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Niles R. Kevern
Major professor

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DISTRIBUTION OF IN-LAKE COARSE WOODY DEBRIS WITHIN OLD-GROWTH AND SECOND-GROWTH FOREST SETTINGS

By

Bruce Martin Peffers

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1995

ABSTRACT

DISTRIBUTION OF IN-LAKE COARSE WOODY DEBRIS WITHIN OLD-GROWTH AND SECOND-GROWTH FOREST SETTINGS

By

Bruce Martin Peffers

The amount of coarse woody debris (CWD) found in lakes within old-growth and second-growth forest settings was investigated to determine if differences in distribution exist. Three lakes in each forest setting were selected in the western Upper Peninsula of Michigan. CWD was quantified using the line-intersect method, noting length, diameter, orientation to shore, and orientation to bottom. Volume for each CWD piece was calculated. Terrestrial variables (percent slope, stem density and diameter at breast height of live trees) above each transect were also measured.

Estimated mean volume and mean number of pieces per hectare were greater in old-growth lakes than in second-growth lakes. No set of characteristics could be determined to adequately define "second-growth" CWD. Basal area of the riparian vegetation may have some value for predicting in-lake CWD volume. We conclude that the second-growth lakes contain less CWD than the old-growth lakes, which has implications for fish habitat.

DEDICATION

This thesis is dedicated to my parents, William and Laurette Peffers, in thanks for their unconditional support and love.

ACKNOWLEDGEMENTS

I wish to thank my major professor, Dr. Niles R. Kevern, for his guidance and patience. I would also like to thank my committee members, Dr. Thomas Coon, Dr. Richard Merritt, and Dr. Clayton Edwards. I have learned so much from them, and have benefitted from their friendship. I would also like to thank my (soon-to-be) wife Rita for her love and support, especially during the hectic writing phase.

This project was funded through a contract with the North Central Forest Experiment Station, U.S.D.A. Forest Service, of Rhinelander, Wisconsin. My travel was funded in 1992 by the Fish Habitat Relationship Program of the U.S.D.A. Forest Service Rocky Mountain Region. I also wish to express my gratitude to the University of Notre Dame Environmental Research Center, especially Drs. Ron Hellenthal and Marty Berg, for the use of their beautiful facilities and their hospitality.

I wish to thank my intern, DawnMarie Welcher, for keeping me in line and always asking the right questions. Her delight in the out-of-doors made me smile again at so many things I had taken for granted.

Thanks are also due to my sister Lisa, her husband Don, and their children Jessica, Peter, and Luke for their support (and many free meals).

And last (but not least), I wish to thank the employees and "ologists" of the various National Forests who were so helpful in this project. The National Forests they work in are the Chequamegon, the Chippewa, the Hiawatha, the Huron-Manistee, the Nicolet, and the Ottawa. They are (in alphabetical order): Jeff Allison, Chuck Bassett, Chantel Cook, Jerry Edde, Bob Evans, Beth Gardner, Don Hair, Joe Kastenholz, Mary-Ann Kipper, Deyna Kuntzsch, Dave Mandrella, Mark Prout, Sue Reinecke, Bill Reardon, Dave Roerick, Bob Steuber, and "Black Bart" Tobin. Thanks to all.

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INTRODUCTION

The importance of large woody debris (LWD) in terrestrial and aquatic systems was often overlooked in natural resources management plans prior to the 1970s, primarily because of the systematic removal of such debris by humans for centuries, most notably in streams. Deforestation often indirectly reduces the amount of LWD that enters a system (Fausch and Northcote 1992). Humans have also altered the natural disturbance regimes by suppression of fire and flood. Rather than remaining intact for 250 to 500 years, which is the interval for natural catastrophic events (Triska and Cromack 1980), forests are being cut on 80-year cycles. Younger, healthier forests produce much less woody debris than older, mature stands. Thinning of forests decreases woody debris inputs by suppressing tree mortality (Spies *et al.* 1988). As a consequence, natural inputs and distributions of woody debris can only be estimated (Harmon *et al.* 1986). There is concern that sufficient LWD is no longer being produced and recruited into aquatic systems.

A distinction has been made between LWD and coarse woody debris (CWD) based on the size of the debris. The distinction appears to be relative, and depends on the author. Large woody debris has been generally defined as greater than 10 cm in diameter and greater than 1 - 1.5 m in length (Murphy and Hall 1981, Johnson and Heifetz 1985, Lienkaemper and Swanson 1987, Murphy and Koski 1989, Van Sickle and Gregory 1990). Bilby and Ward (1989 & 1991) required the length to be >2 m, and Bryant (1985) defined LWD as >30 cm diameter and >2 m in length. Coarse woody debris is smaller, from >2.5 cm diameter (Harmon *et al.* 1986) to >10 cm diameter (Bryant 1985), with Robison and Beschta (1990) defining CWD as >0.2 m in diameter and >1.5 m in length. In west coast studies, where trees tend to be larger than 60 cm diameter breast height (DBH), this may be a necessary distinction. For the purpose of this study, where old-growth trees rarely exceeded 50 cm DBH, coarse woody debris was defined as having a diameter greater than or equal to 10 cm, with no limits on length.

Considerable work has been done on woody debris since 1970, especially its role in stream systems. Gregory and Davis (1992) provide a detailed overview of previous research with emphasis on channel management. Woody debris can significantly affect the morphology of the channel, retention and movement of sediment and fine organic matter, and the type of habitat available for biological communities (Harmon *et al.* 1986, Andrus *et al.* 1988, Bilby and Ward 1989 and 1991). The dynamic nature of stream systems affects the distribution and movement of woody debris. Once the debris enters the system, it is subject to currents and floods, and may not be retained. The role of woody debris in lake systems is not as dramatic, however, and little work has been done to document its importance in the lentic environment. Water movement is limited in lakes, and in-lake CWD has a much greater chance of remaining in the system. Submerged wood has a very slow decay rate, and is less susceptible to invertebrate breakdown than terrestrial woody debris (Harmon *et al.* 1986), leading to the possibility of in-lake CWD persisting for long periods of time if undisturbed. This may mean that CWD deficiencies may be less severe in lake systems than in stream systems.

It is believed that fish assemblages found in lakes surrounded by standing timber have evolved with woody debris as a natural component of the available habitat. With the advent of logging, this habitat component was assumed to be in short supply, as has been found in streams (Angermeier and Karr 1984, Bryant 1985, Sedell *et al.* 1984). A common fish management technique has been the addition of woody structure (whole trees or artificial constructs) to subsidize existing lake habitat. The U.S.D.A. Forest Service has used this technique in many of its lakes in Michigan, Wisconsin, and Minnesota.

The objective of this study was primarily to determine if differences in the amount and distribution of in-lake CWD existed when comparing lakes surrounded by old-growth forest to similar lakes within second-growth forests. Lakes found in old-growth settings should contain amounts of CWD close to pristine levels, and provide a base-line; lakes surrounded by second-growth would be CWD-deficient. Secondarily, I wished to determine if attributes of the surrounding shoreline such as slope, stem density, basal area, and DBH of live trees could be used to predict the amounts of in-lake CWD, as found by Carlson *et al.* (1990) for streams. Such a predictive model would be valuable to the Forest Service biologists in preparation of the lake management component of Forest Plans.

DESCRIPTION OF STUDY AREAS

Study Sites

The old-growth site selected for the study was the Sylvania Wilderness Area (SWA), part of the Ottawa National Forest in Gogebic County of the western Upper Peninsula of Michigan (centered at 46° 12′ N, 89° 18′ W). The SWA is one of the few forested regions in the upper Great Lakes area that has remained relatively undisturbed by humans. The Sylvania tract comprises over 7400 ha (18,327 acres) of undisturbed old-growth hemlock-hardwood forest. Lakes make up about 20 percent of that area. The majority of the Sylvania lakes are seepage lakes with low chemical concentrations (Crumrine and Beeton 1975). Common tree species found in the SWA are eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), paper birch (*B. papyrifera*), red maple (*A. rubrum*), balsam fir (*Abies balsamea*), and white cedar (*Thuja occidentalis*). Hemlock makes up roughly 55 to 80 percent of the trees >10 cm DBH, and stand ages have been estimated in excess of 300 years (Tyrrell and Crow 1994). From prior to 1900 up to 1966, the SWA was in private ownership as a hunting and fishing preserve. In 1966, the tract was purchased by the U.S.D.A. Forest Service, and designated a semi-wilderness area. The tract became the Sylvania Wilderness Area in 1987.

The second-growth site is the 2975 ha (7345 acres) University of Notre Dame Environmental Research Center (UNDERC), located 6.5 km west of the Sylvania Wilderness Area, centered at 46° 13′ N, 89° 32′ E. The property is bounded on three sides by the Ottawa National Forest. The majority of the property lies in Michigan's Gogebic County, but a portion of the UNDERC property is in Vilas County, Wisconsin. Lakes and bogs make up 16.5 percent of the surface area (Anonymous 1991). The property has been owned by the University of Notre Dame since the 1940s, and the lakes have been studied since the 1920s. Access to all lakes on the property is restricted and requires the permission of the UNDERC director. Common tree species found on the shorelines of UNDERC lakes are black spruce (*Picea mariana*), eastern hemlock, white cedar, red maple, balsam fir, and red and white pines (*Pinus* spp.). Calculating the forest stand ages using the average hemlock DBH and regressions developed by Tyrrell and Crow (1994), the UNDERC stands may be as much as 125 to 160 years old, although smaller hemlock are difficult to age in this manner. The last known logging occurred in the late 1940s (R. Hellenthal, pers. comm. 1995).

Both sites lie in a geologically distinctive region, located on the continental divide between the St. Lawrence and Mississippi river drainages (Clady *et al.* 1975). The bedrock is mainly granites and gneisses common to the Laurentian Shield, covered with glacial deposits of acid, sandy loam from 30 to 60 m thick (Crumrine and Beeton 1975, Spies and Barnes 1985). Nutrient availability and productivity of these lakes are low, and the lakes are prone to acid rain impact. Kettle lakes are a common feature, and can be found relatively close-spaced. These adjacent lakes can often exhibit differences in elevation of 2 - 3 m. Most of the lakes have no inlets or outlets. Underlying outwash deposits result in steep shorelines along most of the lakes.

Study Lakes

Two lakes from each setting were selected for the study in 1992. A third lake was added for both settings in 1993 (Figure 1). Lake size was limited to 30 hectares. Corey, Katherine, and Snap Jack lakes are found in the Sylvania Wilderness Area. Corey Lake (Figure 2) is the smallest of the study lakes at 9.3 ha. Fish species found in Corey include largemouth bass (*Micropterus salmoides*) and yellow perch (*Perca flavescens*). Katherine Lake (Figure 3) is 19.4 ha in area, located fairly close to the SWA campground. Katherine's fish population is dominated by smallmouth bass (*M. dolomieu*). Snap Jack (Figure 4) is the largest old-growth lake at 23.9 ha. A portion of the south shoreline of this lake was once the site of an old Civilian Conservation Corps camp, and is presently in old-field vegetation. Bluegill (*Lepomis macrochirus*) are plentiful in this lake, as are largemouth bass. No-kill, artificial lure only regulations are in effect for these lakes (Miller 1992). Bergner, Brown, and Crampton lakes are the UNDERC lakes used in the study. Bergner (Figure 5) is a two-lobed lake surrounded on three sides by bog-mat and leatherleaf, with an area of 16.8 ha. Bluegill and largemouth bass were observed in this lake; fishing is prohibited.

An intermittent outlet at the north end of the lake has been blocked by beaver activity for an undetermined time (vegetation has taken root atop the dam). Brown (Figure 6) is a wide, shallow lake with poor clarity, 14.6 ha in area. It is the only lake with a true outlet. Northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), and bluegill are reported in this lake. Crampton (Figure 7) is 29 ha in size, with fairly steep shorelines. Largemouth bass are numerous. Crampton Lake is located in Wisconsin; all other study lakes are in Michigan.

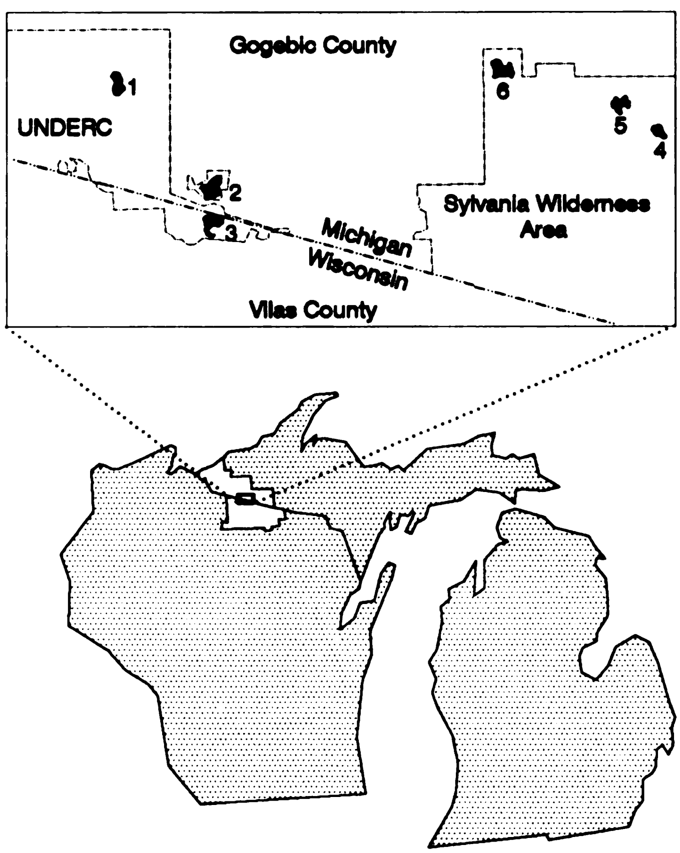

Figure 1. Location of old-growth and second-growth study areas, showing study lakes. The lakes are: 1) Bergner, 2) Brown, 3) Crampton, 4) Corey, 5) Katherine, and 6) Snap Jack.

