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SHORELINE VEGETATION IN AXE LAKE, ONTARIO: EFFECTS OF EXPOSURE ON ZONATION PATTERNS[1]

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Abstract. This study tests several hypotheses relating community structure to environmental disturbance, by testing for changes in the zonation patterns of lakeshore vegetation. Twenty-five transects were examined at different positions along an exposure gradient. The range of water depths tolerated by individual species (realized niche width) changed with exposure. Some (*Lobelia dortmanna, Utricularia cornuta*) reached their maximum on exposed shores, others (*Drosera intermedia, Cladium mariscoides*) at intermediate exposure, and others (*Pontederia cordata, Triadenum fraseri*) on sheltered shores. Species richness peaked significantly at intermediate levels of exposure ($P < .01$). In spite of changes in both species composition and richness, mean niche width did not change with exposure. The distribution of the upper and lower limits of species along the gradient was examined using measures of boundary clustering. The lower and upper boundaries of species were both significantly clustered ($P < .001$), suggesting discrete communities exist on the shoreline gradient. As exposure increased, upper boundaries became more clustered ($P < .002$); lower boundaries were unaffected. The distribution of boundaries shifted landward with increasing exposure. This fact is possibly related to an identical landward shift in the lower boundaries of shoreline shrubs, which appear to have a major influence on the distribution of herbaceous shoreline vegetation.

Key words: aquatic plants; disturbance; exposure; gradients; lakes; marshes; niche width; shoreline plants; shrubs; species richness; wetlands.

INTRODUCTION

The species composition of lakeshore vegetation varies greatly from one point on a lakeshore to another. Although there are many descriptive studies of this variation, there are at present few quantitative studies of lakeshores that relate species composition and community structure to physical factors. By way of contrast, studies on marshes have proceeded considerably further (Harris and Marshall 1963, Walker and Wehrhahn 1971, Auclair et al. 1976*a, b,* van der Valk and Davis 1978). The variation in lakeshore vegetation provides an ideal opportunity to test hypotheses relating species richness and community structure to environmental gradients. The methods chosen for this investigation exploit an a priori knowledge of two major gradients found within lakes: (1) water depth, and (2) wave energy.

The rapid changes in species composition with water depth produce distinct zones characterized by one or more plant species (zonation patterns). While these zones are obvious to the naturalist, and have often been mentioned in the literature (e.g., Pearsall 1920, Dansereau 1959, Mandossian and McIntosh 1960, Bernatowiscz and Zachwieja 1966, Wassen 1966, Spence 1967, Wright and Bent 1968, Hutchinson 1975), only recently have statistical tests been developed to provide methods for asking ecologically meaningful questions about these patterns (Routledge 1975, Pielou and Routledge 1976, Pielou 1977, Underwood 1978*a*, Pielou 1979).

The role of wave energy in controlling the distributions of aquatic macrophytes has often been qualitatively discussed (e.g., Pearsall 1920, Vaarama 1938, Swindale and Curtis 1957, Bernatowicz and Zachwieja 1966, Spence 1967, Aiken and Gillet 1974, Hutchinson 1975, Nicholson et al. 1975). Waves may have direct effects on vegetation; for example, through removing biomass, uprooting seedlings, and transporting propagules. Similarly, they may have many indirect effects through the erosion, transport, and deposition of sediment. Rather than separate these complex and highly correlated effects at present, I have proposed (Keddy 1982) that they all be combined under the term exposure, or the total effect of waves on shoreline vegetation.

In this study I will treat the distribution of species along the vertical gradient (water depth or relative height) as the dependent variable. This gradient not only includes water availability, but correlated factors such as light, nutrients, and substrate particle size (e.g., Pearsall 1920, Spence 1967, Hutchinson 1975). Two attributes of plant zonation are of particular interest. First, the range of relative heights that a species occupies can be considered a measure of realized niche width. Thus, it is possible to measure realized niche widths of species or groups of species on a particular shoreline. Second, the distribution of upper and lower boundaries of species can be examined to test whether they occur in a regular pattern, at random, or in clusters at certain relative heights. Many other studies have looked at the distribution of individual species or com-

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munities along environmental gradients: intertidal invertebrates (Connell 1961, Underwood 1978*b*, Lubchenco 1980), birds on mountainsides (Terborgh 1971, Diamond 1973), mosses in bogs (Vitt and Slack 1975), vascular plants in salt marshes (Pielou and Routledge 1976), desert cacti (Yeaton and Cody 1979), mangroves on shorelines (Rabinowitz 1978), trees on altitudinal gradients (Whittaker 1956), and insects on altitudinal gradients (Dearn 1977).

The independent variable will be exposure. Exposure is clearly correlated with environmental disturbance, and it is therefore possible first to test the intermediate disturbance hypothesis (Connell 1978, Huston 1979, Sousa 1979), which predicts that species richness should peak at intermediate levels of environmental disturbance. By studying these gradients, however, it is possible to determine not only whether disturbance affects the number of species, but whether it affects their interactions. Two questions can be asked: (1) Does environmental disturbance affect the mean niche width of lakeshore assemblages? (2) Does environmental disturbance affect the degree to which groups of lakeshore species share similar upper or lower depth limits? Thus, it is possible to determine whether environmental disturbance affects either the degree of specialization of species, or their tendency to occur in discrete "communities."

The effects of exposure may also be summarized in the terminology of Sanders (1968), who proposed that communities could be arranged along a gradient from "biologically accommodated" to "physically controlled" conditions. The former refers to communities where physical conditions are rather constant, and physiological stress arises predominantly from biological interactions (e.g., competition). The latter refers to communities where physiological stress results primarily from physical factors (e.g., fluctuations in temperature or salinity), and thus where biological interactions are less important. Grime (1977) has recently proposed that two distinct sets of such physical factors influence plants: disturbance and stress. The former is associated with partial or total destruction of plant biomass; the latter is associated with conditions that restrict production (e.g., shortages of light, water, or mineral nutrients). He concludes that plants have different adaptive strategies for these two types of physical control. Both of these factors are likely correlated with exposure, since more exposed shores are not only more disturbed, but tend to have coarse nutrient-poor substrates; the fine, nutrient-rich particles and organic matter are removed and deposited in sheltered areas (e.g., Pearsall 1920, Spence 1967, Hutchinson 1975, Keddy 1982). Huston (1979) has emphasized that the balance between frequency of disturbance and rate of competitive displacement should ultimately determine the species composition of an assemblage. The rate of competitive displacement, in turn, is a function of growth rates of competitive dominants. Lakeshores with high disturbance have nutrient-poor sediments, and therefore low potential for plant growth. Any decreases in nutrient availability with increasing exposure therefore ought to accentuate, not mask, the effects of disturbance.

