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QUANTIFYING WITHIN-LAKE GRADIENTS OF WAVE ENERGY: INTERRELATIONSHIPS OF WAVE ENERGY, SUBSTRATE PARTICLE SIZE AND SHORELINE PLANTS IN AXE LAKE, ONTARIO

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ABSTRACT

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Exposure is defined as the total effect of waves on lakeshore vegetation. Waves may affect shoreline plants directly (e.g., by uprooting seedlings) or indirectly (e.g., by eroding fine sediments). Exposure may be an important ecological factor affecting the within-lake distribution of shoreline plants. The object of this study was to develop a method for identifying exposure gradients, using wind data and fetch measurements. Fetch was either (1) measured directly from aerial photographs for 16 compass bearings ("direct fetch") or (2) calculated from 32 compass bearings to compensate for the shape of the lake basin ("effective fetch"). Wind data were either (1) mean wind velocity multiplied by directional percent frequency or (2) exceedance by direction. Four time periods (1) May, (2) growing season, (3) ice-free season and (4) entire year, were considered. This yielded 2 × 2 × 4 = 16 measures of exposure. Twenty-five points on a 600 m section of shoreline on Axe Lake, Ontario, Canada were sampled for sediment characteristics (proportion silt and clay; sand sorting coefficient) and shoreline plants (depth ranges occupied by six selected species). Exposure values then were calculated for all 25 points using the 16 different methods of calculation. Spearman rank correlation coefficients were used to determine the correlation between calculated exposure values, sediment characteristics and species distributions. The sand sorting coefficient, *Eriocaulon septangulare* With., *Nymphoides cordata* (Ell.) Fern. and *Utricularia cornuta* Michx. were positively correlated with all measures of exposure. Proportion silt and clay, *Brasenia schreberi* Gmel., *Dulichium arundinaceum* (L.) Britt. and *Pontederia cordata* L. were negatively correlated with all measures of exposure. Calculations based on direct fetch yielded the strongest correlations. When effective fetch was used, measurements based on annual or May exceedance by direction values yielded the best results. It is concluded that calculated measures of exposure provided a biologically meaningful way to rank areas of shoreline along an exposure gradient.

Keddy 1982

INTRODUCTION

There is a great deal of within-lake variation in lakeshore vegetation. One of the most likely causes of this variation, aside from water depth, is exposure to wave activity. This may have direct effects on plants by transporting seeds, uprooting seedlings and damaging mature plants. There may also be many indirect effects such as the erosion, transport and deposition of sediment, nutrients, and organic matter. In this paper, I will use the term exposure to refer to the total effect of waves on lakeshore vegetation. In many lakes, exposure, or correlated factors such as substrate particle size, are considered to be a major factor affecting plant distributions (Pearsall, 1920; Vaarama, 1938; Swindale and Curtis, 1957; Bernatowicz and Zachwieja, 1966; Spence, 1967; Aiken and Gillett, 1974; Hutchinson, 1975; Nicholson et al., 1975), although in other lakes it may play a less important role (Howard-Williams and Walker, 1974). There are, however, few quantitative data relating changes in vegetation to exposure. In contrast, studies of marsh vegetation have demonstrated clear relationships between species composition and environmental factors (Harris and Marshall, 1963; Walker and Wehrhahn, 1971; Auclair et al., 1976a, b; van der Valk and Davis, 1978). One of the generalizations which emerges is that both environmental disturbance and substrate characteristics are extremely important in regulating species composition. This emphasizes the importance of seeking quantitative relationships among exposure, substrates and vegetation on lakeshores.

One of the factors which may have hindered botanists in quantifying the effects of exposure on lakeshore vegetation is the difficulty in quantifying exposure itself. While it may be possible to recognize an exposed shore or a sheltered one, identifying extremes alone is not sufficient. The ability to rank areas of shoreline in terms of increasing exposure would permit the application of direct gradient analysis (Whittaker, 1967) to shoreline vegetation. Direct gradient analysis has been used in a wide range of situations, from altitudinal distributions of trees (Whittaker, 1956) and birds (Terborgh, 1971) to the distribution of salt marsh plants (Pielou and Routledge, 1976) and desert succulents (Yeaton and Cody, 1979).

The total effect of waves on a lakeshore (exposure) will be directly related to the amount of energy available for scouring the shoreline. Wave energy is, in turn, related to the square of wave height (Pond and Pickard, 1978). Wave height is known to be a function of three main variables: fetch (the distance over which waves can build up), wind speed, and wind duration (Johnson, 1948; Bretschneider, 1966; Hutchinson, 1975; U.S. Army Coastal Engineering Research Center, 1977; Pond and Pickard, 1978). These three factors are not easily used to predict expected wave height, however. If winds blow for a long duration, then maximum wave height may be determined by fetch; if winds blow for only a short duration, then maximum wave height may be determined by duration alone (Johnson, 1948). Water depth places overall limits on wave height, irrespective of fetch, wind speed and duration (Bretschneider, 1966; U.S. Army Coastal Engineering Research

Center, 1977). Wave period may vary as well as wave height (Pond and Pickard, 1978), Moreover, wave refraction may be an important consideration (Davidson-Arnott and Pollard, 1980).

Thus, the prediction of wave heights alone is a complex problem, even considering only three variables. When water depth, convoluted shorelines, refraction, and the presence of littoral zone vegetation are included, the difficulty of predicting exposure for given points on a lakeshore may seem overwhelming. There were therefore two objectives in this study. The first was to test whether observed variation in substrate characteristics and species distributions on a lakeshore could be related to a simple calculated measure of exposure. If such a relationship could be found, the second objective was to determine which measure of exposure was most strongly correlated with sediment characteristics and species distributions. This would then provide aquatic ecologists with a method of ranking shorelines from high to low exposure. To simplify the procedure further, only a 600 m section of lakeshore was considered in this study. The results are presented as follows: relationships among different measures of exposure, relationships between exposure and substrate characteristics, and then relationships between exposure and selected shoreline species.