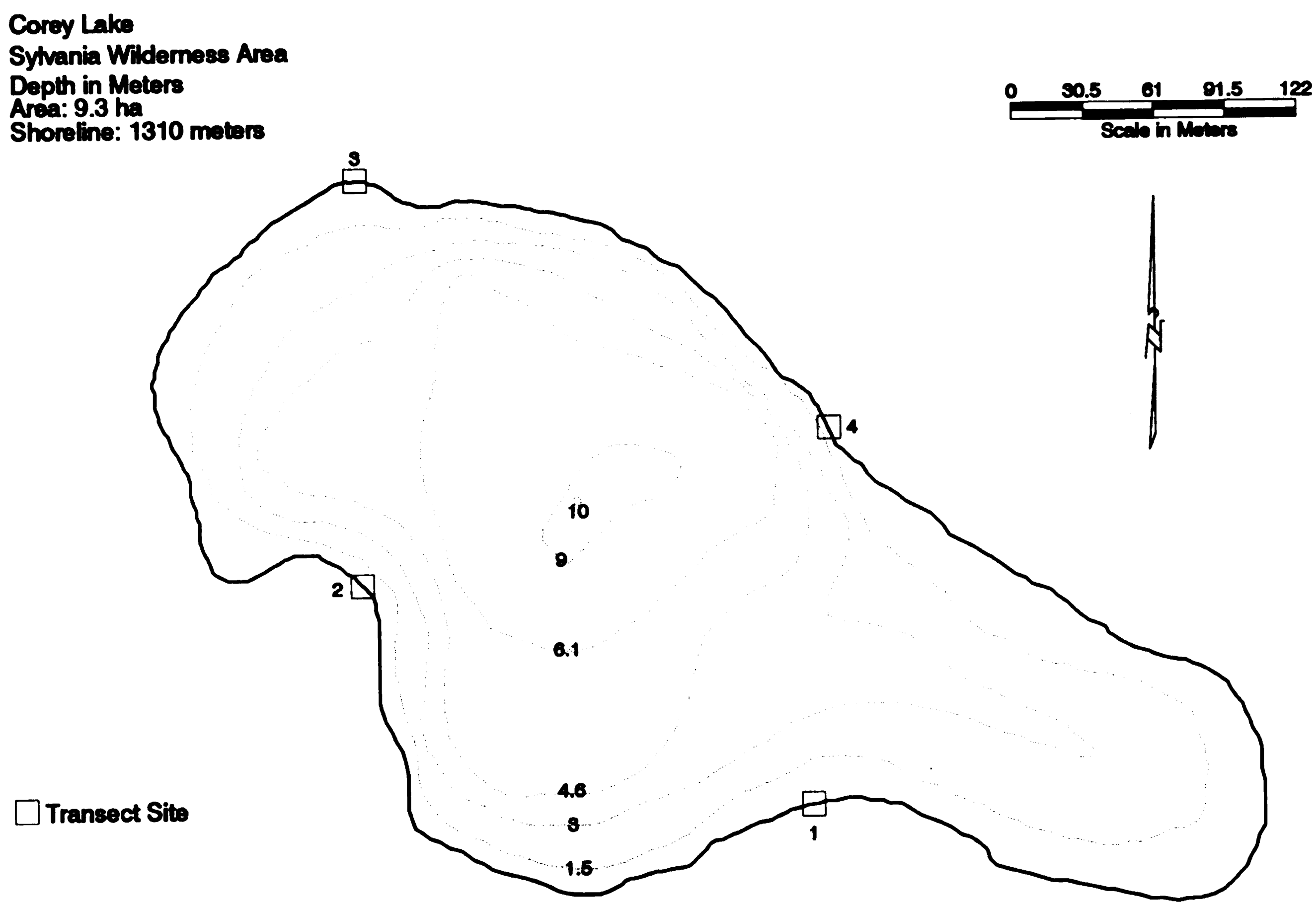

Figure 2. Hydrographic map of Corey Lake, Sylvania Wilderness Area.

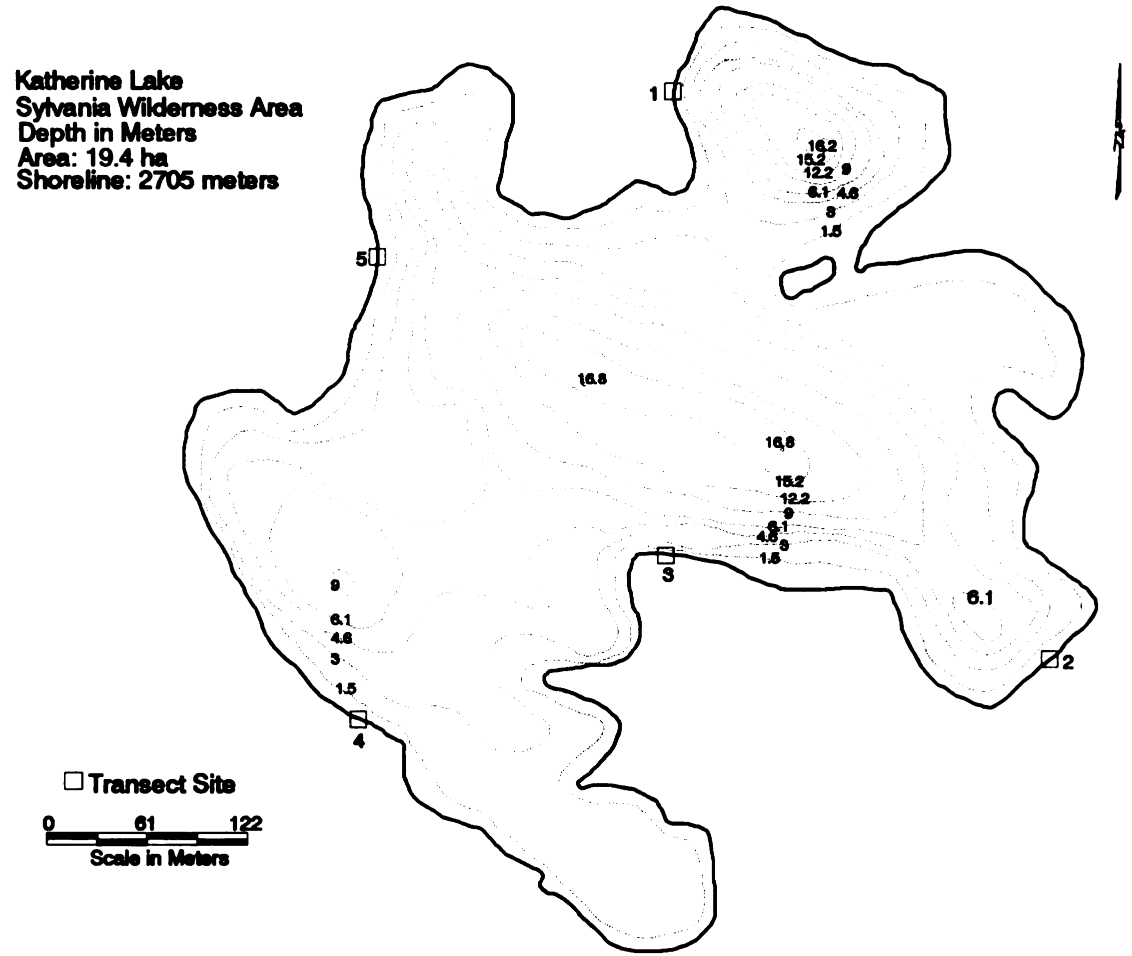

Figure 3. Hydrographic map of Katherine Lake, Sylvania Wilderness Area.

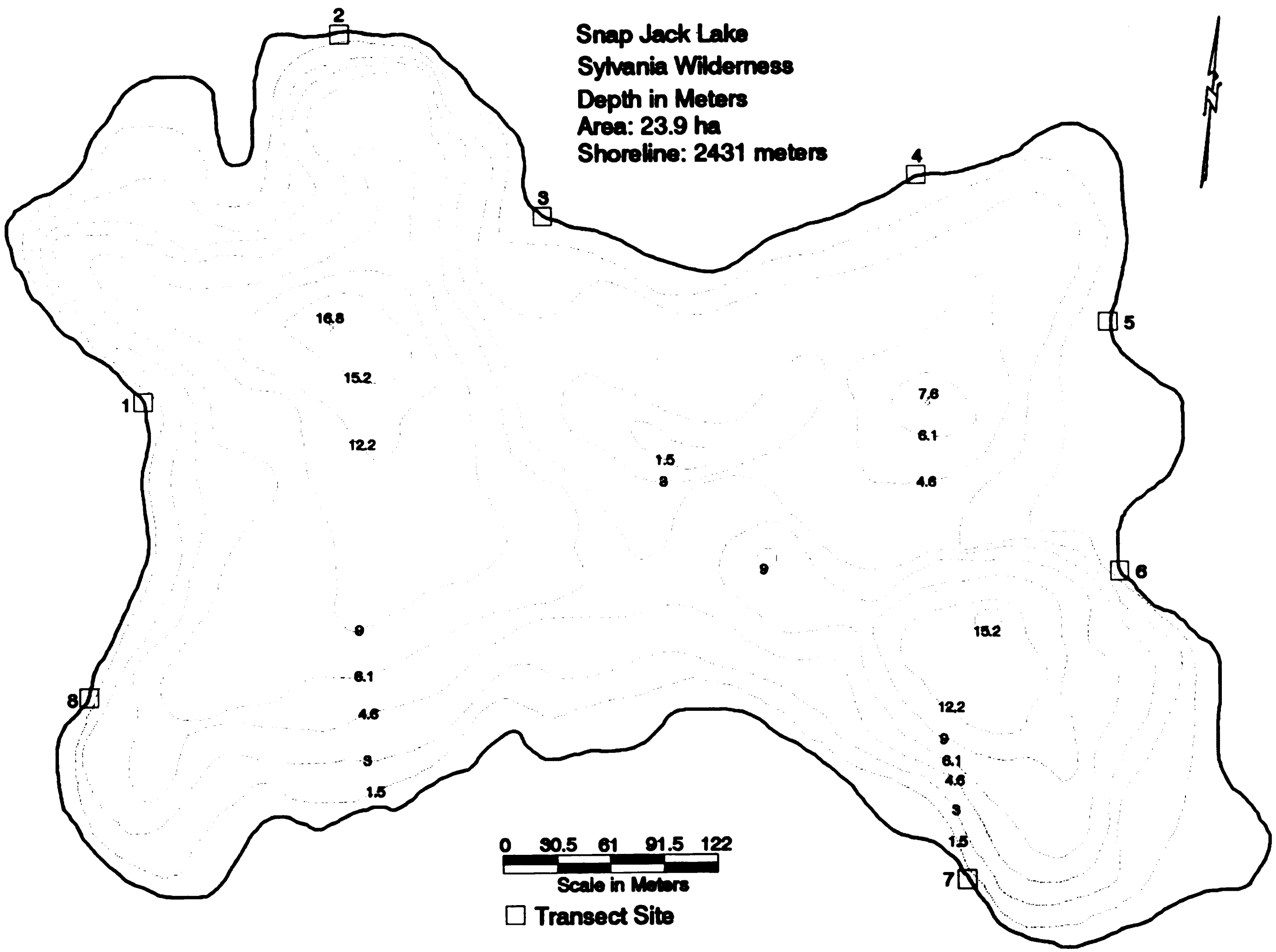

Figure 4. Hydrographic map of Snap Jack Lake, Sylvania Wilderness Area.

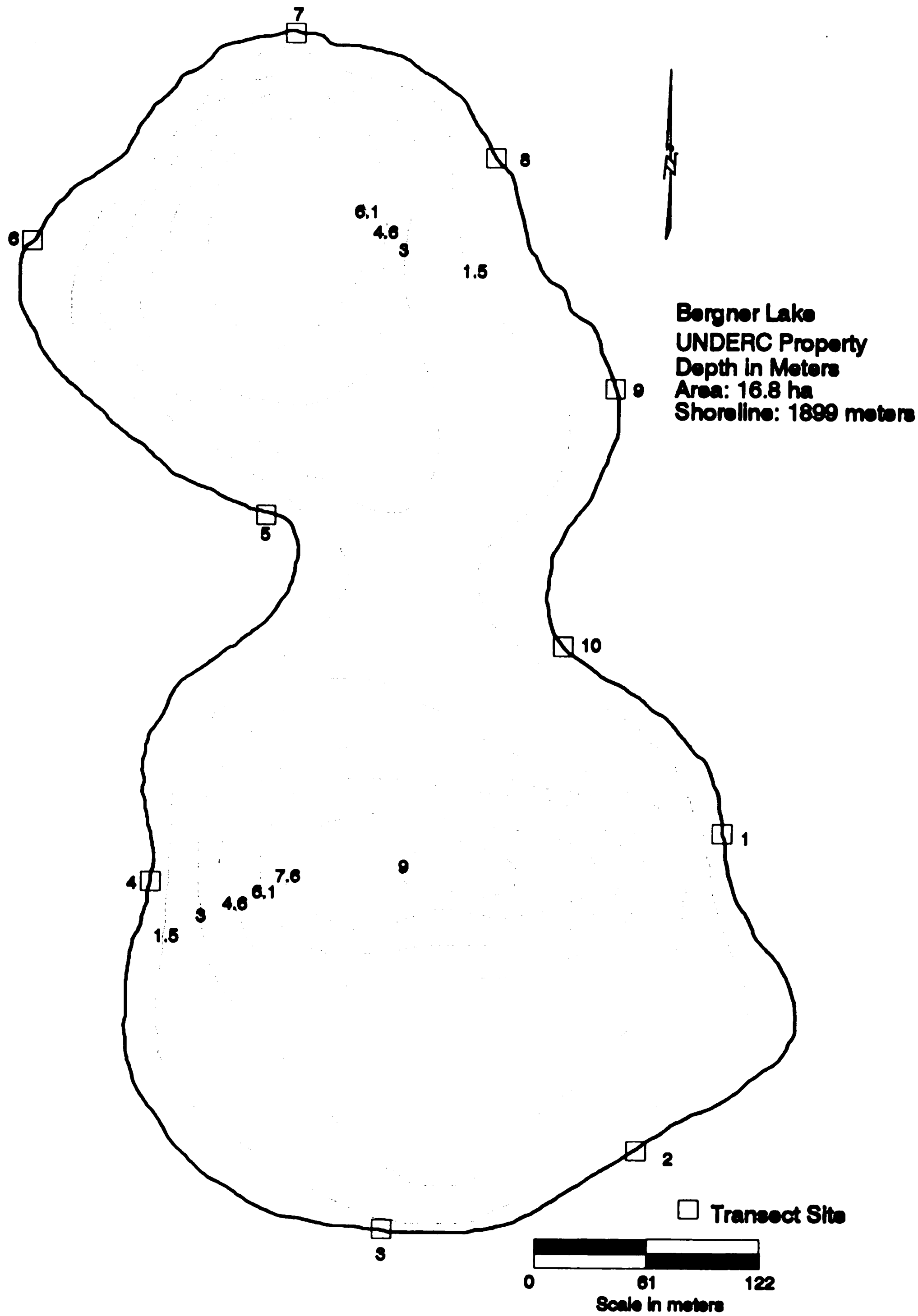

Figure 5. Hydrographic map of Bergner Lake, UNDERC property.