The object of this paper, therefore, is to examine the effect of exposure on zonation patterns. While many studies have examined one gradient, only a few (such as Whittaker 1956) have shown how a second gradient (topography) interacts with a first (altitude). By quantitatively examining how species distributions along a relative height gradient interact with a gradient of increasing wave energy (exposure), I will examine the following questions regarding species composition on lakeshores.

1) Does increasing exposure affect species richness? (I will show that richness peaks at an intermediate level of exposure.)

2) Does increasing exposure affect the mean niche width of a lakeshore assemblage? (I will show that mean niche width is neither a function of exposure nor of species richness.)

3) Does increasing exposure affect the degree to which groups of species share similar upper or lower depth limits? (I will show that the upper limits of species are clustered, as are the lower limits, thereby producing discrete communities along the relative height gradient. The arrangement of clustering changes significantly with exposure.)

In presenting the results, however, the distribution patterns of selected shoreline species will be examined first. This will not only provide some general natural history of the community concerned, but will aid in interpreting the answers to questions 1 through 3.

Description of study area

Axe Lake occurs along the boundary of Parry Sound District and Muskoka District east of Georgian Bay in Ontario, Canada, ≈20 km northwest of the town of Huntsville (Fig. 1). It is an extremely shallow lake with a sandy bottom and very gently sloping shorelines. Most of the upper shoreline is dominated by ericaceous shrubs, 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. Floating bog mats are found around the southern shore. Near the north end is an open sandy area which grades into peat bog shoreline to both the east and the west. Many other small lakes in the area are entirely surrounded by floating bog mats. This gradation from open sand to peat bog was the primary study area. There are marked changes in the species composition of shoreline vegetation along this gradient (Keddy 1981).

The geological history and floristics of Axe Lake are discussed in more detail in Keddy (1981). The lake is a remnant of the former shoreline of glacial Lake Al-

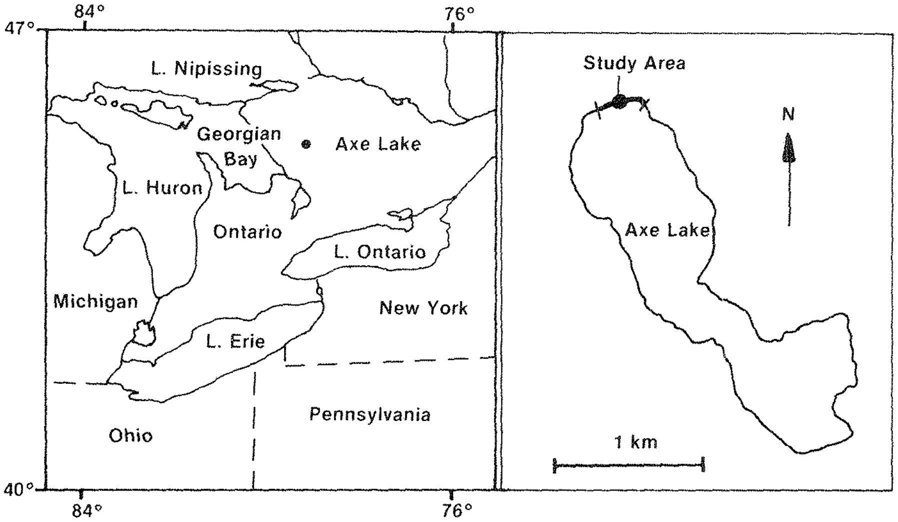

FIG. 1. Location of Axe Lake and the study area.

gonquin, and the flora has affinities to the Atlantic coastal plain of eastern North America. The open sandy shores of Axe Lake support species such as: *Rhexia virginica, Xyris caroliniana, Juncus militaris, Nymphoides cordata, Muhlenbergia uniflora,* and *Rhynchospora capitellata*, which are considered rare in Ontario (Argus and White 1977). These and other species are largely restricted to the Georgian Bay area of Ontario (Keddy and Reznicek 1982), with other disjunct concentrations on the southern end of Lake Michigan (Peattie 1922) and the sand barrens of northwestern Wisconsin (McLaughlin 1932).

The exposure gradient

The size of waves reaching a shoreline will be influenced by many factors including fetch, wind speed, wind duration, and water depth (Keddy 1982). Climatic data show two principal wind directions in this area of Ontario: from the northwest, and from the south. The study area (Fig. 1) has a range of wave energy regimes as a result. The maximum amount of exposure in the study area would be expected at the extreme north end of the lake where the shoreline faces due south and is exposed to south winds with a fetch of at least 1 km. The minimum amount of exposure in the study area would be expected at the northwest end of the lake where the shoreline is protected from both the northwest and south winds. Calculations using wind data from different time periods, and different measures of wind speed, wind duration, and fetch confirmed that such an exposure gradient exists (Keddy 1982). As well as using calculated exposure values, substrate samples were collected in each transect where vegetation was examined. The calculated exposure gradient was strongly positively correlated with a sand-sorting coefficient, and strongly negatively correlated with the proportion of silt and clay in the substrate (Keddy 1982). The rank order of transects along the shore from east to west therefore represents a gradient from lower to higher exposure to wave energy. This rank order of transects is used as the independent variable in figures relating vegetation to exposure, and therefore nonparametric statistical methods are appropriate. The Kendall rank correlation coefficient, τ, (Siegel 1956) is used throughout to test for monotonic trends in vegetation with exposure. To test for a bitonic relationship with exposure, the extension of τ proposed by Ferguson (1965) is used.

METHODS

Sampling procedures

A 600-m section of the perimeter of the northeastern end of the lake was marked; this length of shoreline encompassed most of the range of variation seen in the lake as a whole, from open sand beach to organic shoreline. Random numbers (between 1 and 600) were then chosen until 25 transects were located. These random numbers were accepted subject to the criterion that no pair of transects was to be separated by <10 m, to ensure that the transects would be relatively independent of one another. The transects were then located and sampled in the order in which the random numbers had been drawn. This ensured that variation resulting from changes in observer expertise, working conditions, or plant maturity would be randomly assigned along the shoreline.