METHODS

Description of study area

Axe Lake occurs on the boundary of Parry Sound District and Muskoka District east of Georgian Bay in Ontario, approximately 20 km NW of the town of Huntsville (Fig. 1). The lake is a remnant of the former shoreline of

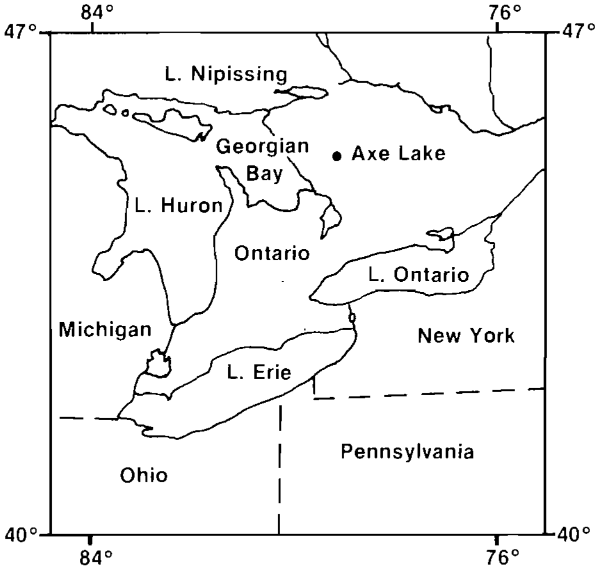

Fig. 1. Location of Axe Lake in Ontario, Canada.

post-glacial Lake Algonquin, with areas of very gently sloping sand shores. At its deepest point, the lake is approximately 12 m deep, but near the shore there are extensive shallow areas less than 2 m deep. These areas have large beds of *Nymphaea odorata* Ait., and often *Nymphoides cordata* (Ell.) Fern. Transects representing 1 m of vertical distance ranged from 40—130 m in length on such shores. The lake is surrounded by deciduous forest on upland sites and coniferous forests in low, poorly-drained sites. Most of the upper shoreline is dominated by shrubs (principally *Myrica gale* L.), often with an adjacent zone of emergent herbaceous species. During the spring, the gently-sloping sand shores are covered in water, but as the summer progresses, expanses of open sand and herbaceous vegetation are exposed by falling water levels. There are no long-term records of water level, but summer water levels have varied among the last three years of field work. Near the north end of the lake the open sandy shores grade into peat shorelines to both the east and west. The southern shore consists largely of floating bog mats. Many other small lakes in the area are entirely surrounded by floating bog mats. The gradation eastward from open sand to peat shores at the north end of the lake was the primary study area (Fig. 2). The geological history and flora of Axe Lake are discussed in more detail in Keddy (1981). The region has a growing season of between 180 and 190 days, with a frost free period of 100—120 days (Department of Energy, Mines and Resources, 1974). The shorelines are frozen from approximately November—April.

Data collection

Vegetation sampling

Random numbers were drawn to select twenty-five points along the 600 m section of lake perimeter, subject to the criterion that all transects must be separated by a minimum of 10 m to ensure relative independence. In the case of transects selected with logs or pools interrupting the monotonic slope, the transect was moved laterally no more than 1 m in either direction. Twenty 5 cm increments of relative height were marked out along each transect. An observer sighted through an automatic level at a measuring pole held by an assistant. As the assistant gradually moved the pole back and forth along the transect, points representing 5 cm height increments were noted and marked. Twenty height increments were thus located in each transect. By recording the presence or absence of each species in each height increment, the depth tolerances of each species in each transect could be determined. The sampling of the vegetation is described in more detail in Keddy (1981). Species nomenclature follows Fernald (1950).

Substrate sampling

At each sample point on the lakeshore, sample units of substrate were collected at the water line and 0.25 m above and below the water line, measured as vertical distance. At each height on the shore, a 3 cm diameter

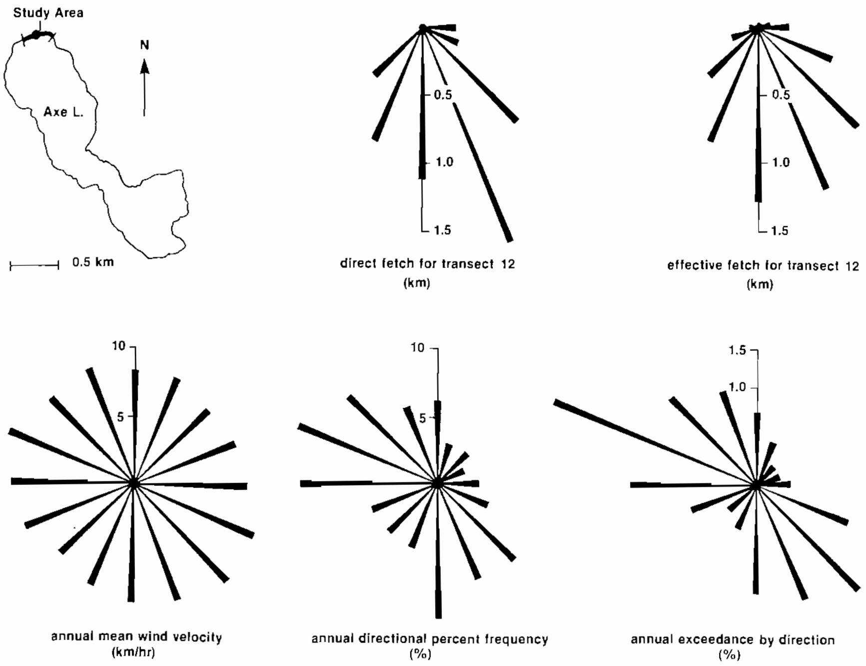

Fig. 2. Calculating exposure for Axe Lake. Upper left shows lake perimeter with the study area and a dot to mark transect 12. Upper centre and right show direct and effective fetch measurements for transect 12. Note that the lake scale is reduced relative to that of the fetch diagrams. Sample wind data in bottom row show data used to calculate annual exposure. Note that the orientation of the study area is such that the winds from the north-west have much less impact than winds from the south-east.