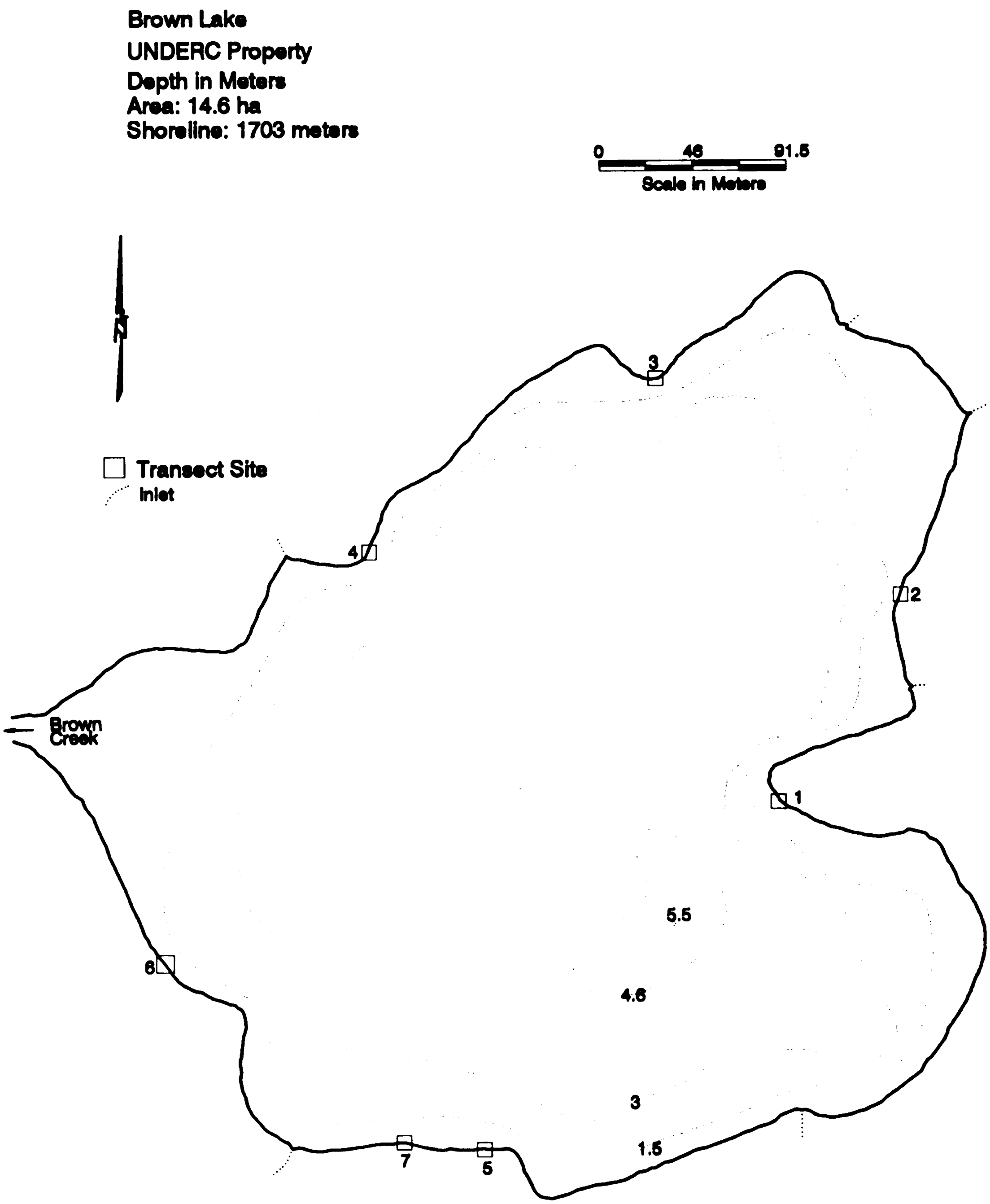

Figure 6. Hydrographic map of Brown Lake, UNDERC property.

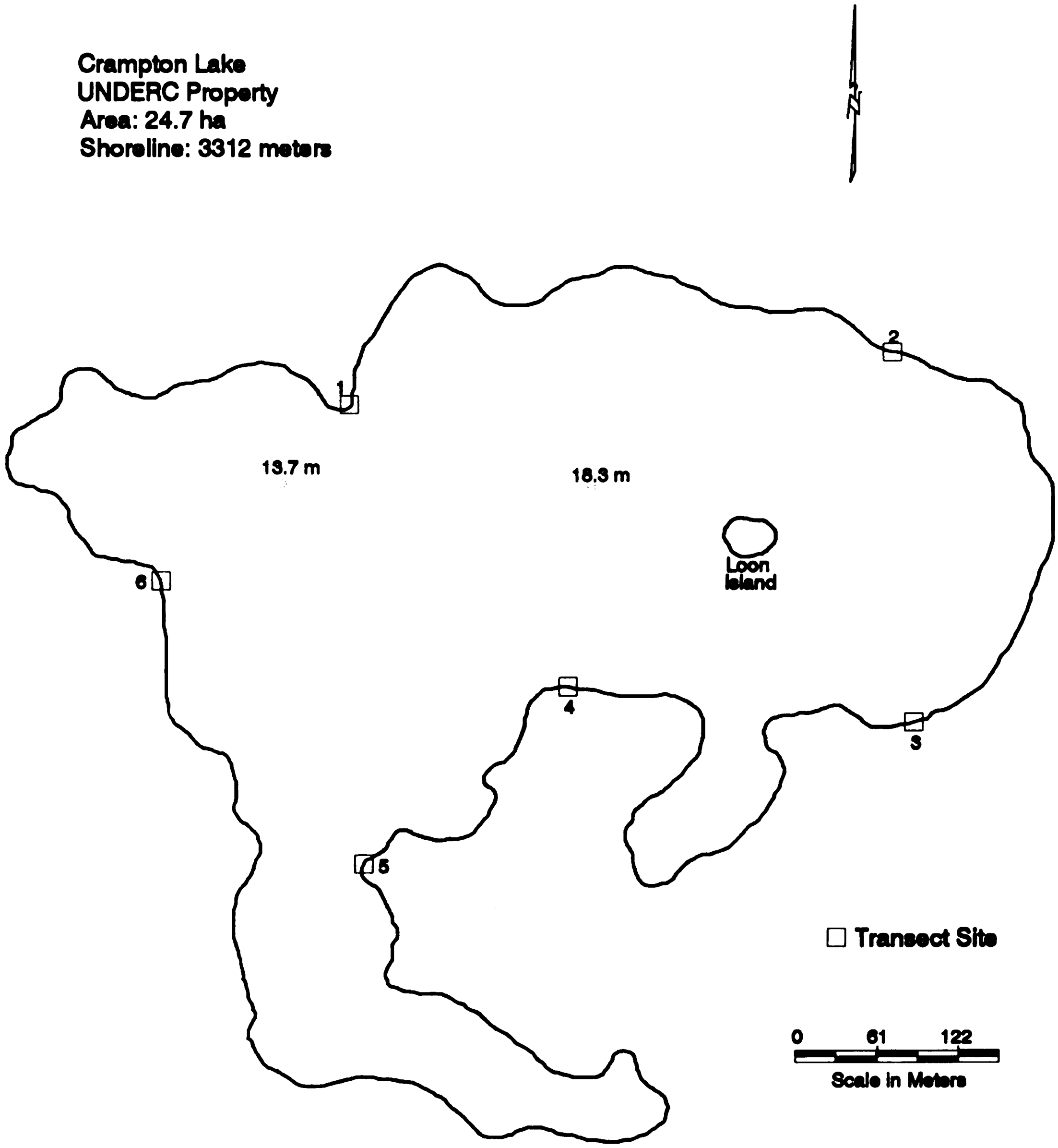

Figure 7. Shoreline map for Crampton Lake, UNDERC property. Known depths are shown in meters.

METHODS

Field Sampling

Standard limnological parameters were measured at surface, mid-depth, and bottom for each study lake. Samples were taken in midwinter, spring (after turnover), and midsummer (after stratification). Samples for alkalinity were stored in 500 ml polyethylene bottles, refrigerated, and tested as soon as possible (usually 3 - 5 hours) after sampling. Alkalinity was determined using the acid titration method and brom-cresol green indicator dye (APHA 1985). Endpoints were checked periodically with a pH meter. Differential titrations (Novak *et al.* 1975) were used to determine the proportion of actual $CaCO_3$ buffer. Lake pH was measured in the field with an Orion model 230A pH meter. Dissolved oxygen and temperature profiles were constructed using a YSI model 50B oxygen meter. Surface conductivity was measured with a YSI model 33 SCT conductivity meter. Secchi transparency was measured using a standard 20 cm black and white quartered disk.

In-lake coarse woody debris was sampled with the line intersect method (DeVries 1974, Wallace and Benke 1984). Transects 15 m in length were placed parallel to and approximately 2-3 m from shore. All debris intersecting the transect line was measured for length, diameter of the larger end, orientation to shoreline (parallel or perpendicular), and orientation to bottom (down on the bottom or suspended above). Measurements were made to the nearest centimeter. A piece was considered perpendicular to shore if it lay >45° to the shoreline; debris was considered off the bottom if any portion of its length was suspended above the substrate. The number of transects per lake was based on the area of the littoral zone (1.25 transects per hectare). Since no hydrographic map could be found for Crampton Lake, the littoral zone area was estimated at 5 ha. The littoral zone was defined as that depth ≤3 m (10 ft).

On-shore (terrestrial) variables were measured in a 15 m by 15 m plot immediately above the in-lake transect line. Percent slope of this terrestrial plot was taken with an inclinometer at two points within the plot, and an average taken. Diameter at breast height (DBH) was measured for all living trees within the plot using a DBH tape. Counts of trees by species in the plots were made in conjunction with DBH measurements. Basal area per plot was calculated using the DBH and stem density per plot data.

Data Analysis

Volume and surface area for each piece was calculated using formulas for the frustum of a cone:

$$V=\frac{\pi l}{3}\left(r_1^2+r_1r_2+r_2^2\right) \qquad (1)$$

$$SA=\pi(r_1+r_2)\sqrt{l^2+(r_1-r_2)^2} \qquad (2)$$

where r_1 is the larger radius, r_2 is the smaller radius, and l is the length of the CWD piece. The smaller radius was calculated with a regression equation derived from actual measurements of fallen trees. The volume and surface area values were used to calculate volume per hectare and surface area per hectare estimates with DeVries' (1974) equation:

$$\hat{X}=\left(\frac{\pi}{2L}\right)\sum\left(\frac{X_i}{l_i}\right) \qquad (3)$$

where L is transect length, X_i is the volume or surface area of the ith piece, and l_i is the length of the ith piece. By substituting 1 for all X_i values, the number of pieces per hectare can be estimated. Equation 3 is an unbiased estimator of the true mean quantity per unit area (DeVries 1974). Variance of the estimate can be given by

$$var\ \hat{X}=\left(\frac{\pi}{2L}\right)^2\sum\left(\frac{X_i}{l_i}\right)^2 \qquad (4)$$

DeVries states that the estimates are independent of width W, and can be applied to the total littoral zone area.

Frequencies of perpendicular and suspended CWD were tested from lake to lake and setting to setting using chi-square contingency analysis. Estimated means of CWD volume per hectare and number of pieces per hectare were compared using the z-test for differences between means, since Equations 3 and 4 provide only one estimate and variance per lake. To examine distributional patterns in more detail, CWD was divided into five 10 cm diameter size classes, and subjected to the same analysis. Volume, length, and diameter relationships were analyzed as general linear models with analysis of covariance (PROC GLM, SAS Institute, 1985); the same procedure tested differences between actual means of the variables with ANOVA for unbalanced samples (Tukey's Studentized Range Test). Linear and multiple regressions were used to determine if relationships existed between shore variables and volume and piece estimates for each transect.

RESULTS

Morphology of the study lakes varied widely (Table 1). Shoreline lengths ranged from 1310 m for Bergner to 3312 m for Crampton. Maximum depths ranged from 5.5 m for Brown Lake to 18.3 m for Crampton Lake. Shoreline development (S_d), an index indicating deviation of the shoreline from the circumference of a circle having the same area as the lake, showed the study lakes to be near the normal range (1.5 to 5.0) for natural lakes (Kevern 1989). Depth profiles along the longest axis of each lake (Figure 8) showed that the bottom gradients for the SWA lakes were relatively steep compared to the two UNDERC lakes having hydrographic maps. From sonar soundings I have done on Crampton Lake, I believe that lake to be very similar to Snap Jack in basin shape.