Each transect contained a belt of vegetation 0.5 m wide. The exact location of the transect was determined by the random number assigned to it, except that transects were in several cases moved laterally up to 2 m to avoid (1) major departures from a monotonic slope (such as deep channels), or (2) obstacles such as large logs. The belt transects were then surveyed into 5 cm height increments using a Sokkisha B4 automatic level (Sokkisha, Limited, Tokyo, Japan). The waterline was used as the reference point, and for each transect 20 such increments were marked out—from 0.5 m above to 0.5 m below the waterline. Since the water level fell during the study period, everything was surveyed relative to 0 m on the day sampling was commenced; daily corrections were made for falling water levels. The gently sloping nature of the sand shores (illustrated in Keddy 1981) meant that these transects were usually ≈40 m long, with extremes up to 130 m.

An observer then started at the top of the transect and recorded the presence of each species in each height increment (initially 45–50 cm above the waterline along the 50 cm wide strip). For sample units deeper than ≈−20 cm, a snorkel and mask were necessary. The final data for each transect then consisted of lists of species occurrences in 20 height increments (quadrats).

The vegetation was sampled in this manner during the period 13–21 July 1979. This was slightly early for best identification; however, many species had been collected the previous year and were already identified. For most taxa encountered a voucher specimen was pressed and used as a reference for the remainder of the transects. These vouchers are on file in the author's herbarium, and duplicates, where available, are deposited in the University of Toronto Herbarium, Toronto, and the National Herbarium, Ottawa, Ontario, Canada. All problematic taxa (*Potamogeton* and *Carex* in particular) were confirmed or annoted by Dr. A. A. Reznicek (University of Michigan) or Dr. P. W. Ball (Erindale College, University of Toronto). Species names follow Fernald (1950) except for the use of *Triadenum fraseri* for *Hypericum virginicum*.

Seedlings of *Acer rubrum,* which germinated in abundance on shores exposed by receding water, were excluded from the data set since they were an ephemeral component of the vegetation. Three species of *Utricularia* (*U. gibba, U. purpurea,* and *U. vulgaris*) were also excluded because they occurred primarily as floating fragments rather than rooted plants, and thus were probably little affected by relative height (or water depth).

Frequently aquatic species such as *Nymphoides cordata* occurred well above the July waterline on open sand beach. To test whether these were ephemeral occupants of this habitat, marked quadrats were established. The object was to test whether these species would die during August from being stranded, and therefore to determine whether zonation patterns changed significantly with the seasons. A row of 10 contiguous 1 × 1 m quadrats was established at each of three heights (28, 22, and 20 cm) above the July water line. These quadrats represented open sand beach. A metre-square quadrat subdivided by strings into 25 20 × 20 cm subquadrats was placed over each quadrat in turn. The presence or absence of *Eriocaulon septangulare, Lobelia dortmanna,* and *Nymphoides cordata* was recorded for each subquadrat, yielding frequency estimates ($n = 750$). This was carried out on 18 July and 22 September 1979 on the same quadrats.

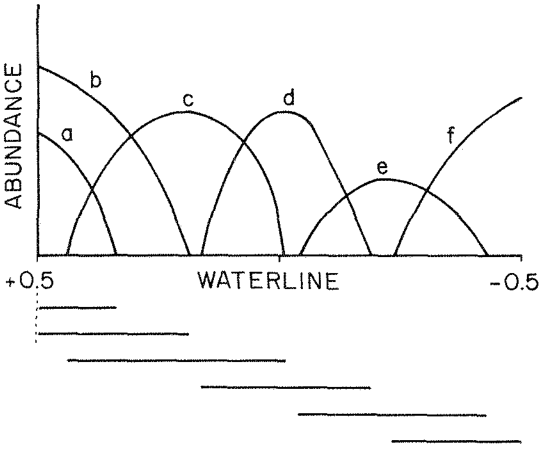

FIG. 2. Hypothetical depth distribution of six species in a lakeshore transect, showing complete species (c, d, e) and incomplete species (a, b, f). The former can be considered true shoreline species, while the latter can be divided into terrestrial species (a, b) and aquatic species (f).

Data analysis

Niche width.—Fig. 2 shows a hypothetical depth distribution for six species in a lakeshore transect. The lower part of the figure shows the presence/absence data, which could easily be recorded as a matrix of zeros and ones. Note that there are two groups of species. One group (to be designated as "shoreline" species) are completely known in terms of their upper and lower limits—Fig. 2c, d, e. The other group is only partly known. Either their landward limits are unknown (for terrestrial species, Fig. 2a, b) or their waterward limits are unknown (for aquatic species, Fig. 2f). First, consider measures of niche width based only on true "shoreline" species. All species that occur in either of the end quadrats on the transect are excluded from the data set. (Note: for the sake of clarity, the term "shoreline species" will be used to refer specifically to this group of species which narrowly span the waterline; the term "lakeshore species" will be used to refer to all species growing in the lakeshore transects.)

Niche width can be defined as the range of relative heights occupied. For any species C, the range occupied would be $C_{max} - C_{min}$. If this species happens by chance to be absent from some intermediate depths, the measure is unaffected. Let W_c represent the range occupied by species C. Then, mean range for a particular transect with s species is simply

$$\left(\sum_{i=1}^{s} W_i\right)/s$$

Return now to the original data set (Fig. 2), and the problem of incompletely known aquatic and terrestrial species. The obvious advantage to considering complete (shoreline) species alone is that both their upper and lower limits are known for each transect. The main disadvantage to excluding aquatic and terrestrial species is that large amounts of data are lost, and these data are related to specific ecological groups. In Fig. 2, data from terrestrial species (a, b) and aquatic species (f) would be lost. This might obscure real ecological trends. For example, as the number of shoreline species in a transect increases, the terrestrial plants may be excluded landward, and the aquatic plants excluded to the deeper areas. We would fail to detect this by excluding these species from the analysis.