core of sediment 10 cm deep was removed at the four corners and centre of a 0.5 m X 0.5 quadrat. These five cores were combined to represent that height and position on the lake perimeter. All sample units were collected on a single day by visiting transects in the random order in which they had been sampled for vegetation. All sample units were frozen that night.

Substrate sample analysis

Samples were thawed and dried in a forced draught oven at 30° C. A portion was then split off for texture analysis (approximately 50 g). It is necessary to remove organic matter prior to texture analysis (Folk, 1968), but standard peroxide treatment (Day, 1965) proved inadequate because of the large peat fraction in some samples (as high as 50% loss on ignition). The entire portion split off was therefore ignited at 400° C to remove organic matter and determine percent loss on ignition. The remaining material was then dry-sieved to determine sand fractions from very coarse sand through to very fine sand (VCS, 1—2 mm; CS, 0.5—1 mm; MS, 0.25—50 mm; FS, 0.10—0.25 mm; VFS, 0.05—0.10 mm). The material finer than 0.05 mm, which collected in the bottom pan, was combined silt and clay particles. Baking samples with clay can turn the entire sample to brick (Folk, 1968), however, the careful drying of the sample before ignition prevented this problem. Where microscopic inspection showed that sieving had not separated aggregations of clay and sand, the sample was lightly ground with a rubber stopper and then resieved. Trial runs with extra sample units had shown that the ash from the ignited peat sieved out largely in the silt and clay category. If this were not corrected for, increasing silt and clay values might actually reflect increased organic matter. The expected weight of ash could be estimated from percent loss on ignition (0.05 of original weight of organic matter), and this expected ash component was subtracted from the silt and clay component.

The following texture characteristics were then used in the analysis:

(i) proportion silt and clay (the proportion of the total sample mass consisting of silt and clay), and

(ii) sand sorting coefficient (the dispersion of the sand particles over the five sand particle size classes, measured as the standard deviation calculated from the proportion of these five size class fractions within the sand category).

Measuring exposure

Fetch

Fetch was measured directly from an enlarged aerial photograph (scale: 10 cm = 1 km). A transparency with 32 lines radiating (at 11.25° intervals) from a single point was superimposed over each point on the lake perimeter where substrate and vegetation data were collected. The distance to the adjacent shoreline along each line was then determined to the nearest 10 m (1 mm on the aerial photograph). Thus, for Axe Lake (25 transects), a 25 × 32 fetch matrix was obtained.

(1) Direct fetch. Let the term direct fetch refer to measurements taken directly from the aerial photograph. Wind data were available for 16 compass bearings. By taking every second fetch measurement, that is, fetch measurements at 22.5° intervals, it was possible to obtain a direct measure of fetch corresponding to each of 16 compass bearings. This yielded a 25 × 16 direct fetch matrix.

(2) Effective fetch. The shape of a body of water will affect its wave generation (U.S. Army Coastal Engineering Research Center, 1977). Thus, a large fetch value may be less meaningful if it represents a narrow arm on the opposite shore than if it represents a large bay. By taking adjacent fetch measures into account, a correction can be made for the shape of the opposite shore, and a measure of effective fetch calculated. In the manner described by the U.S. Army Coastal Engineering Research Center (1977) effective fetch was calculated for each of 16 compass directions. Each effective fetch value (F_E) was composed from weighted direct fetch values (F) for all adjacent fetches less than 45° away.

$$F_{\mathrm{E}} = [F(\alpha) \cos \alpha + \sum_{i=1}^{3} F(\alpha + 11.25i) \cos (\alpha + 11.25i) + \sum_{i=1}^{3} F(\alpha - 11.25i) \cos (\alpha + 11.25i)] / [\cos \alpha + 2(\sum_{i=1}^{3} \cos (\alpha + 11.25i))]$$

where α is set to zero for each F_{E} calculated.

By calculating the effective fetch for 16 compass directions in 25 transects, a 25 × 16 effective fetch matrix was produced. Figure 2 (upper centre and right) shows direct and effective fetch for a typical transect.

Climatic data

The nearest weather station is Muskoka airport, 50 km southeast of Axe Lake. The data used in the calculations were as follows:

(1) Mean wind velocity, for each of 16 compass bearings, based on one minute averages taken on the hour from 1955 to 1972. These were obtained from Canadian Normals (Atmospheric Environment Service, 1975). Annual mean wind velocity is shown in Fig. 2 (lower left).

(2) Directional percent frequency, the percentage of time in which winds blew from each of 16 compass bearings, based on hourly readings from 1955 to 1972. These were obtained from Canadian Normals (Atmospheric Environment Service, 1975). Annual directional percent frequency is shown in Fig. 2 (lower centre).