On-shore slopes above the lakes were usually steep because of their glacial ice block origin (Crumrine and Beeton 1975). Corey Lake had the highest average slope at 44.6 percent, which means that the shoreline would rise 44.6 cm for every 100 cm of linear distance away from the lake. Crampton Lake was also steep-sided, averaging 41.6 percent slope. Katherine and Snap Jack lakes were intermediate, with average slopes at 20.9 and 31 percent. Bergner and Brown lakes, with average slopes of 15 and 10 percent respectively, reflected the shallow shape of their basins.

The study lakes exhibited thermal and dissolved oxygen characteristics typical of north temperate lakes. Stratification occurred by mid-June in all lakes (Figure 9), and continued through final sampling in September. Dissolved oxygen levels were usually near zero in the hypolimnion of each study lake. Metalimnions were found from 2 to 3 m in Bergner, Brown, and Corey lakes. Metalimnions occurred from 4 to 6 m in Crampton, Katherine, and Snap Jack lakes.

Table 1. Physical parameters of the study lakes: surface area, length of shoreline, shoreline development (S_d), and maximum depth.

LAKE	AREA (ha)	SHORELINE (m)	S_d	MAXIMUM DEPTH (m)
Old Growth Lakes - Sylvania Wilderness Area				
Corey	9.3	1310	1.21	10.0
Katherine	19.4	2705	1.73	16.8
Snap Jack	23.9	2431	1.40	16.8
Second Growth Lakes - UNDERC Property				
Bergner	16.8	1899	1.31	10.0
Brown	14.6	1703	1.26	5.5
Crampton	24.7	3312	1.88	18.3

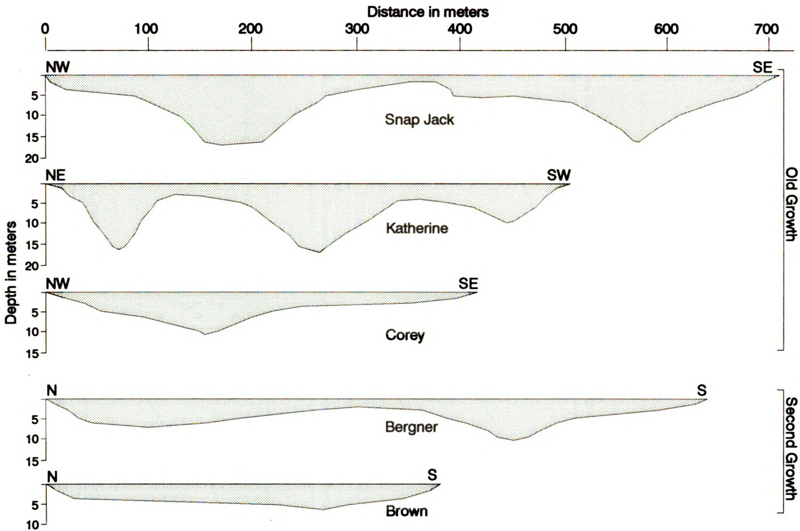

Figure 8. Depth profiles along the longest axis of the study lakes. No depth data available for Crampton Lake.

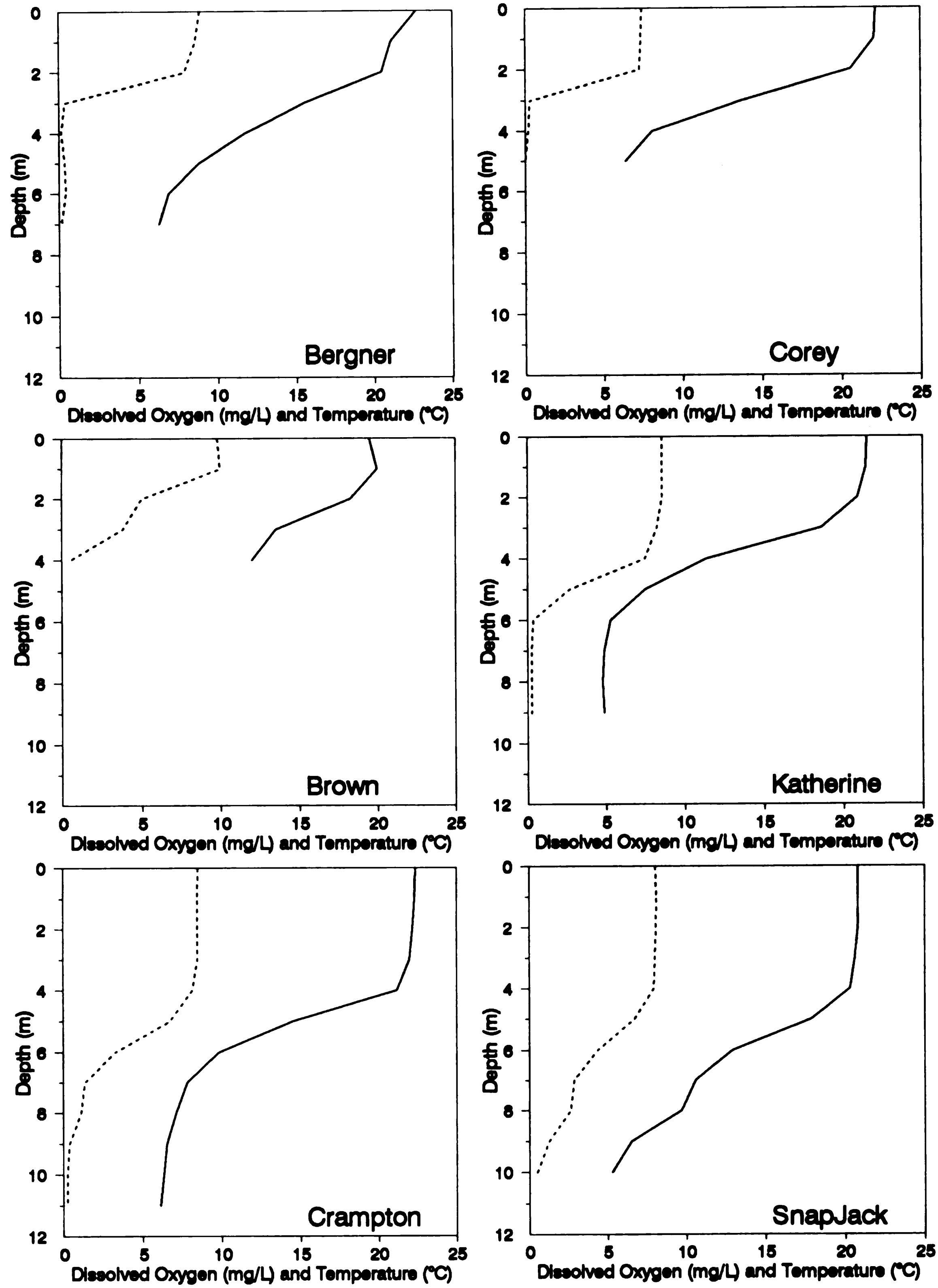

Figure 9. Dissolved oxygen and temperature profiles of the six study lakes at midsummer. Solid lines are temperature curves; dotted lines are dissolved oxygen.

Chemical characteristics of the study lakes were also consistent with other lakes of this region, with the exception of Brown Lake (Table 2). Excluding Brown Lake, average pH was 5.7 and specific conductivity averaged 22 μmhos/cm at 25C. Alkalinity averaged 3.5 mg/L $CaCO_3$. Differential titration performed on samples from Bergner, Crampton, Corey, and Katherine lakes demonstrated that most of this buffering was in the form of organic acids. Brown Lake was consistently higher for all parameters. Most of the lakes were stained to some degree, possibly due to the organic acid content. Secchi depth averaged 2.8 m for all lakes. The lowest value was for Brown Lake, with a

Table 2. Mid-summer chemical parameters of the study lakes: pH, alkalinity (mg/L $CaCO_3$), specific conductance (μmhos/cm @ 25°C), and Secchi depth in meters.

LAKE	pH	ALKALINITY	SPECIFIC CONDUCTANCE	SECCHI DEPTH
Old Growth Lakes - Sylvania Wilderness Area				
Corey	5.8	4.2	33.8	2.5
Katherine	5.4	3.1	21.4	2.25
Snap Jack	6.3	3.0	22.0	3.5
Second Growth Lakes - UNDERC Property				
Bergner	5.6	3.2	13.6	2.5
Brown	7.6	65.0	127.8	1.5
Crampton	6.1	3.8	18.9	4.75

Secchi depth of 1.5 m. This lake was normally very turbid, and Secchi depths as low as 0.4 m have been recorded (Anon. 1991). Crampton Lake was the most transparent, with a Secchi depth of 4.75 meters.

A total of 134 pieces of CWD was measured in 17 transects in the SWA lakes. Of these pieces, 117 (87.3%) lay perpendicular to the shoreline. Only 25 pieces (18.7%) were off the lake bottom, 23 of which were also perpendicular to shore. A total of 59 pieces were measured along 23 transects in the UNDERC lakes, with 47 pieces (79.7%) being perpendicular to shore. Only 19 of these pieces (32.2%) were off the bottom, and also perpendicular to the shoreline.

By-lake comparisons (chi-square) of the frequencies of the combined orientation (perpendicular to shore/parallel to shore) and aspect (up off bottom/down on bottom) distributions are detailed in Table 3. Data were separated into four categories: perpendicular-up, perpendicular-down, parallel-up, and parallel-down. Brown Lake differed significantly from both Bergner and Crampton lakes, with a greater frequency of perpendicular-down CWD. Snap Jack Lake was significantly different from Katherine Lake, with greater frequencies of parallel-down and perpendicular-down CWD. Due to the low sample size for the parallel-up category, X^2 was inappropriate when including this category. Only two pieces were recorded in this category, both in Corey Lake. No significant difference ($p=0.343$) was found between Corey and Snap Jack lakes after removal of this category. Between settings, combined second-growth distributions differed significantly from old-growth ($p=0.012$). A greater percentage of CWD in the perpendicular-up classification was found in the second-growth setting lakes, while a larger percentage of CWD in the perpendicular-down classification was found in the old-growth setting lakes.

Table 3. Matrix of Chi-square probabilities for differences between lakes within settings (combined orientation and aspect count data*). Probabilities ≤0.1 are in bold text.

LAKE	Brown	Crampton	Second-growth combined
Bergner	**0.042**	0.209	
Brown		**0.041**	
	Katherine	Snap Jack	
Corey	0.381	0.150	
Katherine		**0.046**	
Old-growth combined			**0.012**

*Orientation: perpendicular or parallel; Aspect: up off bottom or down on bottom.

Orientation and aspect were tested separately to determine which characteristic contributed most to the differences in Table 3. Brown Lake differed significantly in orientation from both Bergner and Crampton lakes, with a higher percentage of perpendicular CWD (Table 4), consistent with the differences seen in Table 3. However, Table 5 showed the reverse of Table 3 for upright CWD frequencies of the second-growth lakes: Crampton Lake had a higher frequency of upright CWD than Bergner Lake, while Brown Lake was not significantly different from either Bergner or Crampton lakes. Old-growth lake results in Tables 4 and 5 agree with Table 3: Snap Jack Lake's percentage of perpendicular CWD was lower than Katherine's ($p=0.100$). The frequency of CWD down on the bottom in Snap Jack Lake was much greater than Katherine Lake ($p=0.034$). Between settings, second-growth differed from old-growth in both orientation ($p=0.170$) and aspect ($p=0.039$).

Table 4. Matrix of Chi-square probabilities for differences between lakes in orientation (perpendicular/parallel) count data. Probabilities ≤0.1 are in bold text.

LAKE	Brown	Crampton	Second-growth combined
Bergner	**0.012**	0.351	
Brown		**0.070**	
	Katherine	Snap Jack	
Corey	0.255	0.497	
Katherine		**0.100**	
Old-growth combined			0.170

Table 5. Matrix of Chi-square probabilities for differences between lakes in aspect (up/down) count data. Probabilities ≤0.1 are in bold text.

LAKE	Brown	Crampton	Second-growth combined
Bergner	0.378	**0.078**	
Brown		0.280	
	Katherine	Snap Jack	
Corey	0.387	0.195	
Katherine		**0.034**	
Old-growth combined			**0.039**

Regression analysis of the diameters of downed trees demonstrated an exponential relationship between the distance from the base (d) and percent of base diameter remaining(*%R*): $\%R = 0.867e^{-0.00098d}$ ($r^2 = 0.998$). This relationship was used to estimate the terminal diameter of each piece for volume and surface area calculations.

Box-and-whisker plots (boxplots) described by Hartwig and Dearing (1979) are used to illustrate the actual distributions of diameter, length, and volume CWD measures. The boxplots show important percentiles and mean, maximum, and minimum values at a glance. The rectangle of the plot is bounded by the 25^{th} and 75^{th} percentiles, the central horizontal line is the median, the small square is the mean, the whisker ends are the 5^{th} and 95^{th} percentiles, and the small circles are the extreme values.

Diameter distributions by lake (Figure 10) show Brown Lake to have more larger diameters than all other lakes; the other second-growth lakes are skewed to the smaller diameters. Length distributions by lake (Figure 11) likewise show CWD was longer in Brown Lake compared to all other lakes, while the other second-growth lakes were skewed to shorter lengths. Volume distributions by lake (Figure 12) are skewed to smaller values in all lakes, but Brown Lake again had a larger proportion of large volumes. Brown Lake distributions were dissimilar from those of all other study lakes for all three measures.

Tukey's test of differences between means found differences between several lakes (Table 6). For the diameter and volume means, Brown Lake was significantly larger than all lakes but Katherine Lake ($\alpha = 0.05$). For the variable length, the Brown Lake mean was significantly larger than those of Bergner and Crampton lakes ($\alpha = 0.05$) only. Mean length for Bergner Lake was significantly smaller when compared to Katherine Lake ($\alpha = 0.05$).