Since it was unclear whether only shoreline species, or all species in a transect, ought to be considered, the tests for variation in niche width with exposure were carried out on both data sets. An additional problem in analyzing these transect data was the occasional difficulty in defining shoreline species. Aquatic species such as *Eriocaulon septangulare* or *Nymphoides cordata,* which regularly grew in water depths exceeding 1 m, occasionally were absent from the lowest depth interval examined in a transect. According to the above criteria (Fig. 2), they would then have been included as shoreline species in that transect. This was not only biologically wrong, but added variation among transects, as a wide-ranging species such as *E. septangulare* would be randomly included or excluded from the shoreline group based solely upon presence or absence in the lowest height increment in each transect. To avoid these problems, species which regularly occurred above or below the limits of the height intervals examined (species regularly occurring above ± 0.5 m or below −0.5 m) were categorized a priori as terrestrial or aquatic species. This ensured the analysis of shoreline species was based on a conservative list. On average, this reduced the number of shoreline species by two species in each transect. Species treated in this manner included shrubs which occurred near the upper fringe of the shoreline (*Myrica gale, Alnus rugosa, Nemopanthus mucronata, Spiraea alba, Viburnum cassinoides, Vaccinium macrocarpon, Ilex verticillata, Chamaedaphne calyculata, Pyrus floribunda, Vaccinium oxycoccos*) and aquatics that regularly extended deeper into the lake (*Eriocaulon septangulare, Nymphoides cordata, Myriophyllum tenellum, Brasenia schreberi, Nymphaea odorata*).

Boundary clustering.—One of the tests developed by Pielou (1977) provides a method for determining whether the upper (or lower) boundaries of individual species tend to occur nonrandomly. Pielou notes that there are three possible arrangements of the upper boundaries of a group of species growing along an environmental gradient. (1) The boundaries may be randomly arranged, that is, the upper boundary of each species occurs independently of the others. (2) The boundaries may be clustered, that is, large numbers of species reach similar limits at certain points on the gradient, and other areas of the gradient have fewer species boundaries than expected. This would correspond to having discrete communities along the gradient. (3) The boundaries may be regularly spread out like shingles on a roof. Pielou and Routledge (1976) applied the method to investigate salt marsh zonation patterns. Underwood (1978*b*) criticized the statistical assumptions in the method and proposed an alternative approach. Pielou (1979) demonstrated that there are several methods to approaching the problem of boundary clustering, and that neither of the previously published methods was incorrect. Given that the data from Axe Lake were collected in discrete height increments, rather than randomly placed quadrats, Underwood's method was used to test for pattern in upper and lower boundaries. (Note, however, if using Underwood's (1978*a*) technique, that the formula for standard error at the top of page 325 is actually the formula for standard deviation.)

RESULTS

Species composition

There was a wide range of responses of lakeshore species to exposure. Fig. 3 shows the distributions of six selected lakeshore species. The range of heights occupied represents the realized niche width of each species at each level of exposure. Some species, such as *Lobelia dortmanna* and *Utricularia cornuta,* showed an increasing range with increasing exposure. Species such as *Pontederia cordata* occurred only on sheltered shores, while others such as *Triadenum fraseri* peaked on sheltered shores and showed a decreasing range with increasing exposure. Other species, represented here by *Drosera intermedia* and *Cladium mariscoides,* reached a maximum range at intermediate exposure levels.

Note as well the changes in position along the gradient which accompany these changes in range. The increased range of *Lobelia dortmanna* appears to result from survival in higher relative heights with high exposure. It occurs above the waterline only on exposed sites. Similarly, *Drosera intermedia* appears to survive in higher relative heights at intermediate exposures, whereas its lower limit stays relatively constant at the July waterline. Conversely, *Triadenum fraseri* has fairly constant upper limits, and increasing range in the sheltered transects results from the species extending closer to the waterline. *Cladium mariscoides* also extends lower on the gradient in the sheltered transects.

Fig. 3 shows that there were marked changes in the ranges of selected species as exposure increased. Many other species also had distributions which changed along this gradient (Keddy 1981). Of the shoreline Cyperaceae, *Scirpus subterminalis, Rhynchospora fus-*

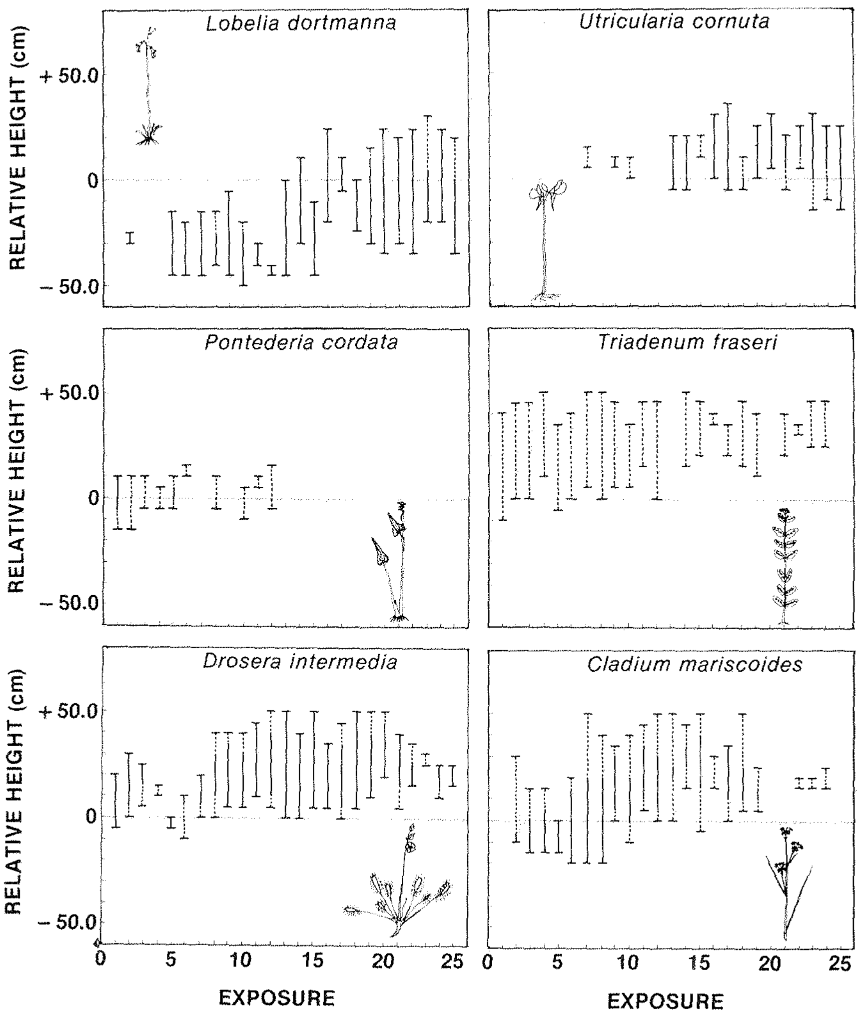

FIG. 3. The distributions of six selected lakeshore species with respect to relative height and exposure. Solid lines indicate flowering individuals present during the period of data collection. In the ordinate scale, 0 denotes the waterline location in July 1979, when sampling began.

ca, *Cladium mariscoides*, and *Scirpus torreyi* occurred on the more exposed shores, while *Eleocharis palustris*, *Carex rostrata*, and *Dulichium arundinaceum* were restricted to the more sheltered shores. *Eriocaulon septangulare*, *Myriophyllum tenellum*, and *Lobelia dortmanna* (illustrated in Fig. 3) extended well above the waterline only in high-exposure areas. Species such as *Brasenia schreberi*, *Nymphaea odorata* and *Potamogeton oakesianus* were restricted to the sheltered shores.