(3) Exceedance, the proportion of winds exceeding 12 mph (19.3 km h^{-1}), for each of 16 compass bearings, based on hourly readings. Exceedance might be important if it is only extreme conditions which affect exposure. Exceedance tables give exceedance by direction for different wind speeds (1—3, 4—7, 8—12, 13—19, 19—24, . . . , 75 mph); 12 mph was chosen as a reasonable extreme since only 14% of winds exceeded this at Axe Lake over the entire year (maximum = 21% in April, minimum = 7% in August). For each month, and each compass direction, the percent of hours with wind speeds equal to or greater than 12 mph (19.3 km h^{-1}) were tabulated. A mean vector was used for calculations based on data from more than one month. These data were obtained from the Hourly Data Summary No. 86 for Muskoka Airport (Atmospheric Environment Service, 1971, Environment Canada, 18 pp.). Annual exceedance by direction is shown in Fig. 2 (lower right).

Time of year

Wind data are available on a month by month basis, so calculations can be based on wind data for any period of months selected. Four time periods were tried.

(1) May. If ice scouring during spring break up has a major effect on sediment and plants, wind directions from this month alone might be the best predictors of exposure. As well, there would be little or no aboveground vegetation present to stabilize sediments or dissipate wave energy.
(2) Growing season (June to September, inclusive). This is the time when plants would be actively growing and might be directly affected by wave damage.
(3) Ice free season (May to October inclusive). This allows for effects on sediment or vegetation for the entire year except when the lakeshore is covered by ice. It is likely that little sediment movement or vegetation damage from waves occurs from November to April, since at least the shoreline areas should be frozen during this period. No long term data on mean ice-free periods are available.
(4) Annual. Since this includes periods when the lake is covered in ice it would initially seem to be the least useful choice.

Calculations

The effects of exposure on substrate characteristics and species distributions should be related to the wave energy regime of a particular shore. Ideally one would determine the total wave energy incident on a given shore over a given time period. Wave energy is related to the square of wave height, and for sinusoidal waves, half is potential energy and half is kinetic energy (Pond and Pickard, 1978). Given that wave height, in turn, is a complex function of fetch, wind speed, duration, and water depth, it seems unrealistic to expect more than to be able to calculate a measure proportional to wave height. This would allow the ranking of points along a shoreline in order of increasing wave energy.

Using the fetch matrices and the wind data matrices it is possible to generate several different values which should be related to the size of waves arriving at given shorelines. One measure of exposure (E_M) is based on mean wind velocity

$$E_M = \sum_{i=1}^{16} \text{mean wind velocity}_{22.5\,i^\circ} \times \text{percent frequency}_{22.5\,i^\circ} \times \text{fetch}_{22.5\,i^\circ}$$

The summation occurs over the 16 compass directions, although, in practice, a given transect receives waves from a more restricted set of directions. Thus, there are many zeros in the fetch matrix corresponding to directions from which waves cannot arrive.

A second measure of exposure (E_E) is based on exceedance. Since exceedance already incorporates the velocity component by considering only winds > 12 mph, values based on exceedance are calculated as

$$E_E = \sum_{i=1}^{16} \text{exceedance}_{22.5\,i^\circ} \times \text{fetch}_{22.5\,i^\circ}$$

Thus, it is possible to calculate measures of exposure using one of two fetch matrices (direct, effective) and one of two measures of windspeed (mean, exceedance). Windspeed data are available for four time periods (May, growing-season, ice-free season, annual). This yields 2 × 2 × 4 = 16 different measures of exposure which can be calculated for each transect in turn.

Duration is not directly included in these calculations, except as it is reflected in percent frequency. If winds from a given direction are of long duration, then, in general, this will be reflected in measures of frequency (which are based on hourly readings). Although wind duration may be important for determining wave height where fetch and water depth are not limiting, in lakes (which are small and shallow, relative to oceans) fetch (Johnson, 1948) or water depth (Bretchneider, 1966) may place an upper limit on wave heights. Waves in small lakes might therefore be relatively insensitive to wind duration.

Fetch is measured in km and wind speed in km h^{-1}. Exceedance and percent frequency have no units. Therefore, measures based on mean windspeed would be expressed as km^2 h^{-1}, and measures based on exceedance would be expressed as km. Since the object is to produce a measure related to the size of waves arriving on a shore, integrated over a particular time period, these units are not relevant. The values calculated are therefore treated as dimensionless measures of exposure.

Water depth was not included as a variable in this study, although water depth is an important variable (Bretschneider, 1966; U.S. Army Coastal Engineering Research Center, 1977). All transects faced the same open area of Axe Lake, and all had very gentle slopes (maximum slope 1 : 38, or 19 m horizontally to 0.5 m water depth; minimum slope 1 : 286, or 143 m horizontally to 0.5 m water depth). Given this extremely shallow water adjacent to these transects, variation in water depth seemed unlikely to influence differences among transects.

To determine which of the 16 measures of exposure was most closely related to substrate characteristics, the correlation between substrate characteristics and calculated exposure values was calculated (n = 75 based on n = 3 depths × n = 25 transects). There was no reason to expect a linear relationship between substrate characteristics and the calculated values of exposure, so the Spearman rank correlation coefficient (Siegel, 1956) was used as a measure of correlation. The analyses were, however, duplicated using parametric correlation coefficients, and similar results were obtained. The same techniques were used to examine the relationships between exposure and the depth range occupied by each species (n = 25 transects).

RESULTS

Figure 3 shows the 16 measures of exposure plotted against the rank order of transects from east to west along the 600 m section of lakeshore.

