bin length (b), as follows:

$$\hat{K}(t_m \rightarrow t_{m+1}) = n^{-1} \sum_{i \neq j} \sum_{i \neq j} I_{t_m \rightarrow (t_{m+1})} \left(u_{ij} \right) \qquad (2)$$

Table 1
Stream and wood characteristics for sites in the White Mountains of New Hampshire and the western Adirondack Mountains of New York State. Bin percentages were calculated using 5-m bin intervals.

Stream	Mean bankful width (m)	Reach length (m)	Gradient	# LWD per 100 m	# Dams per 100 m	% Wood in dams	% Bins segregated	# Bins aggregated/periodic	# Bins random
White Mountain streams, NH									
Trib b/t Can and Zig	1.4	200	17.7%	20.0	10.5	58%	0%	0%	100%
HBEF W1	2.2	238	19.2%	34.0	14.3	52%	4%	13%	83%
HBEF W6	2.9	246	23.6%	30.1	8.1	47%	46%	21%	33%
Crazy Brook	3.0	200	10.0%	30.0	6.5	45%	25%	10%	65%
HBEF W7	3.8	400	10.5%	25.3	3.3	44%	60%	13%	28%
HBEF W3	4.0	300	20.8%	26.7	3.0	31%	19%	13%	68%
Bear Brook	4.5	200	19.4%	29.5	4.5	32%	20%	30%	50%
Zig Zag_western trib	6.3	500	7.3%	18.6	2.4	34%	24%	30%	46%
Zig Zag_Mainstem	6.5	500	7.3%	20.6	1.8	60%	44%	26%	30%
Hubbard Brk_Upper Mainstem	8.5	700	1.5%	19.9	0.7	42%	40%	29%	31%
Hubbard BK_Lower Mainstem	15.2	1200	2.9%	6.2	0.5	26%	13%	22%	65%
Adirondack Mountain streams, NY									
Beth's Brook	3.7	150	1.2%	24.7	2.7	19%	0%	0%	100%
Otter Brook	5.0	200	0.8%	43.0	2.0	14%	0%	0%	100%
LML_outlet_blockdam	7.0	325	2.5%	35.4	3.7	38%	38%	9%	53%
Pico Creek	8.0	200	2.9%	47.5	6.5	81%	35%	20%	45%
LML outlet — Oxbow	10.5	500	2.5%	14.0	1.4	43%	20%	22%	58%
Canachagala Brook	10.9	250	2.3%	7.6	0.4	43%	12%	8%	80%

where n is the number of points in the stream reach; u_{ij} is the distance between points i and j; $I_{t_m \to (t_{m+1})}$ is the counter variable, which equals 1 if $t_m \leq u \leq t_{m+1}$ and equals 0 if $u > t_{m+1}$ or $u < t_m$. This is similar to the previously used neighbor-K statistic except that the summation is over all pairs of points within a distance bin $t_m \to t_{m+1}$.

For each spatial point pattern analysis, the test statistic was calculated for the observed distribution of all pieces of wood within a particular stream reach, after which this value was compared with those from 1000 Monte Carlo simulated wood distributions. For each Monte Carlo run, simulated instream wood locations were randomly selected (without replacement) from within a stream-specific length of reach, and the number of pieces of wood was specified by the actual number of pieces observed within the study reach. Spatial regularity in the presence or absence of wood was determined relative to the randomized data. Results from this analysis are referred to as 'significant' when observed wood distributions included more wood than expected at a particular binned distance in >97.5% of randomized simulations or less wood than expected within that binned distance in <2.5% of simulations, thereby mimicking a two-tailed test with a p-value of 0.05. Given the potential for one out of every twenty bins to be assigned significance by chance using these criteria, we discuss below the selection of an appropriate bin size to balance information gained versus inappropriately characterizing a pattern as significant.

2.3. Evaluating instream wood distribution patterns

We provide two specific examples comparing results from the previously developed neighbor-K statistic presented by Kraft and Warren (2003) and the binned neighbor-K statistic described by Eq. (2). These comparisons used data from Bear Brook, a small Hubbard Brook tributary (bankfull width = 4.5 m) and from a larger stream, Little Moose Lake outlet (at Oxbow) in the Adirondack Mountains (bankfull width = 10.5 m). Using data from these two streams, results were also compared using three different bin sizes (5, 10, and 20 m) with the binned neighbor-K metric.