I suspected that some aspects of these patterns might change with the seasons. For example, the above-water occurrence of *Lobelia dortmanna*, *Nymphoides cordata*, and *Eriocaulon septangulare* could reflect plants that washed ashore in spring but died from desiccation as the summer progressed. Table 1 shows, however, that the frequency of these species remained virtually constant from 18 July to 22 September 1979.

The general morphology of species also changed with exposure. Many of the shoreline species on the sheltered shores were large, leafy, erect perennials (e.g., *Calamagrostis canadensis*, *Carex rostrata*, *Cladium mariscoides*, *Dulichium arundinaceum*, *Glyceria can-*

TABLE 1. The frequency of three "aquatic" species occurring above the waterline on exposed shorelines. Values are frequency of occurrence in 750 20 × 20 cm quadrats in July (when zonation data were collected) and the following September. All quadrats represented relative heights >20 cm above the July waterline.

	Species		
Date	*L. dortmanna*	*N. cordata*	*E. septangulare*
18 July	0.047	0.247	0.594
22 September	0.041	0.264	0.616

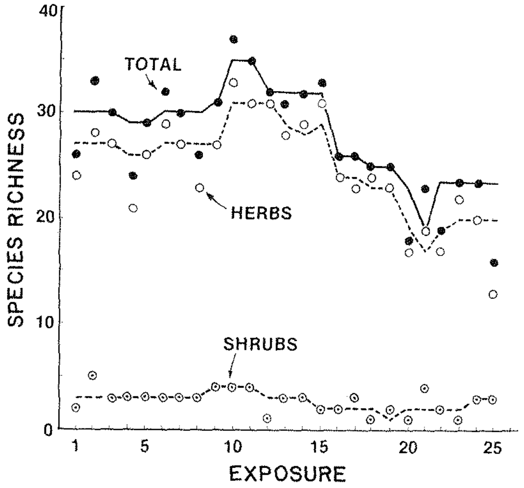

FIG. 4. Species richness plotted against exposure. There is a significant bitonic (quadratic) relationship (τ = .375, $P <$ .01) between total richness and exposure. Lines are three-point running medians with end-point smoothing (Tukey 1977).

adensis). On exposed shores they were replaced by small rosette or creeping species (e.g., *Drosera intermedia, Eriocaulon septangulare, Lobelia dortmanna, Utricularia cornuta, U. resupinata,* and *Myriophyllum tenellum.* The annual *Eleocharis olivacea* also occurred on the exposed shoreline. Aquatic species with large floating leaves such as *Brasenia schreberi* and *Nymphaea odorata* disappeared from shallow water on the exposed shore. Another qualitative observation was that total cover decreased with exposure, leaving large areas of substrate unvegetated on the exposed shores.

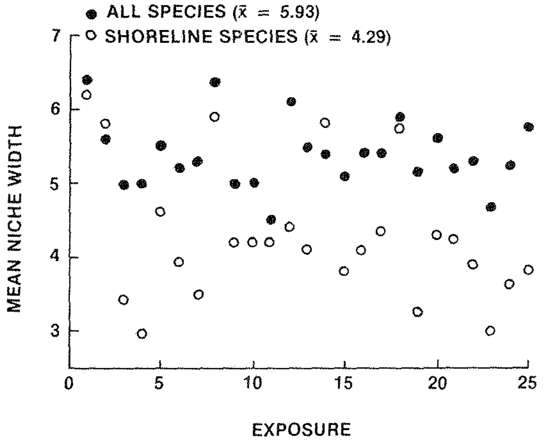

FIG. 5. Mean realized niche width (mean range) plotted against exposure for all species in a transect (lakeshore species) and for shoreline species only.

Species richness

There was a significant bitonic, or quadratic, relationship between species richness and exposure (τ = .375, $P <$ .01). Species richness therefore peaked at an intermediate level of exposure. Fig. 4 shows that most of this variation was the result of changes in the number of herbaceous species.

Niche width

Fig. 3 showed that individual species exhibited marked changes in ranges with exposure. Now consider the results when all species in a transect are considered collectively. Fig. 5 shows that there was no relationship between mean range (mean niche width) and exposure for either shoreline species alone (τ =

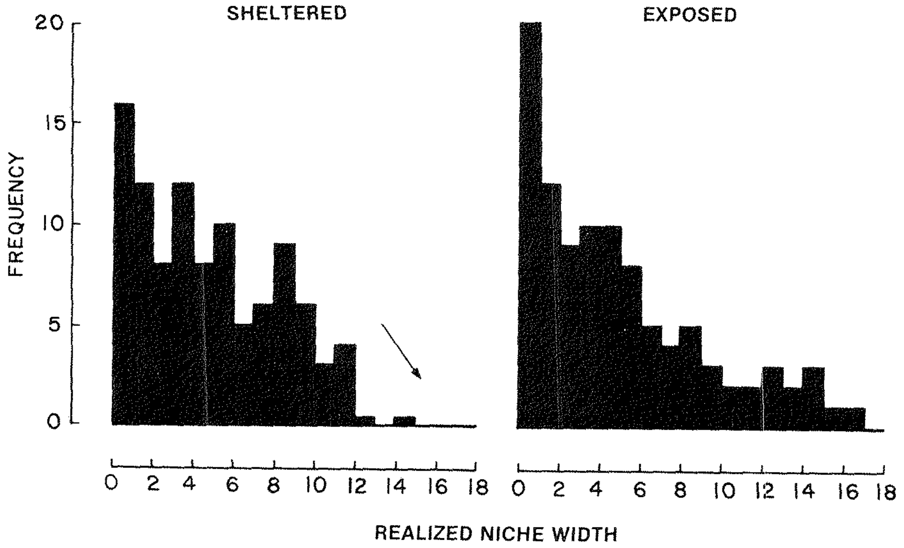

FIG. 6. The distribution of realized niche widths (ranges) for all species in the 10 most sheltered transects (left) and the 10 most exposed transects (right).