Analysis of covariance (general linear models) was performed using diameter and length as covariates, with lake and interaction of lake and setting as main effects. Brown Lake was found to be significantly different from both Bergner and Crampton lakes ($p = 0.0004$) within the second-growth setting. Crampton Lake was not significantly different from the old-growth lakes ($p = 0.3096$). Katherine Lake was significantly different from Snap Jack Lake ($p = 0.0858$) within the old-growth setting.

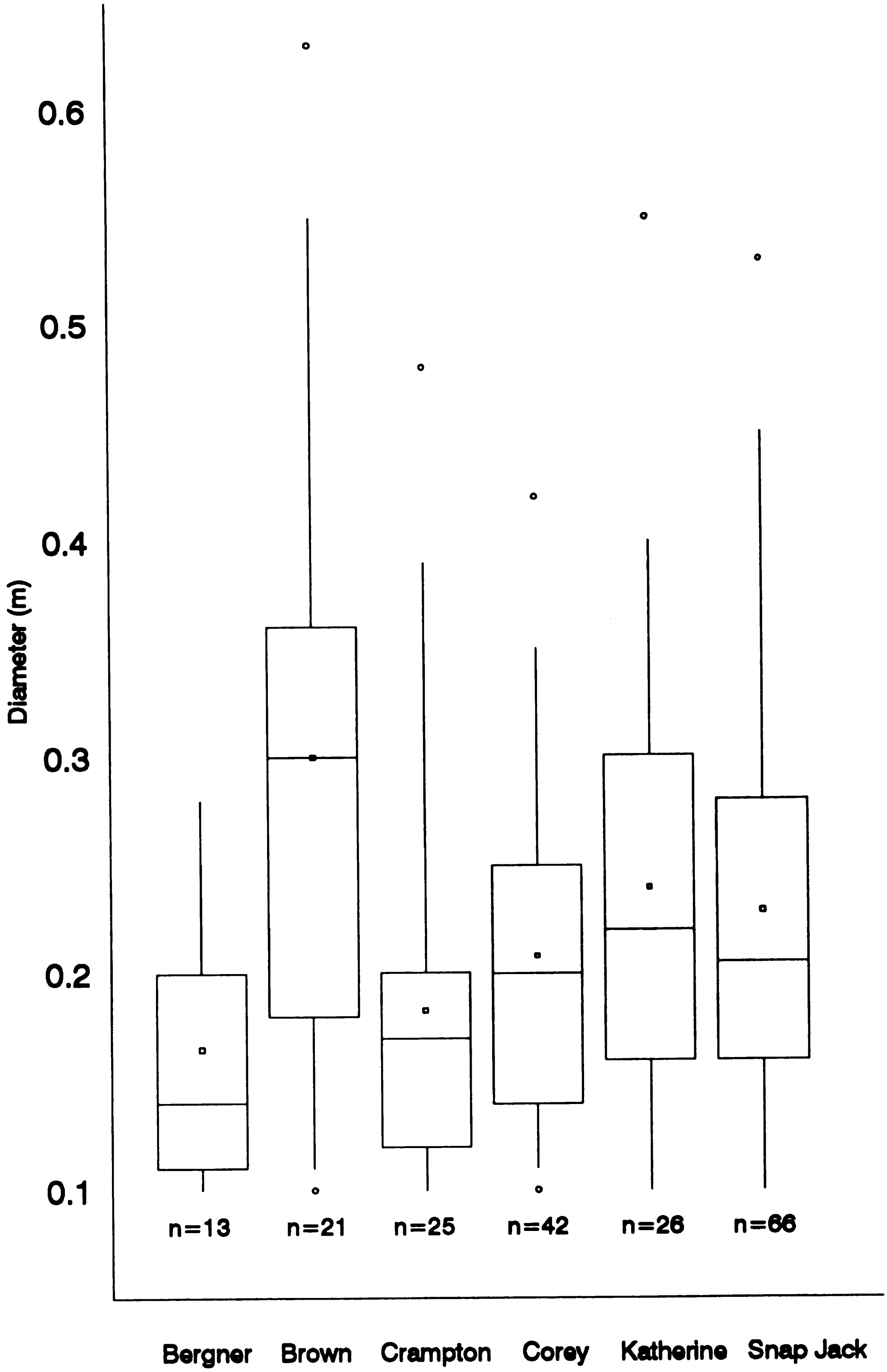

Figure 10. Diameter distributions of CWD for each of the study lakes.

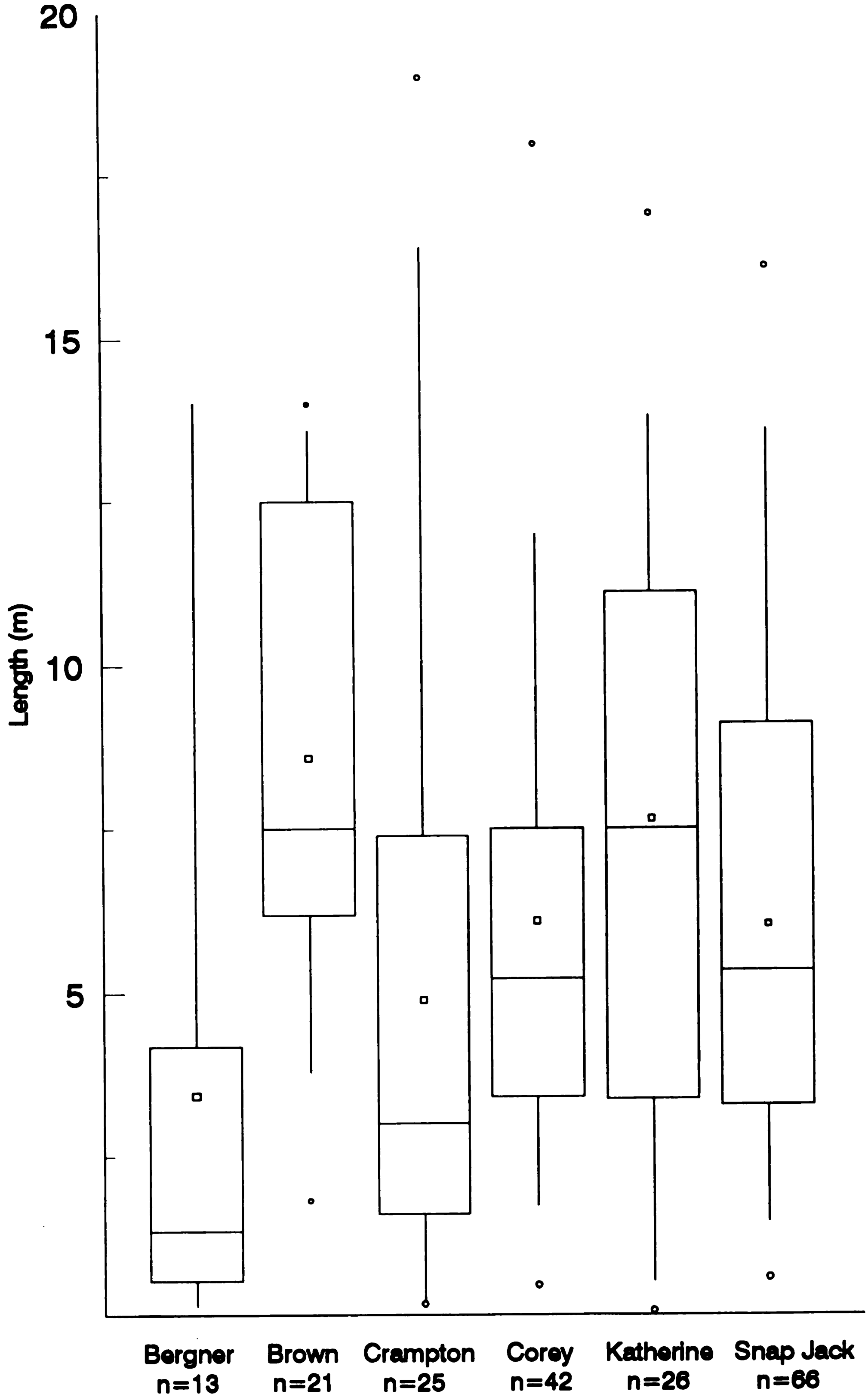

Figure 11. Length distributions of CWD for each of the study lakes.

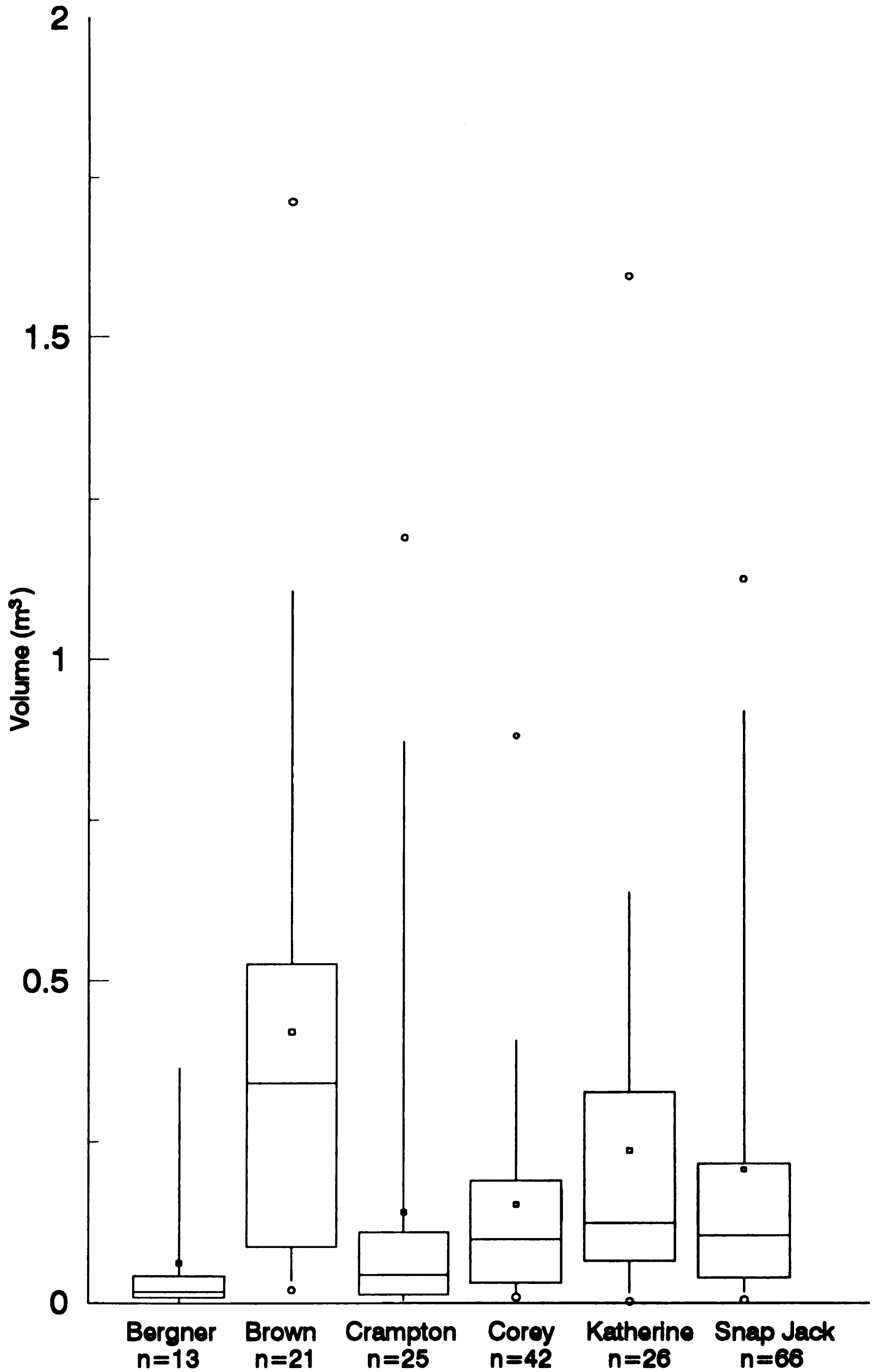

Figure 12. Volume distributions of CWD for each of the study lakes.

Table 6. Comparison of means significant at $\alpha=0.05$ level for diameter (D), length (L), and volume (V) of CWD (Tukey's Studentized Range Test).

LAKE	Bergner	Crampton	Corey	Katherine	Snap Jack
Brown	D,L,V	D,L,V	D,V		D,V
Katherine	L				

For portions of the analysis, CWD was divided by diameter into five size classes in 10 cm intervals. Smaller diameter pieces constituted the majority of CWD in all lakes. Over 62% of the total number of CWD pieces in second-growth lakes was contained in the 10 - 20 cm size class (Figure 13). The percentage increased to 79.6% when the next larger size class was added. For the old-growth setting, the 10 - 20 cm size class accounts for 51.5% of the total number of pieces, increasing to 82.1% when including the next size class. The contribution of total CWD volume for the first size class was 10% for second-growth and 14% for old-growth. Adding the next size class increased the percentage to 28% and 43% for second-growth and old-growth, respectively. The single size class with the greatest contribution to second-growth total volume was the 31 - 40 cm size class, with 28% of the CWD volume accounted for by 11.9% of the pieces. The 21 - 30 cm size class, with 30.6% of the pieces, accounted for 29.2% of the old-growth CWD volume.