The binned neighbor-K analysis was subsequently applied as a regional analysis of instream wood distributions in 17 study streams, using 5-m bin intervals. First, the statistic was used to determine the proportion of bins in each stream in which a "significantly" greater occurrence or absence of wood was observed than would be expected

by random chance. Next, the amount of regularity in wood occurrence (percentage of bins with wood occurring more often than expected at a given distance interval) and regularity in wood absence (percentage of bins in which wood occurred less frequently than expected at a given distance interval) was evaluated as a function of bankfull width for each study stream. The proportion of bins in which the occurrence of wood was not significantly different from a random distribution was used as an overall measure of the amount of organization of the wood distributed within a particular stream. The overall proportion of "random" bins (those with values that did not differ significantly different from random) was evaluated as a function of bankfull width for streams in each of the two regions. In order to evaluate the association between these two metrics of wood organization, the proportion of bins with regularity in wood occurrence was evaluated as a function of the proportion of bins in which wood was consistently absent in that same stream.

3. Results

3.1. Comparing the two spatial pattern metrics

The original neighbor-K statistic indicated the presence of wood aggregations at spatial extents ranging from 0 to 20 m and from 40 to 57 m in the 200-m study reach of Bear Brook, but no areas of segregation (less wood than expected by chance) were revealed by this analysis (Fig. 1). By contrast, the modified analysis using a binned neighbor-K statistic (Eq. 2) indicated the presence of wood aggregations within the first 5-m distance bin (0–5 m), as well as aggregation/periodicity at distances extending from 35 to 39, 45 to 49, 50 to 54, 60 to 64, and 90 to 94 m (Fig. 2A). The binned neighbor-K analysis also showed the presence of wood segregation (regularly spaced intervals without wood) at four distance intervals: 15–19, 70–74, 75–79 m, and 95–99 m (Fig. 2A).

In Little Moose Lake outlet, the original neighbor-K analysis indicated a high degree of aggregation at almost all spatial scales (Fig. 3). This suggested that wood was not randomly distributed at almost every spatial extent, an observation that was largely uninformative by comparison with the revised, binned analysis that revealed wood aggregation, periodicity, and segregation at various distance intervals in this stream reach (Fig. 4A).
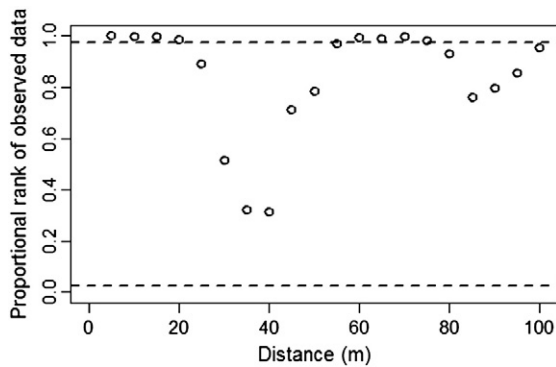
Fig. 1. Circles show output from the initial modified neighbor-K statistic for observed wood distribution in Bear Brook; solid lines show upper (>97.5%) and lower bound (<2.5%) for 1000 Monte Carlo simulations.
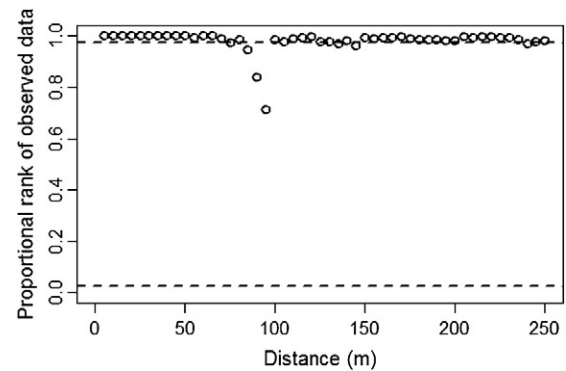

Fig. 3. Circles show output from the initial modified neighbor-K statistic for observed wood distribution in Little Moose Lake outlet (at Oxbow); solid lines show upper (>97.5%) and lower bound (<2.5%) for 1000 Monte Carlo simulations.