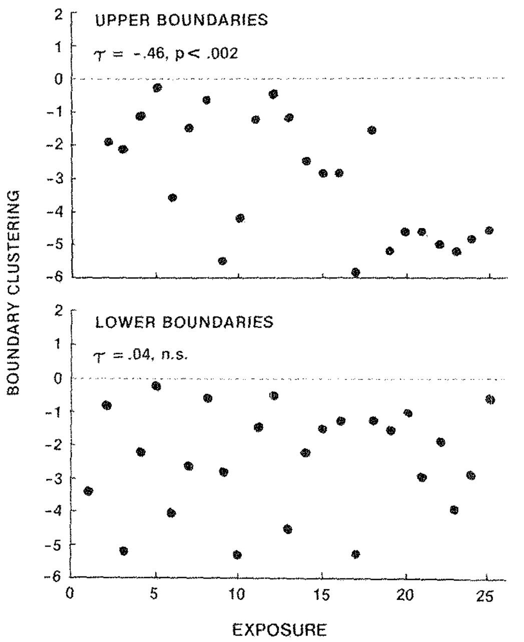

Fig. 7. Boundary clustering plotted against exposure for upper (landward) and lower (waterward) boundaries of lakeshore plants. Note that the more negative the value, the stronger is the degree of clustering.

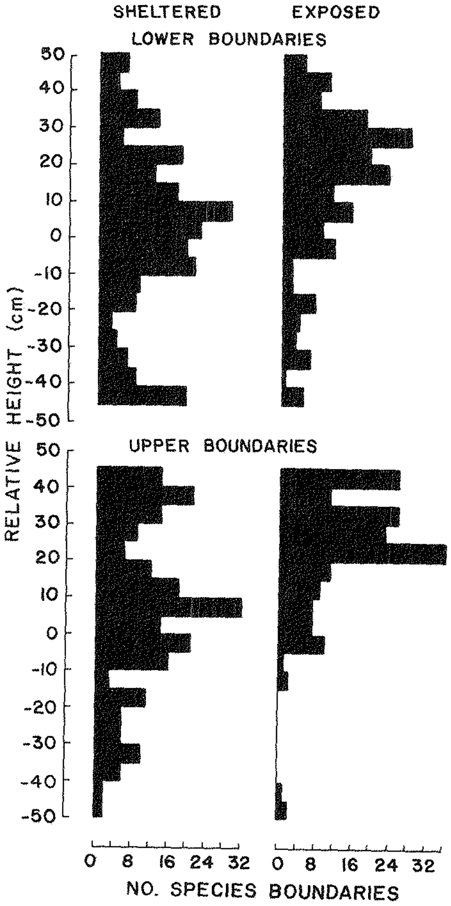

Fig. 8. The distribution of species' boundaries along a lakeshore gradient from 50 cm above to 50 cm below the July waterline in the 10 most sheltered transects (left) and 10 most exposed transects (right).

−.19, NS) or all species on the shoreline ($\tau = -.01$, NS). Fig. 6 shows, however, that while mean range was unrelated to exposure, there were differences in the relative abundances of ranges ($\chi^2 = 35.9$, df = 12, $P < .001$). On the exposed shores there were proportionately more generalist species, that is, more with comparatively broad ranges. On the sheltered shore, in contrast, a more equitable distribution occurred. Thus, while the mean range for the lakeshore assemblage did not change with exposure, one subgroup of species did apparently increase in range (arrow, Fig. 6). This subgroup consists largely of aquatics such as *Eriocaulon septangulare* and *Nymphoides cordata* extending landward.

Boundary clustering

There are three possible arrangements of the lower (or upper) boundaries of a group of species growing on an environmental gradient (Pielou 1977); they may be regularly arranged, randomly arranged, or clustered. If discrete groups (or communities of species) occur on a gradient, one would expect to find clustered lower (or upper) boundaries.

I asked two questions: (1) how are the lower or upper boundaries clustered, and (2) does this arrangement change with exposure? The null hypotheses were, respectively, (1) random arrangement of boundaries, and (2) no change with exposure. Consider the first question. The lower boundaries of species were significantly clustered ($t = 7.52$, $P < .001$) as were upper boundaries ($t = 7.12$, $P < .001$). Thus, certain relative heights had more rapid species turnover than others. Now consider the second question. Fig. 7 shows the relationship between degree of clustering and exposure; the horizontal dashed line at zero corresponds to a random arrangement of boundaries. This figure shows that there was no relationship between lower boundary clustering and exposure ($\tau = .04$). The clustering of upper boundaries, however, increased significantly with exposure ($\tau = -.46$, $P < .002$).

To simplify interpretation of the above results, Fig. 8 shows the number of species boundaries occurring in each height increment for the 10 most exposed and 10 most sheltered transects. Consider lower boundaries first. Although there was no correlation between degree of clustering and exposure, the level at which most species reach their lower limit shifts upward with increasing exposure, from near the water line on the sheltered shore to ≈25 cm above the water line on the exposed shore. (Recall the individual species responses illustrated earlier in Fig. 3 where *Triadenum*

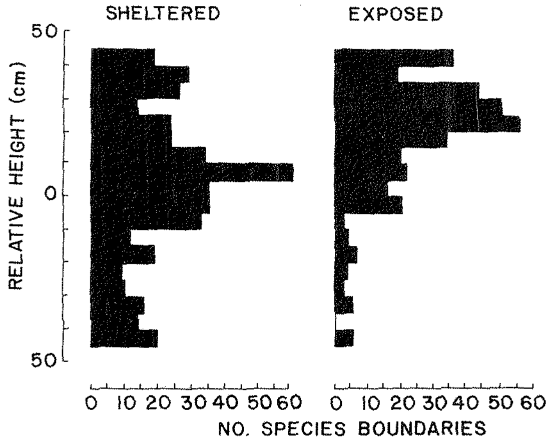

FIG. 9. The total distribution of species boundaries (upper and lower combined) along a lakeshore gradient, comparing the 10 most sheltered transects (left) to the 10 most exposed transects (right).

fraseri and *Cladium mariscoides* both extended lower on the gradient in sheltered areas.)