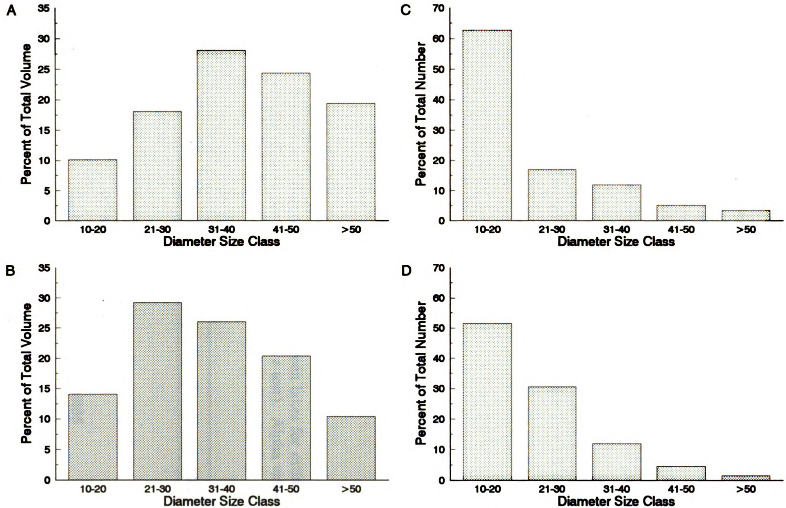

Figure 13. The distribution of A) second-growth and B) old-growth CWD volumes per size class, and numbers of pieces for C) second-growth and D) old-growth.

Estimates of the mean volume of CWD per hectare calculated with Equation 3 (Figure 14) are shown with one standard deviation. All second-growth lake volume estimates were significantly different from each other (Table 7). Bergner Lake and Crampton Lake, with the lowest volume estimates, were significantly different from all other study lakes. Corey and Snap Jack estimates for mean volume of CWD were significantly higher than all second-growth lakes. The volume estimate for Katherine Lake was similar to Brown Lake ($\alpha=0.3446$), significantly higher than Bergner ($\alpha=0.0005$) and Crampton ($\alpha=0.0368$) lakes, and significantly lower than Corey ($\alpha=0.0885$) and Snap Jack ($\alpha=0.1021$) lakes.

Table 7. Significant differences (α values) between lakes for estimated mean volumes per hectare (one-tailed *z* test). Alpha values $\leq$0.1 are in bold text.

LAKE	Bergner	Brown	Crampton	Corey	Katherine
Brown	**0.0020**				
Crampton	**0.0047**	**0.0885**			
Corey	**<0.0001**	**0.0401**	**0.0005**		
Katherine	**0.0005**	0.3446	**0.0368**	**0.0885**	
Snap Jack	**<0.0001**	**0.0427**	**0.0001**	0.4139	**0.1021**

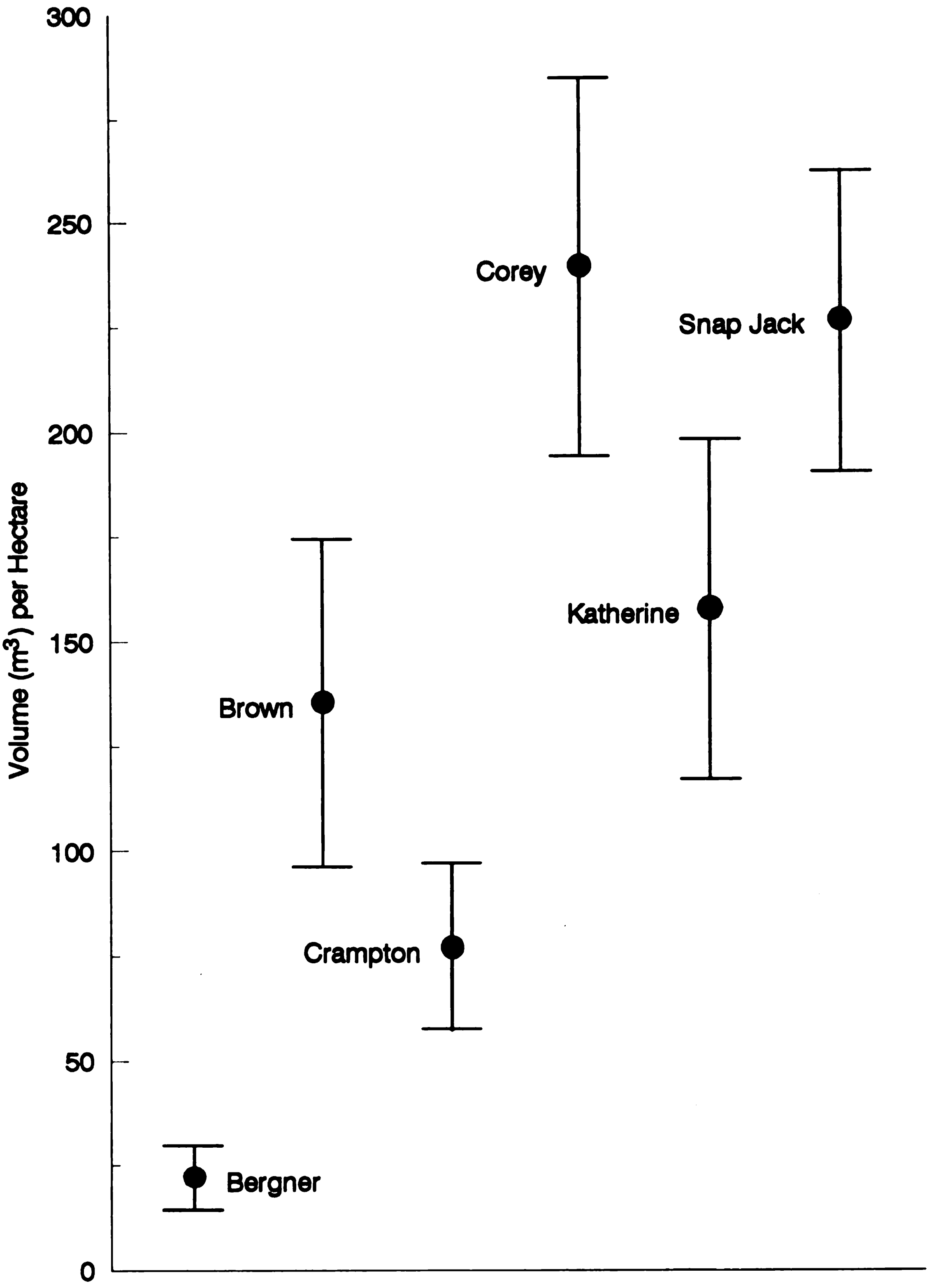

Figure 14. Estimated mean volume (± one standard deviation) of coarse woody debris per hectare of littoral zone for each of the six study lakes.

Estimates of the mean total number of pieces of CWD per hectare calculated with Equation 3 (Figure 15) are shown with one standard deviation. Brown Lake piece estimates were significantly lower than all other lakes (Table 8). Bergner Lake piece estimates were significantly lower than Crampton ($\alpha = 0.1021$) and Corey ($\alpha = 0.0808$) lakes, but not Katherine or Snap Jack lakes. The Crampton Lake piece estimate was similar to the old-growth lake estimates. There were no significant differences in total piece estimates between old-growth lakes.

Table 8. Significant differences (α values) between lakes for estimated mean pieces of CWD per hectare (one-tailed *z* test). Alpha values ≤ 0.1 are in bold text.

LAKE	Bergner	Brown	Crampton	Corey	Katherine
Brown	**0.0376**				
Crampton	**0.1021**	**0.0062**			
Corey	**0.0808**	**0.0003**	0.4169		
Katherine	0.2878	**0.0736**	0.3300	0.3745	
Snap Jack	0.2389	**<0.0001**	0.1698	0.1492	0.4052

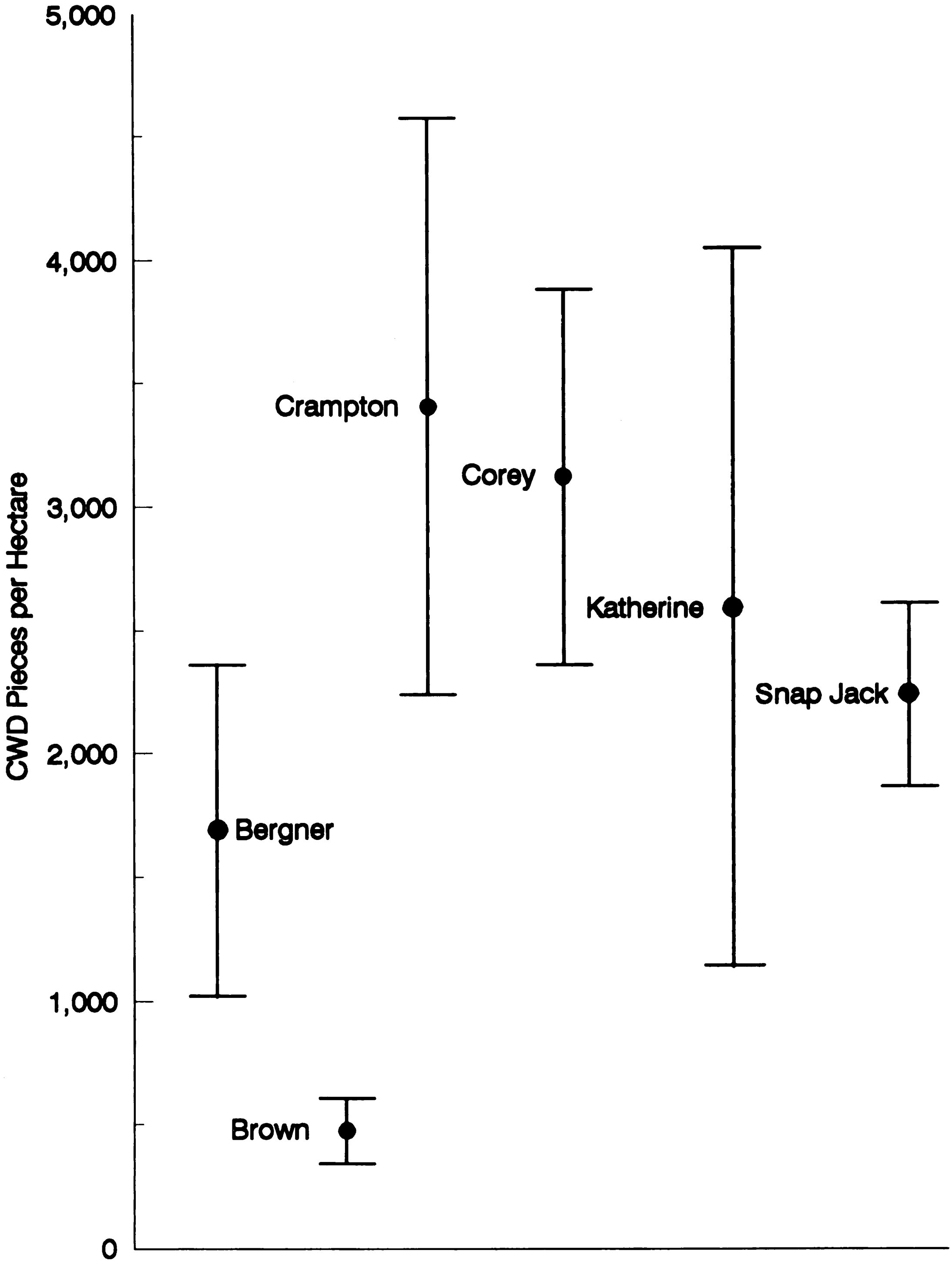

Figure 15. Estimated mean number (± one standard deviation) of coarse woody debris pieces per hectare for all study lakes.

Division of the estimated mean volume per hectare by the estimated mean number of pieces per hectare yields the estimated mean volume per piece of CWD for each lake (Table 9). Bergner and Crampton lakes had very small values. The old-growth setting lakes had slightly larger volume per piece estimates. The highest estimate was obtained for Brown Lake, in the second-growth setting.

Table 9. Estimated mean volume per piece of CWD for the study lakes, obtained by dividing the volume per hectare estimate by the estimated number of pieces per hectare.

SETTING	LAKE		
Second-Growth	Bergner	Brown	Crampton
volume (m^3)	0.0131	0.2861	0.0226
Old-Growth	Corey	Katherine	Snap Jack
volume (m^3)	0.0768	0.0606	0.1013

Comparisons of volume estimates by diameter size class provide greater detail into differences in distribution. Due to the small sample size for the larger diameter size classes (>40 cm), only the first three size classes are used in

Table 10 and Figure 16. Within-setting comparisons of volume estimates show that all second-growth lakes were equivalent for the 21 - 30 cm size class, where total volume estimates were significantly different in Table 7. The 10 - 20 cm size class volume of Crampton Lake was significantly higher than both Bergner and Brown lakes ($\alpha=0.003$). The 31 - 40 cm size class volume of Brown Lake was significantly higher than Crampton Lake ($\alpha=0.041$). No estimate was made for Bergner Lake for the 31 - 40 cm size class because no CWD in that class was measured.

Comparisons of mean piece number estimates by diameter size class also provides increased resolution of differences in distribution (Table 11, Figure 16). Within-setting comparisons of piece estimates show that all second-growth lakes were again equivalent for the 21 - 30 cm size class, where total piece estimates were significantly different (Table 8). The estimate of the mean number of pieces in the 10 - 20 cm size class for Brown Lake was significantly lower than those for Bergner ($\alpha=0.027$) and Crampton ($\alpha=0.089$) lakes. Within the old-growth setting, no significant differences were found between lakes, confirming the mean total piece comparison results of Table 8.

Table 10. Significant differences (α values) between lakes for estimated mean volumes per diameter size class per hectare (one-tailed *z* test). Only the first three size classes are shown: 1) 10 - 20 cm, 2) 21 - 30 cm, and 3) 31 - 40 cm. Alpha values ≤0.1 are in bold text. There is no 31 - 40 cm estimate for Bergner Lake.