3.2. Bin size comparisons

In comparing results from the three bin sizes, the proportion of bins indicating wood organization (bins with more or less wood than expected by random chance) varied somewhat with bin size, but the trends remained the same. In Bear Brook, 30% of the 5-m bins indicated that wood occurred at specific distance intervals more often than expected by random chance (aggregation and/or periodicity), 25% of the bins indicated that wood occurred less frequently than expected at those given intervals (segregation), and the observed wood distribution corresponded with a random distribution in 45% of the distance interval bins (Fig. 2). When bin size was increased to 10 m, 30% of the bins again had more wood than expected, 20% had less wood than expected, and 50% indicated a wood distribution consistent with a random distribution. Results using 20-m bin intervals were somewhat similar despite the small number (5) of bins evaluated, with 40% (2) indicating aggregation/periodicity, 20% (1) indicating segregation, and 40% (2) indicating a random distribution of instream wood. A similar comparison using data from Little Moose Lake outlet showed a comparable pattern, in that

changing bin sizes did not substantially alter the relative amount of wood organization, though some differences between the bin sizes tested were evident in the spatial extent of wood organization (Fig. 4). Overall, although the patterns of proportional organization remained generally consistent, the ability to discriminate patterns in wood distribution was reduced when larger bin sizes were used (Fig. 4). Notably, the use of fewer bins decreased the possibility of falsely classifying significance at any given distance interval, therefore some intermediate bin size is preferable so that spatial pattern can be discriminated without evaluating such a large number of bins that nonrandom distributions are inevitably observed.

3.3. Patterns of instream wood distribution

The proportion of bins in which wood occurred with greater frequency than expected for a random distribution (aggregation and periodicity) was, as predicted, relatively low in small streams. This proportion increased with increasing stream size up to a mean bankfull width of 8–10 m in study streams. The largest streams in both the Adirondacks (NY) and White Mountains (NH) exhibited a
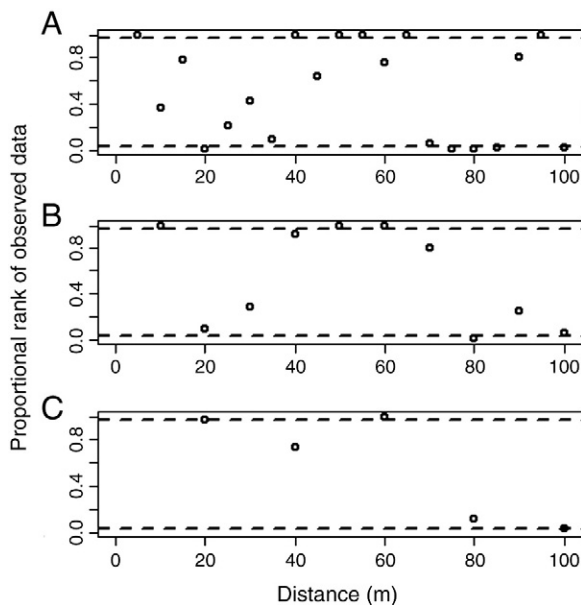