Now consider upper boundaries. Fig. 8 illustrates the increase in clustering with exposure; it also shows that the level at which most species reach their upper limit shifts from near the waterline on sheltered shores to ≈25 cm above the waterline on exposed shores. (Recall that *Lobelia dortmanna* [Fig. 3] was a species which showed such a shift in its upper limit from sheltered to exposed sites.)

Combining both upper and lower boundaries in one plot illustrates those points along the gradient at which species composition changes most rapidly. Fig. 9 shows that on sheltered shores species composition changes rapidly at the waterline. On exposed shores, however, species composition changes most rapidly at 25 cm above the waterline. In both cases, the rate of change of species composition with height is least rapid below the waterline.

DISCUSSION

Species composition

While it is a standard field observation that species composition is different on shorelines with different exposure, some interesting observations emerge from taking a more quantitative approach. It might initially be expected that a particular species' depth range would be fairly constant around a lake. Yet many species examined showed differences in depth distribution with exposure; species reached their maximum range of depths at different points along the exposure gradient. Species such as *Lobelia dortmanna* and *Utricularia cornuta* had widest depth ranges at high exposures; species such as *Cladium mariscoides* and *Drosera intermedia* peaked at intermediate levels of exposure, and species such as *Triadenum fraseri* and *Pontederia cordata* peaked at low exposure. Given the large number of ecological factors included in the term exposure (e.g., wave damage, ice scour, sediment transport, organic matter accumulation) I will not speculate which factor or combination of factors is producing these distributions, with one exception.

One of the most conspicuous (and consistent) effects of exposure was its effect on the distribution on species such as *Lobelia dortmanna* (Fig. 3), *Utricularia cornuta* (Fig. 3), *Eriocaulon septangulare* and *Nymphoides cordata*. These species occurred mainly below the waterline in sheltered areas, but increased their range of heights occupied by growing well above the waterline in exposed areas. This was particularly striking with *Nymphoides cordata*, an aquatic which often formed extensive colonies in water more than a metre deep. A first hypothesis was that *Eriocaulon septangulare*, *Lobelia dortmanna*, and *Nymphoides cordata* rosettes were merely transients washed ashore each spring to die as the water level receded. Quantitative data on rosette frequency in Table 1 showed, however, that their September abundance was similar to that in mid-July. An alternate hypothesis which might be suggested is that waves on the exposed shore keep these plants moist, whereas they die of desiccation in the sheltered bay. Waves >10 cm high are infrequent during the growing season, however, and given the gentle slope of the shoreline, plants growing 25 cm above the waterline may be horizontally 5 m distant from it. A third hypothesis is that these plants are intolerant of competition, and cannot grow in sheltered areas where the shoreline is dominated by the species of Cyperaceae, particularly *C. mariscoides* and *C. rostrata*. The growth form of these species is consistent with this hypothesis: *Utricularia cornuta* has tiny leaves which grow from creeping horizontal stems; the other three species all have rosettes. Thus they would be at a strong disadvantage compared with taller species. On more sheltered shores, if found at all, they occur only in small clearings in an otherwise solid mat of Cyperaceae. This change in the distribution of these species, therefore, may well reflect changes in competitive interactions with exposure.

Species richness

There are reasons for expecting species richness to peak at intermediate levels of environmental disturbance (Connell 1978, Huston 1979, Sousa 1979) rather than in the least disturbed areas (Sanders 1968). In Axe Lake, species richness peaked at an intermediate level of exposure ($\tau = .38$, $P < .01$), with sheltered shores having approximately nine-tenths as many species as intermediate shores, and exposed shores having approximately half as many species as intermediate shores. Transect data may not be the best choice for testing the intermediate disturbance hypothesis, since the gradient of water depth interacted with exposure. Fig. 10 shows species richness plotted

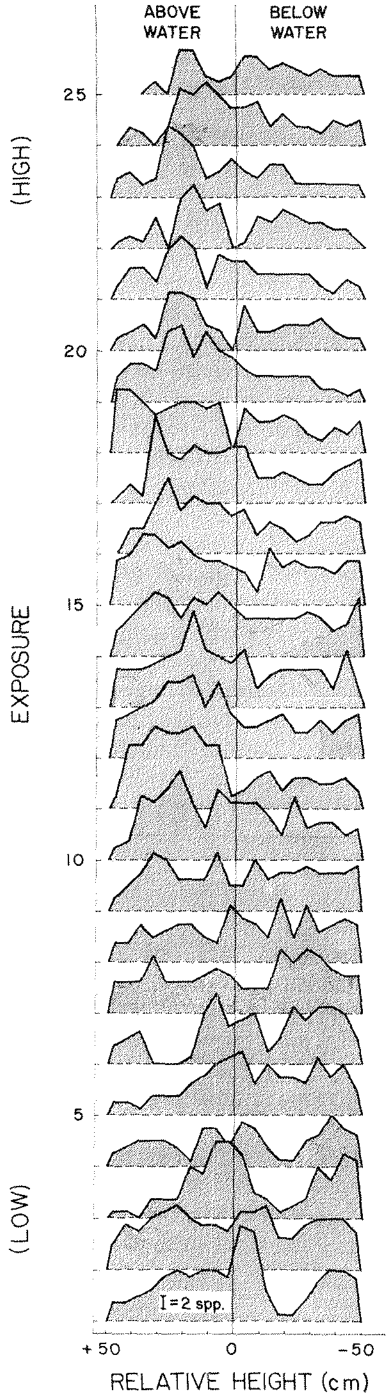

FIG. 10. Species richness plotted against relative height, for all 25 transects with their various exposure levels.

against relative height for all 25 transects. (Note that this is the only figure in which relative height is on the horizontal axis.) There is a suggestion, for example, that species richness peaked above the waterline at intermediate exposures but near or below the waterline at low exposure. Terrestrial, shoreline, and aquatic species may be regulated independently, and combining all three may confound changes in species richness with exposure.