	Size Class	Bergner	Brown	Crampton	Corey	Katherine
	1	0.456				
Brown	2	0.195				
	3					
	1	**0.003**	**0.003**			
Crampton	2	0.421	0.245			
	3		**0.041**			
	1	**0.0001**	**0.0001**	**0.068**		
Corey	2	**0.001**	**0.005**	**0.002**		
	3		0.319	**0.054**		
	1	**0.062**	**0.058**	0.119	**0.007**	
Katherine	2	**0.014**	**0.061**	**0.019**	**0.104**	
	3		0.309	**0.051**	0.488	
	1	**0.0001**	**0.0001**	0.252	0.157	**0.026**
Snap Jack	2	**0.001**	**0.011**	**0.001**	0.136	0.371
	3		0.475	**0.019**	0.390	0.379

Table 11. Significant differences (α values) between lakes for estimated mean number of pieces per diameter class per hectare (one-tailed z test). Only the first three size classes are shown: 1) 10 - 20 cm, 2) 21 - 30 cm, 3) 31 - 40 cm. Alpha values ≤0.1 are in bold text. There is no 31 - 40 cm estimate for Bergner Lake.

	Size Class	Bergner	Brown	Crampton	Corey	Katherine
	1	**0.027**				
Brown	2	0.295				
	3					
	1	**0.089**	**0.004**			
Crampton	2	0.224	0.281			
	3		**0.020**			
	1	0.201	**0.002**	0.236		
Corey	2	**0.042**	**0.003**	**0.001**		
	3		0.184	**0.056**		
	1	0.360	**0.100**	0.252	0.437	
Katherine	2	0.215	**0.039**	**0.020**	0.138	
	3		0.239	**0.062**	0.402	
	1	0.452	**0.0001**	**0.078**	0.184	0.375
Snap Jack	2	**0.084**	**0.003**	**0.001**	0.275	0.271
	3		0.285	**0.008**	0.268	0.352

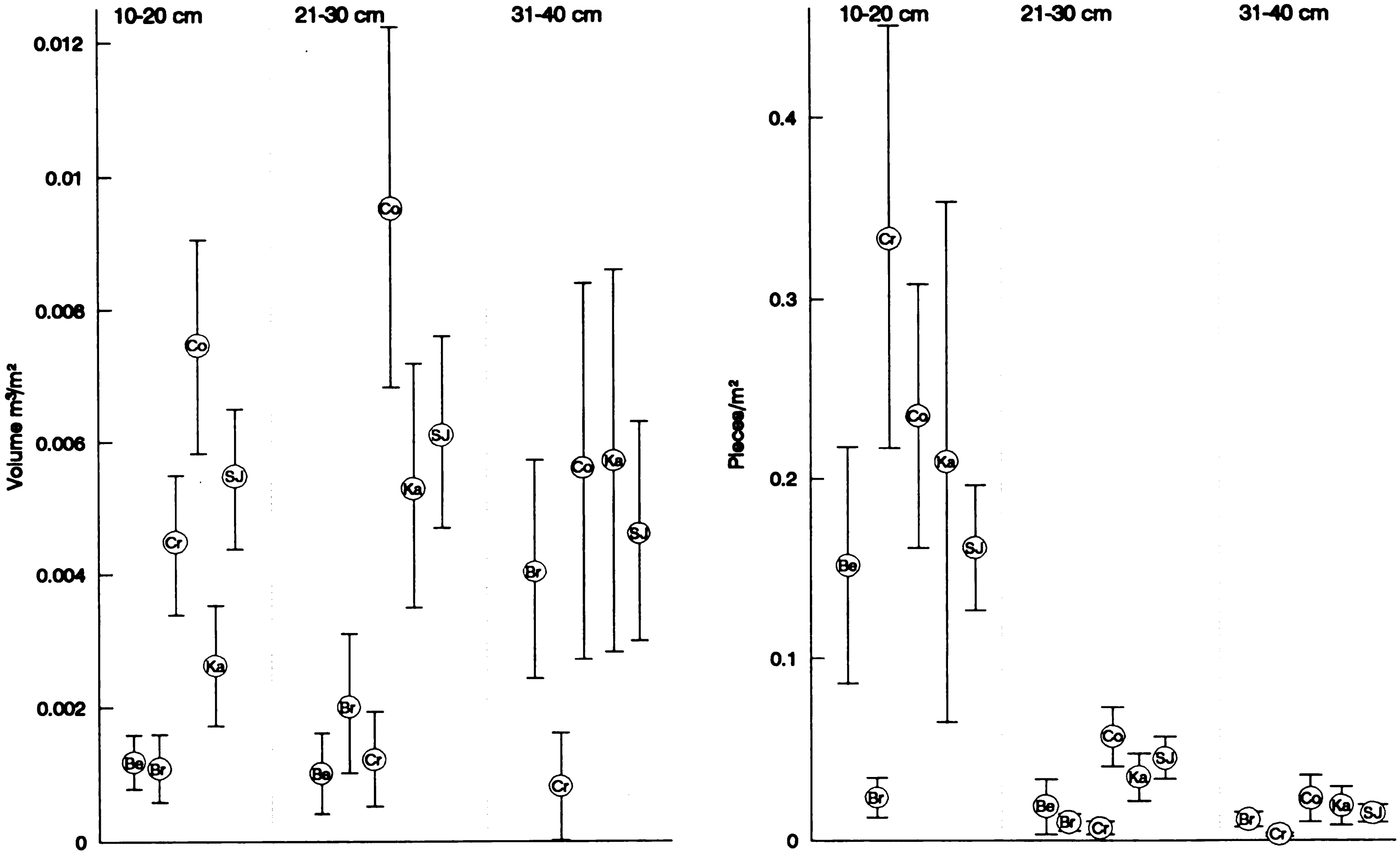

Figure 16. Volume and piece estimates (± one standard deviation) per m^2 for the first three size classes. Lake abbreviations are: Be - Bergner, Br - Brown, Cr - Crampton, Co - Corey, Ka - Katherine, and SJ - Snap Jack.

Care should be taken when considering the calculated volume per hectare and piece per hectare estimates. The calculated values give the impression of evenly-distributed CWD across the littoral zone. This is not the case, as the CWD more frequently displayed clumped distributions. The number of pieces within Snap Jack Lake ranged from 1 to 16 pieces per transect; half the transects in Bergner Lake contained no CWD at all. The volume and piece estimates per transect (Table 12) show that some second-growth transects contain as much CWD as old-growth transects, and some old-growth transects were as sparse as second-growth transects. The *quality* of the CWD available as habitat may be equal between the two settings; old-growth lakes simply have more of this quality habitat available.

Average on-shore stem densities of the live trees ≥10 cm DBH for each second-growth lake ranged from 3.2 to 10.1 stems per 15 m by 15 m plot (Table 13). Old-growth lake stem densities ranged from 6.6 to 11.8 stems per plot. Averages by setting were 6.3 stems per plot for second-growth and 9.6 stems per plot for old-growth. Total basal area (TBA) of trees ≥10 cm DBH ranged from 0.19 m^2 to 0.61 m^2 per plot for the second-growth lakes, and 0.83 m^2 to 1.51 m^2 per plot for the old-growth lakes. Average TBA for each setting was 0.32 m^2 per plot for second-growth and 1.18 m^2 per plot for old-growth.

Table 12. Estimated mean volume per m², estimated mean pieces per m², and actual number of CWD pieces measured for each transect in the study lakes.

Second-growth					Old-growth				
Lake	Transect	Vol./m²	Piece/m²	Measured	Lake	Transect	Vol./m²	piece/m²	Measured
Bergner	1	0.0007	0.349	1	Corey	1	0.0205	0.322	9
	2,3,5,7,9	0.0	0.0	0		2	0.0436	0.388	15
	4	0.0033	0.047	2		3	0.0209	0.441	12
	6	0.0058	0.212	3		4	0.0108	0.095	6
	8	0.0095	0.455	4	Katherine	1	0.0232	0.107	9
	10	0.0029	0.629	3		2	0.0012	0.020	1
Brown	1	0.0141	0.017	1		3	0.0174	0.105	5
	2	0.0037	0.010	1		4	0.0169	0.968	5
	3	0.0094	0.046	3		5	0.0202	0.098	6
	4	0.0009	0.024	1	Snap Jack	1	0.0300	0.088	6
	5	0.0225	0.037	4		2	0.0420	0.153	13
	6	0.0355	0.182	9		3	0.0238	0.666	16
	7	0.0089	0.017	2		4	0.0050	0.020	1
Crampton	1	0.0166	0.115	5		5	0.0144	0.350	8
	2	0.0	0.0	0		6	0.0041	0.038	2
	3	0.0078	0.227	5		7	0.0120	0.271	9
	4	0.0059	0.836	4		8	0.0499	0.204	11
	5	0.0025	0.011	1					
	6	0.0135	0.856	9					

Table 13. Average characteristics of 15 m by 15 m shoreline plots above lake transects.

LAKE	PERCENT SLOPE	STEM DENSITY	TOTAL BASAL AREA (m^2)
Corey	44.6	11.8	1.51
Katherine	20.9	6.6	0.83
Snap Jack	31.0	10.4	1.24
Old-growth Average	*31.2*	*9.6*	*1.18*
Bergner	15.1	3.2	0.19
Brown	10.4	10.1	0.61
Crampton	41.6	7.2	0.20
Second-growth Average	*20.6*	*6.3*	*0.32*

Basal area and estimated volume exhibited a weak linear relationship (r^2=0.26). A larger sample size may show that basal area has predictive potential for estimating in-lake CWD volume. Multiple regression with estimated volume as the dependent variable, and percent slope, basal area, and stem density as the independent variables resulted in an r^2 of 0.34; larger samples may be able to fine-tune these relationships as a predictive model for CWD volume.

DISCUSSION

The difference in morphologies of the study lakes between settings is most probably an artifact of random chance rather than an actual distinction. The old-growth lakes selected tend to be steeper-bottomed and deeper, but an examination of available hydrographic maps show that not all old-growth lakes in the SWA are similar. Likewise, the second-growth lakes selected tend to be shallow-sloped and less deep, but maps of other UNDERC lakes show a variety of morphologies. The depth of a lake may have an influence on the amount of CWD remaining in the littoral zone: Moring *et al.* (1986) described the gradual migration of submerged logs to deeper portions of a reservoir due to wave and ice action. Such logs would be less important ecologically because summer dissolved oxygen levels are usually very low in deeper water. In addition, the low dissolved oxygen levels in the hypolimnions of the study lakes in midsummer indicates the presence of oxygen-consuming materials in the deeper portions of the lakes (Crumrine and Beeton 1975), which may include woody debris that had migrated.

Shoreline slopes above the transects averaged higher for old-growth settings, but this would again be due to random chance. Crampton Lake, in the second-growth setting, averaged 41.6 percent slope, at the upper end of the range for slopes in this region; the average slope found in the SWA has been reported as less than ten percent (Spies and Barnes 1985). The average slopes of the study lakes were consistently higher than this. The two lowest average slopes, 15.1% (Bergner) and 10.4% (Brown), are found in the second-growth setting.

The second-growth setting shoreline plots averaged lower for both stem densities ≥10 cm DBH and total basal area. This is not surprising, since the old-growth trees are larger diameter, and have had more time to attain this size. What was not recorded were the number of trees below 10 cm DBH observed, which would have increased the second-growth stem densities to numbers surpassing the old-growth densities. Dense stands of balsam fir 3 - 7 cm DBH were common along the second-growth shorelines, but were absent along the old-growth shorelines. These saplings would not increase the total basal area significantly.

The study lakes all shared similar chemical characteristics, with the exception of Brown Lake. Low pH, low alkalinities, and low conductivities were the rule for the five other lakes. The differential titrations performed on samples from Bergner, Crampton, Corey, and Katherine lakes demonstrated that most of the alkalinity measured in these lakes is actually organic acid buffering, and not $CaCO_3$ alkalinity. Organic acids are by-products of the decomposition of organic compounds (such as woody debris), and are also responsible for stained (colored) water, which occurs in all the study lakes except Brown Lake. Brown Lake, with consistently higher pH, alkalinity, and conductivity (Table 2) was the only study lake with surface inlets and an outlet. Groundwater throughput is probably the cause of these higher limnological values (Crumrine and Beeton 1975) and may have been a factor in the differences in CWD distributions to be discussed later. The balance of the study lakes had chemical character similar to precipitation, suggesting little groundwater input.

Recruitment of trees into the water occurs primarily at or near 90° to the shoreline due to a variety of factors: phototropism, bank undercut, slope of the shoreline, and the tendency to produce more biomass on the unshaded side (Robison and Beschta 1990). When trees enter the water naturally, the trunk usually remains associated with the rootwad, anchoring it to shore (Bryant 1985), and props a major portion of the trunk off the lake bottom. Branches extending from the trunk can also hold the debris off bottom. After some time in the water, a combination of decay of branches, biotic activity, sedimentation, and water movements can alter the position or elevation of the CWD. An assumption can be made that pieces of CWD found parallel to the shoreline have moved into this orientation at some point since entering the system (Bilby and Ward 1989), and that CWD lying flat on the bottom has been in the system for a long time.

In the old-growth setting, Corey Lake had the highest values for the terrestrial variables. This lake was the smallest of the study lakes, entirely surrounded by steep (nearly 45%) slopes covered in relatively dense (averaging 11.8 stems per plot) stands of very large trees. The estimate of total volume per hectare was the highest for all study lakes, with the 10 - 20 cm and 21 - 30 cm size classes contributing the largest portion of that volume. The estimated total number of pieces was also high, but not significantly different from other old-growth lakes. The majority of the piece estimate came from the 10 - 20 cm and 21 - 30 cm size classes. The relatively dense stem densities above this lake may account for the greater volume per hectare estimate within Corey Lake.

Percent slope, stem density, and basal area values for Katherine Lake were the lowest of the old-growth lakes. Estimated total volume reflects this, being the lowest estimate for old-growth lakes, significantly lower for the 10 - 20 cm size class. Estimates of number of pieces per hectare were similar to other old-growth lakes. Frequencies of upright and perpendicular CWD suggest that recruitment of the sampled debris was recent. The basin shape of Katherine Lake is the steepest of the study lakes (Figure 8), and older CWD may have migrated to the deeper areas of the lake. Attempts to verify this hypothesis by SCUBA were unsuccessful; visibility below the thermocline was essentially zero.