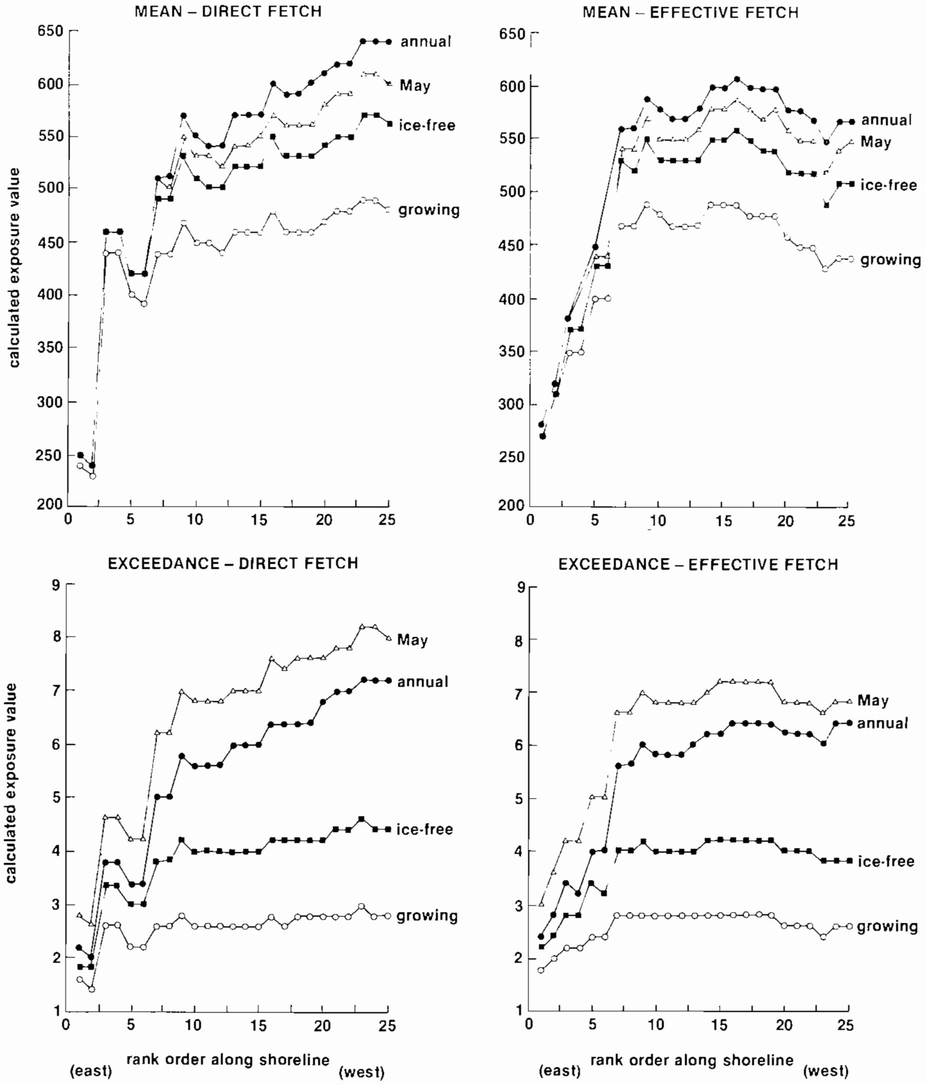

Fig. 3. Calculated exposure values plotted against the rank order of transects along the shoreline from east to west. Upper graphs give values for mean wind speed, lower graphs give values for exceedance. Left graphs give values for direct fetch, right graphs give values for effective fetch. Note that vertical scales differ between the upper and lower graphs.

The graphs permit comparison of mean wind speed (upper) with exceedance (lower), and direct fetch (left side) with effective fetch (right side). First consider the similarities among all four graphs. In general, the calculated values for exposure increase from east to west along the shoreline studied. Values for the annual and May calculations are consistently higher than those

TABLE I

Spearman rank correlations (r_s) among all 16 sets of calculated exposure values*

			Direct fetch								Effective fetch							
			Mean				Exceedance				Mean				Exceedance			
			Annual	May	Growing	Ice-free	Annual	May	Growing	Ice-free	Annual	May	Growing	Ice-free	Annual	May	Growing	Ice-free
Direct fetch	Mean	Annual	1.00															
		May	1.00	1.00														
		Growing	0.99	0.99	1.00													
		Ice-free	1.00	1.00	0.99	1.00												
	Exceedance	Annual	0.99	0.99	0.97	0.99	1.00											
		May	0.99	0.99	0.97	0.99	1.00	1.00										
		Growing	0.97	0.97	0.98	0.97	0.95	0.96	1.00									
		Ice-free	1.00	1.00	0.99	1.00	0.99	0.99	0.97	1.00								
Effective fetch	Mean	Annual	0.57	0.57	0.56	0.57	0.57	0.57	0.52	0.57	1.00							
		May	0.53	0.53	0.52	0.53	0.53	0.53	0.47	0.53	0.99	1.00						
		Growing	0.36	0.36	0.39	0.38	0.35	0.35	0.33	0.38	0.90	0.92	1.00					
		Ice-free	0.37	0.37	0.39	0.38	0.37	0.37	0.32	0.38	0.93	0.95	0.99	1.00				
	Exceedance	Annual	0.84	0.80	0.84	0.84	0.85	0.85	0.78	0.84	0.84	0.81	0.65	0.68	1.00			
		May	0.65	0.65	0.64	0.65	0.65	0.65	0.61	0.65	0.98	0.97	0.86	0.88	0.90	1.00		
		Growing	0.36	0.36	0.39	0.37	0.35	0.35	0.33	0.37	0.90	0.91	1.00	0.98	0.64	0.86	1.00	
		Ice-free	0.37	0.37	0.39	0.38	0.36	0.37	0.32	0.38	0.92	0.95	0.99	1.00	0.67	0.88	0.99	1.00

*$N = 25; r_s \geqslant 0.40, P < 0.05; r_s \geqslant 0.51, P < 0.01$.

for the ice-free season and growing season, a reflection of the strong winter and spring winds in this area. As well, the variation among transects is least for values calculated for the ice-free season and growing season, particularly the exceedance/effective fetch calculations (lower right).