Fig. 2. Results from the new "binned" neighbor-K statistic for observed wood distribution in Bear Brook (circles) for (A) 5-m distance bins (e.g., 0–4 m, 5–9 m, etc.); (B) 10-m distance bins; and (C) 20-m distance bins. Dashed lines show upper (>97.5%) and lower bound (<2.5%) for 1000 Monte Carlo simulations.
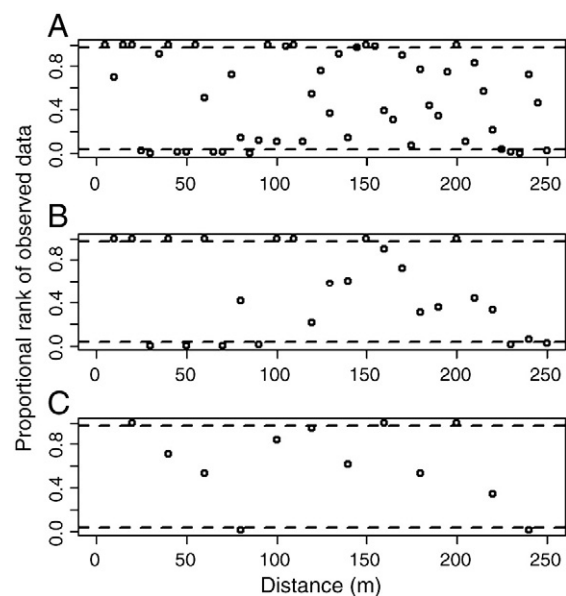

Fig. 4. Results from the new 'binned' neighbor-K statistic for observed wood distribution in Moose Lake outlet (at Oxbow); (circles) for (A) 5-m distance bins (e.g., 0–4 m, 5–9 m, etc.); (B) 10-m distance bins; and (C) 20-m distance bins. Dashed lines show upper (>97.5%) and lower bound (<2.5%) for 1000 Monte Carlo simulations.

lower proportion of bins with regularity in wood occurrence than mid-sized streams, but more than the smallest streams. Yet one consistent difference between regions was the larger proportion of bins with regularity in wood occurrence observed in White Mountain streams for all bin sizes examined. A quadratic fit applied to these data was significant for White Mountain but not Adirondack streams (White Mountain: $n = 11$, $p = 0.006$, $r^2 = 0.71$; Adirondacks: $n = 6$, $p = 0.11$, $r^2 = 0.50$; Fig. 5A), though the fit of this model for White Mountain streams was strongly influenced by one site with great leverage. Regularity in the absence of wood from streams (segregation) followed a similar trend as for wood aggregation/periodicity, but the quadratic fit was not significant for either stream region, though in Adirondack study streams it accounted for more than 75% of the observed variation (White Mountain: $n = 11$, $p = 0.22$, $r^2 = 0.32$; Adirondacks: $n = 6$, $p = 0.10$, $r^2 = 0.78$; Fig. 5B).

The overall proportion of distance intervals at which instream wood was randomly distributed demonstrated the opposite pattern from that of wood organization, with a lower proportion of random bins observed in mid-sized streams compared to both smaller and the largest streams (though mean bankfull width in only three study streams was >10 m). A quadratic fit to these data was significant for White Mountain streams and accounted for a substantial proportion of the variation in the dependent variable (proportion of bins with a random distribution) ($n = 11$, $p = 0.04$, $r^2 = 0.56$; Fig. 6). However, despite accounting for 78% of the observed variation, the relationship was not significant for Adirondack study streams ($n = 6$, $p = 0.10$, $r^2 = 0.78$; Fig. 6). No significant correlation was observed between instream wood aggregation/periodicity and instream wood segregation for either region ($p = 0.30$ and 0.11 for White Mountain and Adirondack streams, respectively).

Fig. 6. Relationship between the proportion of bins with wood distributed as expected by chance (random) relative to bankfull width for streams in the White Mountains, NH (filled diamonds) and the western Adirondack Mountains, NY (open squares), using 5-m bin intervals. The quadratic fit to the data was significant for White Mountain streams (solid line, $n = 11$, $p = 0.04$, $r^2 = 0.56$) but not Adirondack streams (dashed line, $n = 6$, $p = 0.10$, $r^2 = 0.78$).

4. Discussion

Metrics that allow consistent and meaningful assessment of spatial pattern have been useful in developing an understanding of a variety of ecological processes (Fortin and Dale, 2005; Turner, 2005). We developed an improved version of a neighbor-K analysis that provides greater resolution in quantifying the spatial extent of aggregation, periodicity, and segregation exhibited by stream features, such as the distribution of instream wood. In an application of this metric to streams in New Hampshire and northern New York, we found that instream wood was most highly organized — i.e., exhibited the greatest degree of nonrandom distribution patterns — in streams ranging from 6 to 10 m bankfull width. Smaller streams exhibited less wood aggregation and fewer areas of wood segregation; this spatial pattern likely resulted from lower levels of stream energy, greater wood retention and the greater proportion of wood pieces able to span the narrow channels of small streams. This analysis describes the relationship between stream size and the distribution of instream wood, reflecting a strong influence of wood mobility on the spatial arrangement of wood habitat in streams.