The CWD in Snap Jack Lake had the highest percentage of pieces parallel to the shoreline, and the least percentage of pieces up off the bottom, suggesting that the CWD measured had been in the lake for some time. Snap Jack's terrestrial stem density and basal area values were higher than Katherine Lake, but lower than Corey Lake. The estimated volume per hectare was similar to that of Corey Lake, but the estimated number of pieces was lower than the other old-growth lakes. The basin shape of this lake deepens gradually (Figure 8), and migration of CWD may not be as easily accomplished as in Katherine Lake.

Bergner Lake in the second-growth setting had the lowest percentage of perpendicular CWD, and a low percentage of upright CWD as well, suggesting that the CWD within the lake had been present for some time, and had possibly relocated from its original entry point. Bergner Lake, with the lowest basal area, stem density, and low percent slope values for the shoreline plots, would be expected to have very low recruitment rates for CWD. The estimated CWD volume value suggests this low rate. The lack of larger, slower-to-decay CWD in this lake suggests a long time interval since old-growth trees were found close enough to the lake to be recruited into the system, or that any residual CWD may have been covered by the encroaching bog mat. The intermittent outlet (at present dammed by beavers) may also have provided emigration for some CWD in the past. The debris found in Bergner Lake probably was brought in via beaver activity, as most of the CWD was found in transects near the dam.

Crampton Lake (second-growth) had a low percentage of perpendicular CWD, but the highest percentage of suspended CWD of all the study lakes. All of the up-off-bottom CWD was also perpendicular to shore. This suggests recent recruitment of CWD. The shoreline surrounding Crampton Lake has a very high percent slope, but the shore plot stem density and basal area values were relatively low. Any recruitment of CWD would necessarily be in the smaller diameters. The volume and number of piece estimates bear this out: the major contribution to CWD was found in the 10 - 20 cm diameter class (Figure 16).

Brown Lake, a second-growth lake, is more similar to old-growth lakes in shoreline and CWD characteristics. Stem density and basal area values were higher than the other second-growth lakes. Over 95% of the CWD found in the lake was perpendicular to shore, and 28.6% was suspended off the bottom, nearly identical to Katherine Lake in the old-growth setting. All of the suspended CWD was perpendicular. The other second-growth lakes had low frequencies of perpendicular CWD, significantly different from old-growth frequencies ($\alpha = 0.072$), but the frequency of perpendicular CWD in Brown Lake was not significantly different from old-growth ($\alpha = 0.185$). The CWD sampled in Brown Lake had the highest average volume of all the study lakes. Estimated volume per hectare in Brown Lake was higher than the other second-growth lakes, but the estimate of CWD pieces per hectare was much lower than all other lakes. This would correspond to an estimated mean volume per piece of 0.2861 m^3, much higher than all other lakes (Table 9). For this to be true, the CWD in Brown Lake must be consistently longer for any given diameter. The average dimensions of CWD sampled in Brown Lake (Figures 10 and 11) were consistently greater than the other study lakes; the ANCOVA results confirmed that the relationship of diameter and length for Brown Lake was different from all other lakes. Bilby (1984) and Benke and Wallace (1990) found that the longer the piece of CWD, the less likely it is to move from the system. The low number of pieces and relatively large volume of each discrete piece of CWD in Brown Lake would suggest that smaller CWD in the lake has been moved from the lake. Brown Lake does have inlets and an outlet; movement of water through this lake may be a factor in this distinctive distribution of CWD. Because of the higher pH and lower organic acid content in this lake, decomposition of CWD may occur at a faster rate (Wetzel 1983) than the other study lakes, with the smaller pieces breaking down first. The shape of the lake basin and relative lack of wind shelter causes a strong fetch effect (Anonymous 1991), which may also move the CWD away from its original entry point.

Older stands of trees have been proven to produce more woody debris than younger, healthier stands (Andrus *et al.* 1988), and the trees of the second-growth setting of this study contained a higher percentage of deciduous species which have been shown to produce less CWD than coniferous stands (Harmon *et al.* 1986). The lakes in the old-growth setting of this study contained more CWD pieces and volume than the second-growth lakes, which agrees with several studies comparing streams in old-growth vs. second-growth settings (Bilby and Ward 1991, Murphy and Koski 1989, Murphy and Hall 1981), but the percent difference was much less severe than seen in streams. The average second-growth volume per m^2 was 37.6% of the average old-growth volume for the study lakes, compared to an average of 25% for western stream studies; the average number of pieces of CWD per m^2 in second-growth was 70% of the old-growth average for the lakes, contrasted with 50 - 56% for stream systems.

Corey and Snap Jack lakes were the most similar in CWD characteristics of the old-growth lakes studied. Shoreline characteristics were also similar for these two lakes. Katherine Lake, with lower values for shoreline variables, had less potential recruitable volume than the other old-growth lakes, and had less estimated total volume. The estimated number of pieces per hectare was not significantly different among old-growth lakes, meaning the volume per piece for

Katherine Lake would also be less than the other old-growth lakes. However, due to the small number of lakes sampled, it would be inappropriate to conclude that Katherine Lake was "less old-growth" in nature than the other lakes; rather it may be that Katherine Lake was found at one end of a range of characteristics for old-growth.

The lakes in the second-growth setting were more dissimilar than similar for CWD characteristics. No combination of in-lake CWD characteristics or size-class distribution could be used to classify a lake as "second-growth" in nature. Brown Lake, with inlets and an outlet, low-sloped shoreline, and shallow basin shape demonstrated that the CWD content of a lake depends on more than the composition and age of the surrounding forest stands. The small number of lakes used in this study increase the difficulty of making any meaningful generalizations about either setting.

Importance of CWD as Habitat

Although invertebrate and fish abundance were not measured directly in this study, a basis exists to make inferences from the habitat potential of the CWD (Carlson *et al.* 1990). In stream systems, many studies have shown that increases in CWD resulted in increased secondary production (Benke and Wallace 1990), increased invertebrate abundance (Angermeier and Karr 1984), increased invertebrate diversity (Murphy and Hall 1981), increased fish abundance, diversity, and numbers of larger fish (Angermeier and Karr 1984, Murphy and Hall 1981, Sedell *et al.* 1984).

Benke and Wallace (1990) estimated snag surface area in streams to exceed benthic habitat area by 20 to 50 percent. This increased area provides more chemically and biologically active surfaces and attachment sites important for grazing, scraping, and filter-feeding aquatic invertebrates (Triska and Cromack 1980, Harmon *et al.* 1986). This implies that the old-growth lakes in the study, with greater amounts of CWD, can potentially produce more invertebrate biomass than second-growth lakes.

The function of CWD itself as a food source for aquatic invertebrates is less important. Very few insects ingest or bore into submerged or waterlogged wood when compared to terrestrial woody debris (Harmon *et al.* 1986), and this is one of the reasons that CWD persists so long in aquatic systems. It is this stability of CWD in stream systems that makes it attractive as habitat (Benke and Wallace 1990). In lentic systems, where water movements do not supply a constant particulate food source, or require firm attachment to prevent being carried off by the current, CWD may be less important for invertebrate production. Moring *et al.* (1986) found invertebrate densities to be less in areas of log accumulation than adjacent bare sediment, and suggested this as a reason for finding no significant difference in fish abundance between log and non-log areas of the lake. Invertebrate populations in the littoral zone of five of the study lakes may be reduced due to the low pH found in those lakes (Dermott 1985).

For fish, the three-dimensional arrangement is the most important feature, rather than increased invertebrate food supply (Sedell *et al.* 1984). Fish abundance in streams has been shown to increase with increasing structural complexity (Harmon *et al.* 1986, Sedell *et al.* 1984). This phenomenon was also apparent in the study lake systems. In the lakes with good visibility (Crampton and Snap Jack lakes), fish were usually seen associated with the CWD being measured. The debris was being used primarily as cover, although some largemouth bass spawning beds were located adjacent to debris. No feeding behaviors were observed at all, even after allowing fish sufficient time to become used to my presence. In Bergner Lake, where CWD was scarce, the fish populations had switched to the overhanging bog mat for cover requirements, and were not associated with the woody debris in the lake.

It has not been determined whether the presence of CWD is required for fish production, or merely concentrates the fish already present in the system. Triska and Cromack (1980) stated that "wood debris seems to have a direct effect on the size of fish populations but only an indirect influence on their metabolism". I would paraphrase this as "wood debris seems to have a direct effect on the *numbers of fish present in an area* but only an indirect influence on their metabolism". Some species, such as the *Micropterus* species and crappies, do utilize woody debris when spawning by locating nests next to, or broadcasting eggs over, woody debris (Scott and Crossman 1973). Insufficient woody debris could be limiting in this case, and I have observed smallmouth bass in a clean-bottomed lake constructing beds next to discarded beer cans when CWD was absent. For other species, it is more likely that CWD simply provides a stable visual reference in an otherwise featureless environment, or at most provides ambush cover or refuge from predators.

Implications for Management

In general, abundance of in-lake CWD does differ between study lakes in old-growth and second-growth settings, with fewer and smaller pieces occurring in the second-growth setting seepage lakes. The protected nature of the second-growth lakes studied may not be representative of other deforested or reforested settings where human impacts are less controlled. Clearing of CWD for navigation, aesthetics, and swimming beaches will lessen the amount of CWD available as habitat. In these lakes, I believe the addition of woody structure would be indicated and necessary.

The three important questions posed by Sedell *et al.* (1984) are:

1) what kind of structure should be used?

2) where should the structure be placed?

3) how much structure is enough?

I would add a fourth question:

4) how has the change from old-growth to second-growth forest changed the dynamics of the ecosystem?

The answers will depend on the lake and the goals of the manager. The characteristics of the second-growth study lakes demonstrate that each of these lakes was unique in CWD content. Any naturally-occurring CWD will require no management, and provide a template for supplementation. Restoration of CWD to pre-existing conditions is impossible, and should not be attempted (Bryant 1983); rather the focus of CWD management should be to maximize the beneficial aspects of structural additions while offsetting the adverse effects (if any) and the costs of installation. Structures most like natural inputs (tree-drops) at 90° to the shoreline will provide cover at a range of depths, from the land-water interface to the near-pelagic. More branching (complexity) will increase the attractiveness of the structure, and provide a range of interstice sizes for various fish to select from. The importance of the microhabitat size within the macrohabitat of woody structure was emphasized by Johnson *et al.* (1988). I have observed that pine trees recently added to the water, complete with dense needles, were more attractive to a variety of fish species and sizes than bare trunks. Coniferous trees persist longer in aquatic systems (Andrus *et al.* 1988) and would be the preferred species for tree-drops when available. Considering how structure-poor most recreational lakes are, as many of these structures as feasible should be used.

A great deal of emphasis is placed on manipulation of structural habitat by fisheries managers today. Addition of structural habitat is relatively easy and inexpensive, visually impressive, and psychologically satisfying to the users of the resource. I believe that managers should step back and consider the productivity potential of the system before improving habitat.

The old-growth lakes of the Sylvania Wilderness support small populations dominated by older, larger fish (Miller 1992). This is not due to higher growth rates; rather it is due to longevity of the individual fish (Clady *et al.* 1975). I observed no fish utilizing CWD in either Corey or Katherine lakes; this may be because of small numbers present or poor visibility in these lakes. Recruitment in old-growth lakes of the SWA may be reduced due to the low productivity of the lakes (Clady *et al.* 1975), and the low pH. I think it is doubtful that the presence or absence of CWD in these lakes would affect either fish numbers or production. Many fish were observed around the CWD in Snap Jack Lake, but this lake had a higher pH and more light penetration.

The fish populations observed in the second-growth lakes appeared healthy and abundant, in spite of the reduced CWD. The productivity of these lakes must have been altered in some way by the shift from surrounding old-growth to second-growth forest. Replacement of hemlocks with hardwoods has been shown to decrease soil acidity and increase the cycling of nutrients (Hix and Barnes 1984). It is possible that this change has increased the availability of nutrients in the second-growth lakes, and increased overall production. If this is true, increasing woody habitat may benefit the fish population in this case.

CONCLUSIONS

The study lake systems within old-growth forest settings were similar in CWD attributes, although CWD in Katherine Lake was found to be slightly less than Corey or Snap Jack lakes. The CWD distribution in lakes within the second-growth forest settings were not similar to each other, and Brown Lake was dissimilar from all other study lakes. The presence of inlets and an outlet, and subsequent movement of water through the lake, higher decomposition rates allowed by higher pH, and fetch may all attribute to the high degree of difference in Brown Lake's CWD. The CWD distribution (volume and number of pieces) in the second-growth study lakes was less than that of the old-growth study lakes, indicating that the second-growth systems may be CWD-deficient. Lack of CWD may be limiting for secondary production and/or fish habitat requirements. However, the differences in this study between the two settings is not as extreme as those found in similar studies in stream systems.

The dynamic nature of stream systems can drastically affect the amount and distribution of CWD within the banks; changes in CWD input through changes in the riparian forest can decrease the amounts of CWD in the stream system. Lake systems, with their relative lack of dynamic forces, are not as susceptible to movements or emigration of CWD within the lake. Inundated and waterlogged wood decay rates are extremely slow, especially for larger diameter debris and low pH waters. If left undisturbed, in-lake CWD will persist for a long time, even in second-growth settings.

The characteristics of the riparian shoreline vegetation and slope have been useful in modelling CWD inputs to stream systems, and may prove useful as predictors of in-lake CWD content as well. The basal area of live trees along the shoreline may have the most potential for predicting natural CWD volume within the lake. In lakes where human influence has altered or removed most naturally-occurring CWD, analyzing the riparian vegetation could suggest a base guideline for supplementing in-lake woody structure. Placement of this structure to mimic naturally occurring inputs will increase the chance of the added structure being used as habitat.

The small number of lakes and subsequent minimal sample size obtained in this study may not have been sufficient to adequately demonstrate the differences or similarities among lake or settings. Future studies utilizing a larger number of lakes and greater percentage of littoral zone sampled may result in better resolution of CWD characteristics within the lakes of both settings.

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