Comparing calculations based on mean wind speed (upper) with exceedance (lower), the values based on mean wind speed vary less with time of year than those based on exceedance. For example, the mean/direct fetch (upper left) annual and May values are approximately 1.5 times the growing season values. In contrast, exceedance/direct fetch (lower left) annual and May values are approximately 3 times the growing season values. The same is true for values based on effective fetch (upper right compared to lower right). Values based on exceedance also show seasonal differences among sheltered transects, whereas values based on mean wind speed produce largely coincident values in sheltered transects.

A comparison of calculations based on direct fetch (left) with those of effective fetch (right) shows that effective fetch calculations minimized among-transect differences at intermediate and high levels of exposure. As well, direct fetch calculations show exposure increasing monotonically along the shoreline studied, whereas effective fetch calculations suggest that exposure is bitonically related to the rank order of the transects.

Table I shows a Spearman rank correlation matrix for these 16 measures of exposure. In general, all of these measures are highly correlated, and thus might be expected to yield similar results as predictors of exposure. Measures based on direct fetch are poorly correlated with measures based on effective fetch, suggesting that variation in the fetch matrix is more important than variation in the time of year considered. Exposure values for the growing season and ice-free season (using effective fetch) are not significantly correlated with exposure values based on the direct fetch matrix.

There are several ways to compare calculated measures of exposure with substrate characteristics. Table II shows that the range of variation in sediment characteristics was greatest at 0.25 m above the water line, and least at 0.25 m below the water line. Thus all exposure/sediment calculations could be reported for the three water depths independently. Qualitatively the results are similar, so Table III shows only correlations between exposure and all three depths combined (n = 75). The proportion of silt and clay should be greatest in sediments from sheltered areas and it is therefore negatively correlated with all measures of exposure, but most strongly with those based on the direct fetch matrix (Table III, column 1). The sorting coefficient should be greatest in exposed areas, where reworking of sands should have produced a more uniform particle size, and Table III (column 2) shows it is positively correlated with all measures of exposure. Unlike silt and clay, however, it is most strongly correlated with calculations based on the effective fetch matrix.

Table III also shows the correlations between the range of depths occupied by selected species and calculated exposure values. These species were

TABLE II

Within-lake variation in sediment characteristics at three relative heights

Sediment characteristic	Relative height (m)		
	0.25	0*	–0.25
Proportion silt/clay	0.01–0.25	0.01–0.12	0.01–0.02
Sand sorting coefficient	0.18–0.35	0.18–0.35	0.21–0.30

*0 m = water line.

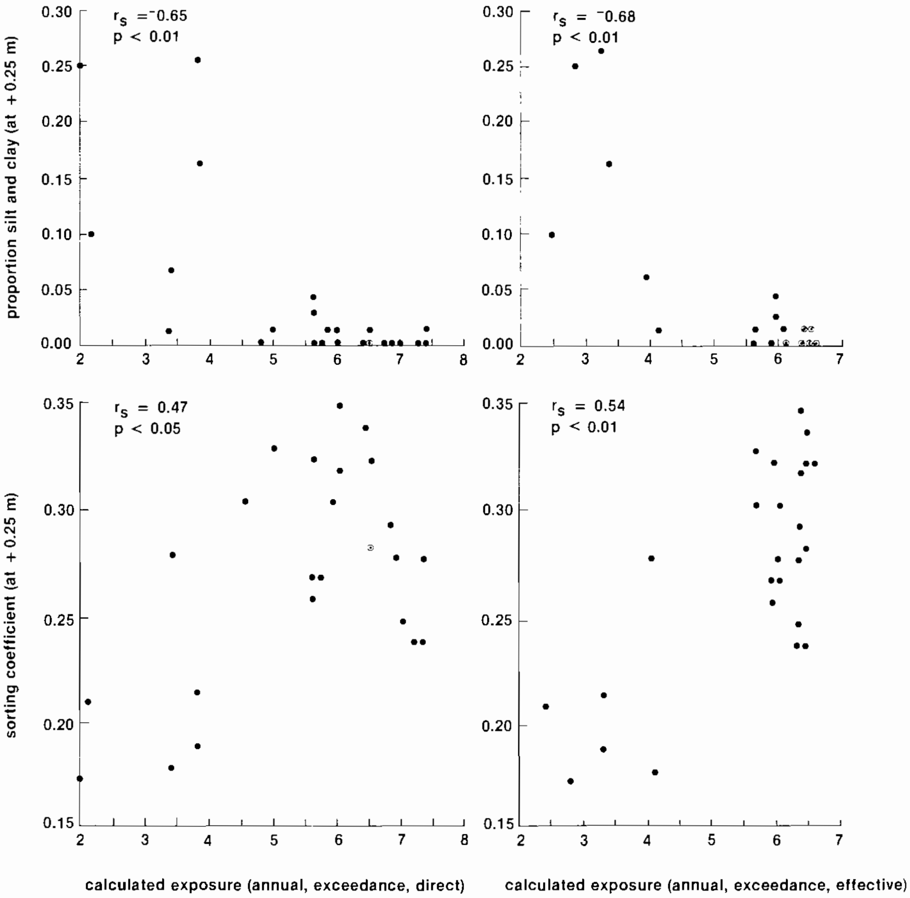

Fig. 4. Proportion silt and clay in the substrate (top) and sorting coefficient of sand fraction (bottom) plotted against two sets of calculated exposure values. Left-hand figures show exposure calculated as annual/exceedance/direct fetch; right-hand figures show exposure calculated as annual/exceedance/effective fetch. Substrate samples were taken at 0.25 m vertical height above the July water line.