Our study results also indicate that the binned neighbor-K approach more accurately represents the spatial extent at which wood accumulates in streams. The broad range of distance intervals over which the unmodified linear neighbor-K statistic identified wood aggregations in such streams as Bear Brook appears to be an artifact of the statistic. This is illustrated by results from the binned neighbor-K statistic, which repeatedly showed an aggregated distribution of wood at spatial extents of 5 m in the Bear Brook example and in other streams evaluated in this study (not shown). This short-distance scale of aggregation is due to the consistent accumulation of individual pieces of wood within debris dams. The calculation used in the unmodified linear neighbor-K statistic erroneously extended this distance scale of aggregation beyond the spatial extent of wood accumulation. This was due to the use of information from debris dam aggregations at distances incrementally extending beyond 5 m. By contrast, the binned statistic only uses information from a specific distance interval, therefore it better reflects the scale of wood accumulation in debris dams.

The binned neighbor-K statistic also more effectively identified recurring intervals in streams within which wood is not present, an aspect of wood distribution that is important in many streams (Martin and Benda, 2001; Angradi et al., 2004). The unmodified linear neighbor-K statistic seldom indicated the presence of segregated
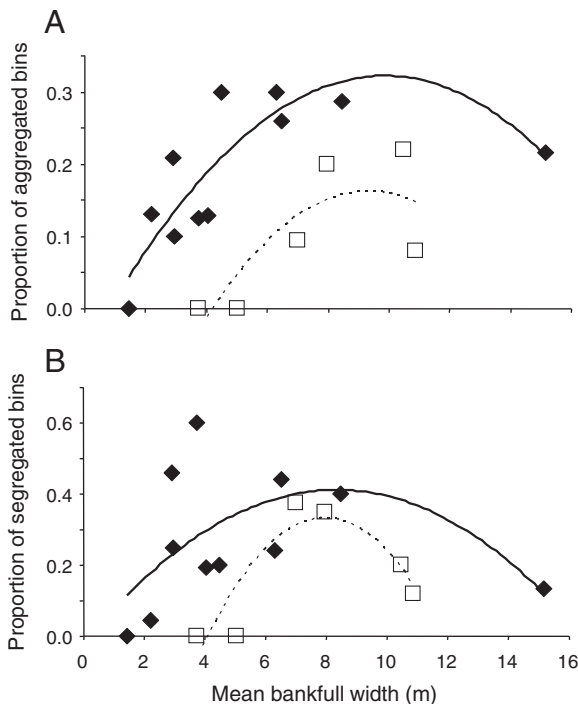

Fig. 5. Proportion of bins with (A) more wood than expected by chance (aggregation/periodicity) and (B) less wood than expected by chance (segregation) as a function of bankfull width for streams in the White Mountains, NH (filled diamonds) and the western Adirondack Mountains, NY (open squares), using 5-m bin intervals. A quadratic fit to the aggregation/periodicity data was significant for White Mountain streams (solid line, $n = 11$, $p = 0.006$, $r^2 = 0.71$) but not Adirondack streams (dashed line, $n = 6$, $p = 0.11$, $r^2 = 0.50$) (bottom panel). A quadratic fit to the segregation data was not significant for either region (White Mountain streams, solid line, $n = 11$, $p = 0.22$, $r^2 = 0.32$; Adirondack streams, dashed line, $n = 6$, $p = 0.10$, $r^2 = 0.78$).
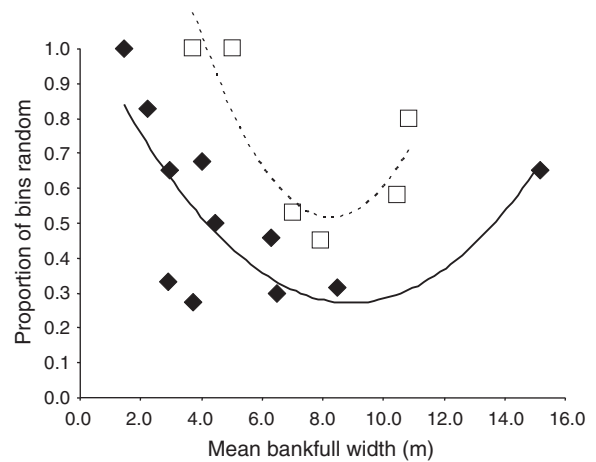
instream wood distributions, as is illustrated by the Bear Brook analysis (Fig. 1). By contrast, the binned neighbor-K analysis of the distribution of wood within Bear Brook shows the presence of regularly spaced intervals without wood at four distance intervals (15–19, 70–74, 75–79, and 95–99 m; Fig. 2). Previously published results by Kraft and Warren (2003) and Bocchiola et al. (2006) using the unmodified linear neighbor-K analysis indicated trends toward segregation, but significant levels of segregation were rarely observed.

Together, the Bear Brook results using the binned neighbor-K statistic indicate that wood within this stream accumulated at small distance intervals (5 m) in debris dams, and a larger distance interval of regularly distributed wood occurred from 45 to 54 m and even beyond to a range of distances extending from 35 to 64 m (Fig. 2). Areas from which wood was absent occurred at distance intervals of 15–19 and 70–79 m. We do not contend that every aspect of regularity in the presence and absence of wood and associated wood distributions can be explained mechanistically. However, the binned statistic is clearly more useful — by comparison with the unmodified linear neighbor-K statistic — in identifying distance intervals at which wood accumulates, as well as interspersed distance intervals from which wood has been mobilized into these aggregations. We note, however, that we have not fully evaluated the statistical properties of the binned neighbor-K statistic in a similar manner as the linear neighbor-K statistic has been evaluated in measuring the aggregation and segregation of events through time (Bhopal et al., 1992; Cressie, 1993; Diggle, 2006). Nevertheless, we have identified an empirical approach that describes observed spatial patterns in stream wood distribution in a fashion that can be readily interpreted.

Another important result of using the metric developed and applied in this study is that it can be used to quantify the 'organization' of wood in streams; that is, the proportion of a stream reach in which wood is aggregated, periodic, or segregated. By developing a metric that quantifies the extent to which the distribution of a stream habitat feature deviates from randomness, we have provided a tool for understanding how the distribution of stream habitats changes temporally and spatially. The tool can also be used to compare streams in various regions. For example, in this study this measure of wood organization provided a cumulative metric that — in conjunction with its component parts (aggregation, segregation, and periodicity) — identified similarities and differences in wood distribution patterns in streams in the two regions evaluated. These patterns likely resulted from landscape (e.g., slope, channel form, and stability) and ecological (e.g., forest age and tree species composition) factors that can be further evaluated by mechanistic studies of instream wood loading, decay, and movement.

Wood distribution patterns in both study regions were partially consistent with our expectations of increased organization at an intermediate stream size. As hypothesized, an increase in wood organization was observed as stream size increased for streams up to about 10 m bankfull width. But in larger streams (>10 m), wood was less organized than in the moderately sized streams in this study (6–10 m). While greater transport capacity in larger streams likely increased wood mobility, this greater mobility of larger pieces also likely reduced the number of key pieces that anchor stable wood structures that retain other pieces of instream wood. For example, the largest White Mountain stream in our study exhibited moderate wood organization but contained the lowest proportion of wood occurring in wood jams.