TABLE III

Spearman rank correlations (r_s) between calculated values of exposure and both two sediment characteristics and depth ranges occupied by six plant species

Exposure			Sediment*		Species**					
			Silt/clay	Sorting	*E. septangulare*	*N. cordata*	*U. cornuta*	*B. schreberi*	*D. arundinaceum*	*P. cordata*
Direct Fetch	Mean	a***	−0.59	0.46	0.57	0.82	0.87	−0.77	−0.81	−0.81
		M	−0.59	0.46	0.57	0.82	0.87	−0.77	−0.81	−0.81
		g	−0.60	0.46	0.55	0.87	0.86	−0.72	−0.79	−0.82
		i	−0.59	0.46	0.57	0.81	0.87	−0.76	−0.80	−0.81
	Exceedance	a	−0.59	0.47	0.58	0.83	0.89	−0.80	−0.83	−0.81
		M	−0.59	0.47	0.58	0.82	0.89	−0.80	−0.83	−0.81
		g	−0.53	0.38	0.48	0.79	0.85	−0.72	−0.82	−0.81
		i	−0.59	0.46	0.57	0.81	0.87	−0.76	−0.80	−0.81
Effective fetch	Mean	a	−0.46	0.61	0.58	0.56	0.57	−0.43	−0.55	−0.69
		M	−0.44	0.61	0.56	0.50	0.54	−0.39	−0.50	−0.66
		g	−0.40	0.61	0.49	0.32	0.38	−0.13	−0.32	−0.57
		i	−0.39	0.62	0.50	0.33	0.40	−0.18	−0.34	−0.56
	Exceedance	a	−0.56	0.54	0.67	0.74	0.81	−0.75	−0.78	−0.81
		M	−0.51	0.60	0.65	0.62	0.65	−0.53	−0.66	−0.77
		g	−0.40	0.62	0.50	0.31	0.38	−0.14	−0.33	−0.58
		i	−0.39	0.61	0.49	0.33	0.39	−0.17	−0.34	−0.56

*$N = 75$; $r_s \geqslant 0.23$, $P < 0.05$; $r_s \geqslant 0.30$, $P < 0.01$.

*$N = 25$; $r_s \geqslant 0.40$, $P < 0.05$; $r_s \geqslant 0.51$, $P < 0.01$.

***a = annual; M = May; g = growing; i = ice free.

selected because of their obvious exposure tolerances from prior field observations on many lakes — *Eriocaulon septangulare* With., *Nymphoides cordata* (Ell.) Fern. and *Utricularia cornuta* Michx. being most abundant on exposed shores and *Brasenia schreberi* Gmel., *Dulichium arundinaceum* (L.) Britt. and *Pontederia cordata* L. being most abundant in sheltered bays. The former three are thus positively correlated, and the latter three negatively correlated with calculated exposure values. In most cases, the distributions of these species are most strongly correlated with measures of exposure based on direct fetch. As with the proportion silt and clay, these species distributions are also strongly correlated with annual/exceedance/effective fetch, but generally poorly correlated with exposure values based on either the growing or ice-free seasons based on effective fetch.

Since correlation coefficients alone can be misleading, Figs. 4 and 5 present scatter plots of sediment characteristics and species distributions. Figure 4 shows the proportion of silt and clay, and sorting coefficients, plotted against two sets of the calculated values for exposure. Figure 5 shows the depth distributions of *Eriocaulon septangulare* and *Brasenia schreberi* plotted against the same two sets of calculated exposure values. These species represent, respectively, species positively and negatively correlated with exposure. The relationships between exposure and both substrate characteristics and plant distributions are generally monotonic. Note that *E. septangulare* exhibits a distribution which changes gradually with exposure, whereas *B. schreberi* shows an abrupt change.

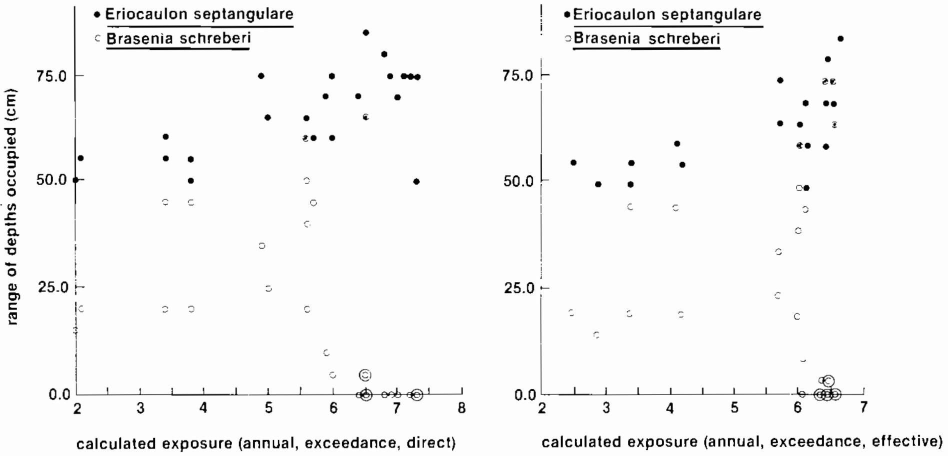

Fig. 5. Depth ranges occupied by *Eriocaulon septangulare* and *Brasenia schreberi* plotted against two sets of calculated exposure values. As in Fig. 4., left-hand figure shows exposure calculated as annual/exceedance/direct fetch, right-hand figure shows exposure calculated as annual/exceedance/effective fetch. Correlation coefficients shown in Table III, $P < 0.01$ in all cases.

results. Secondly, one would expect the annual weather data to yield the poorest results within this category. These difficulties may result from failure to consider water depth or the presence of rooted macrophytes, particularly in those fetch directions running diagonally along the shoreline. It should also be noted that this study considered only one small area of shoreline on a shallow lake basin. Effective fetch values may prove more useful when dealing with lakes in which variation in the shape of the lake basin has a greater effect on wave generation.