Overall, the general shape of the relationship between wood organization and stream size was similar in both regions. Although the quadratic fit was not significant (at p = 0.05) for Adirondack streams, the organization of instream wood in this region followed a similar pattern as White Mountain streams; and the lack of significance was likely influenced by the low number of stream reaches evaluated. In addition, the degree of wood organization was consistently lower in Adirondack streams of all sizes, which was likely

due to differences in stream energy in each of the two regions. Specifically, stream gradients were lower in the Adirondack study streams (Table 1), and large wetlands or lakes located upstream of each Adirondack study reach likely dissipated stream energy during storm events. By contrast, none of the White Mountain stream reaches were located downstream from low gradient areas or wide valleys where stream energy would be dissipated. Comparing study results from stream systems in different geomorphic settings illustrates the value of employing a spatial distribution metric in identifying similarities and differences in patterns of wood distribution that can be linked to landscape and ecological features.

Previous studies have regularly noted that stream bankfull width and the length of wood relative to stream bankfull width are key features influencing wood movement dynamics, (Lienkaemper and Swanson, 1987; Nakamura and Swanson, 1994; Martin and Benda, 2001; Gurnell et al., 2002; Warren and Kraft, 2008). In streams bordered by larger riparian trees, the key pieces of instream wood can effectively span or remain stable in a larger stream channel. Therefore, we speculate that as riparian forest tree size increases, the stream size at which peak wood organization occurs will also increase. This is particularly relevant for study streams in New Hampshire where riparian forests are still approaching maturity and trees have not yet attained the maximum size potential for dominant riparian species (Keeton et al. 2007, Warren et al. 2009). Our results are consistent with previous conceptual models of the storage and dynamics of wood in rivers (Gurnell et al., 2002; Wohl and Jaeger, 2009). Based upon work in the Colorado Front Range, Wohl and Jaeger (2009) suggested that: (i) debris dam formation will be low in small streams where wood is transport limited, (ii) wood jam formation will be maximized in intermediate sized streams where transport is greater but not so large as to reduce wood availability, and (iii) wood jam formation in larger streams will be limited by the availability of wood from greater export and reduced source wood for jams.

The overall metric of wood organization developed in this study reflects the influence of both transport and retention processes. In considering the application and evaluation of instream wood distribution in other regions, other factors to consider as possibly influencing the observed spatial extent of wood organization include — in addition to the size of source wood relative to stream size and stream gradient — the presence of boulders, ice flows, large floods, beavers and factors enhancing wood decay. Boulders can serve as important wood retention structures in recently glaciated regions such as the northeastern U.S., and the loss of wood from high decay rates may also lead to more rapid break-up of wood jams and increased wood transport potential. Ice has the capacity to increase physical stress upon instream wood, breaking downed trees into pieces smaller than that reflected by riparian tree size. The presence and frequency of large flood events can lead to changes in channel location, wholesale removal of wood, or deposition of large amounts of wood at a single location; therefore transport and retention during low flow years may yield greater levels of wood organization than are observed in years with larger flow events (Gurnell et al., 2002).

We acknowledge that we cannot explain the driving mechanisms for some aspects of the spatial distribution metrics reported for our study streams, particularly observations of regularly spaced wood-free reaches. However, by presenting a metric of spatial organization relevant to streams, stream ecologists and geomorphologists can employ this quantitative measure in developing an understanding of why specific features of wood self-organization are observed in streams. Wood transport and retention is dependent on localized variables related to hydraulic geometry, slope, planform morphology, bed roughness and riparian conditions, therefore any regular patterning in the storage of wood jams is likely associated with these non-wood variables. Future investigations can explore associations between observed patterns in wood spatial distribution with other fluvial driving variables.

5. Conclusions

This study demonstrates the utility of a binned neighbor-K statistic to quantify patterns in instream wood aggregation, segregation, and periodicity, which are important stream habitat features. We also used this metric to describe overall wood organization, which provides a metric by which stream transport and retention processes can be evaluated relative to underlying hydrologic and geomorphic characteristics. Patterns in wood distribution observed in northeastern U.S. study streams indicated the presence of high transport zones interspersed with wood retention zones that resulted in maximum wood organization in streams ranging from 6 to 10 m bankfull width. Wood distribution patterns from two different regions in the northeastern U.S. suggest that stream gradient is an important factor leading to observed differences in the degree of wood organization. Although this application of the binned neighbor-K statistic only evaluated the distribution of wood in streams, this metric can be applied to quantify patterns of other stream habitat features such as pools and boulders.

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