It appears that it is possible to calculate values of exposure which will allow aquatic biologists to use direct gradient analysis by ranking shoreline sample sites from low to high exposure. The ultimate test will be to try similar methods on a larger lake with a convoluted shoreline.

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REFERENCES

Aiken, S. and Gillett, J.M., 1974. The distribution of aquatic plants in selected lakes in Gatineau Park, Quebec. Can. Field Nat., 88: 437—448.

Auclair, A.N.D., Bouchard, A. and Pajaczkowski, J., 1976a. Plant standing crop and productivity relations in a *Scirpus—Equisetum* wetland. Ecology, 57: 941—952.

Auclair, A.N.D., Bouchard, A. and Pajaczkowski, J., 1976b. Productivity relations in a *Carex*-dominated ecosystem. Oecologia, 26: 9—31.

Atmospheric Environment Service, 1975. Canadian Normals. Vol. 3. Wind. 1955—1972. Environment Canada, Downsview, Ontario, 139 pp.

Bernatowicz, S. and Zachwieja, J., 1966. Types of littoral found in the lakes of the Masurian and Suwalki lakelands. Ekol. Pol., A 14: 519—545.

Bretschneider, C.L., 1966. Wave generation by wind, deep and shallow water. In: A.T. Ippen (Editor), Estuary and Coastline Hydrodynamics. McGraw-Hill, New York, 744 pp.

Davidson-Arnott, R.G.D. and Pollard, W.H., 1980. Wave climate and potential longshore sediment transport patterns, Nottawasaga Bay, Ontario. J. Great Lakes Res., 6: 45—67.

Day, P.R., 1965. Particle fractionation and particle size analysis. In: C.A. Black (Editor), Methods of Soil Analysis. Vol. 1. American Society of Agronomy, Madison, Wisconsin, pp. 545—567.

Department of Energy, Mines and Resources, 1974. The National Atlas of Canada. 4th edn., Ottawa, Canada, 265 pp.

Fernald, M.L., 1950. Gray's Manual of Botany. 8th edn., D. van Nostrand, NY, 1623 pp.

Folk, R.L., 1968. Petrology of Sedimentary Rocks. Hemphill's, Drawer M, University Station, Austin, Texas, 170 pp.

Howard-Williams, C. and Walker, B.H., 1974. The vegetation of a tropical African Lake: classification and ordination of the vegetation of Lake Chilwa (Malawi). J. Ecol., 62: 831—854.

Harris, S.W. and Marshall, W.H., 1963. Ecology of water-level manipulations on a northern marsh. Ecology, 44: 331—343.

Hutchinson, G.E., 1975. A Treatise on Limnology. Vol. III. Limnological Botany. Wiley, NY, 660 pp.

Johnson, J.W., 1948. The characteristics of wind waves on lakes and protected bays. Trans. Am. Geophys. Union, 29: 671—681.

Keddy, P.A., 1981. Vegetation with Atlantic Coastal Plain affinities in Axe Lake, near Georgian Bay, Ontario. Can. Field Nat., 95: 241—248.

Nicholson, S.A., Levey, R.A. and Clute, P.R., 1975. Macrophyte—sediment relationships in Chautauqua Lake. Verh. Internat. Verein Theor. Angew. Limnol., 19: 2758—2764.

Pearsall, W.H., 1920. The aquatic vegetation of the English Lakes. J. Ecol., 8: 163—201.

Pielou, E.C. and Routledge, R.D., 1976. Salt marsh vegetation: latitudinal variation in the zonation patterns. Oecologia, 24: 311—321.

Pond, S. and Pickard, G.L., 1978. Introductory Dynamic Oceanography. Pergamon, Oxford, 241 pp.

Siegel, S., 1956. Nonparametic Statistics for the Behavioral Sciences. McGraw-Hill, NY, 312 pp.

Spence, D.H.N., 1967. Factors controlling the distribution of macrophytes with particular reference to the Lochs of Scotland. J. Ecol., 55: 147—170.

Swindale, D.N. and Curtis, J.T., 1957. Phytosociology of the larger submerged plants in Wisconsin Lakes. Ecology, 38: 397—407.

Terborgh, J., 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology, 52: 23—40.

U.S. Army Coastal Engineering Research Center, 1977. Shore Protection Manual. Vol. 1. 3rd edn., U.S. Government Printing Office, Washington, DC, 514 pp.

Vaarama, A., 1938. Wasservegetation Studien am Grosssee Kallavesi. Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo, 13: 1—318.

Van der Valk, A.G. and Davis, C.B., 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology, 59: 322—335.

Walker, B.H. and Wehrhahn, C.F., 1971. Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. Ecology, 52: 85—95.

Whittaker, R.H., 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr., 26: 1—80.

Whittaker, R.H., 1967. Gradient analysis of vegetation. Biol. Rev., 42: 207—264.

Yeaton, R.I. and Cody, M.L., 1979. The distribution of cacti along environmental gradients in the Sonoran and Mojave deserts. J. Ecol., 67: 529—541.