Niche width

Figs. 3 and 4 illustrated the changes in species composition and richness with exposure. Fig. 5 showed, however, that there was no relationship between mean range and exposure. That is, the mean niche width of species, or the mean range of heights utilized along the depth gradient, remained constant. Thus increased specialization along this gradient does not occur in spite of almost twice as many species co-occurring in sheltered areas. It also contradicts Sanders' (1968) prediction that species of biologically accommodated communities should be more specialized than species of physically controlled communities. One interpretation of this would be that competition did not affect the zonation of these lakeshore plants, since twice as many species occur on the sheltered shores without any reduction in the mean range of resources utilized. Unfortunately there are several complicating factors. Since this study examined only one axis of niche hyperspace, it could be that increased richness was accommodated by increased specialization along other axes such as light or nutrients. The axis of relative height, however, not only incorporated moisture, but also other correlated factors such as light and nutrient availability and substrate particle sizes. It is also possible that the methods were not sufficiently discriminating to detect the occurrence of changes. Mean range may have been underestimated on exposed shores. Since some species tended to be rare, their ranges were often measured by a few sporadic occurrences, none of which would necessarily represent the extreme of the range of conditions that those species could occupy. Using only the mean value for each transect may also have been misleading. For example, Fig. 6 showed that on the exposed shore, there were more extreme generalists than on the sheltered shore, although the mean range of the species on each shoreline type was the same. To choose real examples, recall *Eriocaulon septangulare* or *Lobelia dortmanna,* two of the species which extended their ranges greatly on exposed shores, at the same time that species such as *Cladium mariscoides* and *Nymphaea odorata* exhibited greatly reduced ranges. One possible interpretation of this is that as ecological dominants are gradually eliminated from exposed shores, other "exposure tolerant" species expand to fill the space available (as discussed earlier). The arrows on Fig. 6 illustrate this process. Thus, on Axe Lake, I propose that while competition may affect the depth distribution of particular species, as one species disappears because of exposure-related effects, it is replaced by another, leaving the mean range of the assemblage unaffected. If a greater range of exposures were examined, increases in mean niche width might be observed at high exposures.

Boundary clustering

The distribution of species along environmental gradients has been of considerable interest to ecologists. Whittaker (1967) concluded that composition of communities changes continuously along environmental gradients. Terborgh (1971) proposed three different models to explain distributions along an environmental gradient. In Model I, the distributional limits of species on a gradient are determined by factors in the physical or biological environment that vary continuously and in parallel with the gradient. In Model II, the distributional limits are determined by competitive exclusion. In Model III, distributional limits are determined by habitat discontinuities (ecotones). Terborgh used species abundance data for birds along an altitudinal gradient in Peru to examine these models. He concluded that gradually changing conditions account for approximately one-half of the limits, competitive exclusion about one-third, and ecotones <20%. (He also warned against the use of temperate localities, as well as the use of plants in such studies!)

Boundary clustering techniques, on the other hand, test whether for a distribution pattern as a whole, species are arranged regularly, at random, or in clusters along a gradient. These alternatives are not directly comparable to Terborgh's three models. If species are arranged independently along a gradient (the individualistic concept of Gleason [1926]), then we might expect species boundaries to be randomly arranged along it. Whittaker (1967) argues, however, that competitive interactions should cause species to evolve toward dispersion of their distributional centers, which might, in turn, produce a regular arrangement of species along a gradient. Neither of these alternatives was found. In Axe Lake both the upper and lower boundaries of lakeshore plants are significantly clustered, indicating that discrete associations of shoreline plants occur along the relative height gradient. In contrast, Pielou and Routledge (1976) found that in salt marshes the lower boundaries of vascular plants were regularly spaced, although the upper ones were more clustered. Underwood (1978*a*) found no clustering of species boundaries among organisms in the rocky intertidal zone. Pielou and Routledge (1976) also found that lower boundaries are more clustered than upper boundaries. While this may be true for the most sheltered shores of Axe Lake (Fig. 7, extreme left), exactly the opposite is found on the exposed shores.

These results of boundary clustering analyses must be interpreted with caution. Interpretation may be aided by considering the way in which clustering changes with exposure. Consider the summary below extracted from Figs. 7–9.

1) In sheltered areas, upper boundaries are more randomly distributed (less clustered) than in exposed areas.
2) As exposure increases, upper boundaries become more clustered than lower boundaries.
3) Among-transect variation appears to decrease with increasing exposure.
4) Upper and lower boundaries tend to cluster at the same depth for a given level of exposure.
5) Upper and lower boundaries both shift upward with increasing exposure.
6) Although there is a suggestion of several peaks in boundary occurrences in the sheltered areas, increased exposure results in only a single large peak.
7) Lower boundary clustering is unaffected by exposure.

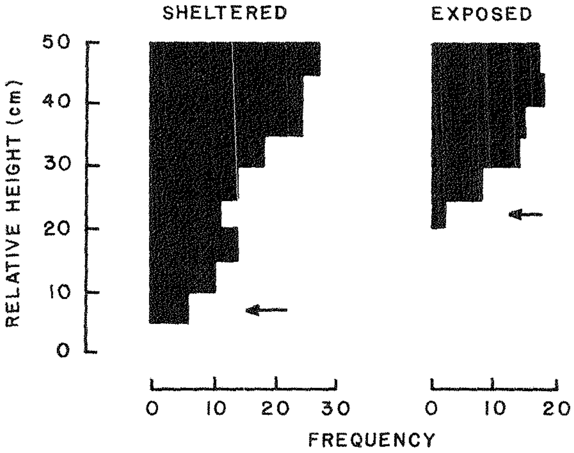

FIG. 11. The total frequency of shrub species occurrence in 10 combined transects, plotted against relative height, comparing the 10 most sheltered transects (left) to the 10 most exposed transects (right). The arrows mark the location of the maximum number of species boundaries (height of most rapid species turnover) as taken from Fig. 9.

As exposure increases, the clustering becomes more pronounced and both upper and lower boundaries shift upward from +10 to +25 cm (observations 1, 2 and 3). This is the approximate lower limit of shrubs, principally *Myrica gale*. Thus, the following hypothesis is suggested: the point of most rapid change in species composition on a shoreline is determined by the lower limit of the shoreline shrubs, and their abundance (and lower limit) is pushed upward with exposure.

To examine this hypothesis, data on shrub distributions are needed for both sheltered and exposed shores. Since cover data were not taken, shrub abundance at each relative height was estimated by summing all species occurrences over all 10 transects for either the 10 most exposed or the 10 most sheltered transects. This simple measure of abundance incorporates both the number of species which occurred, and their frequency over 10 transects.

Fig. 11 shows the lower limit and frequency of shrubs in the exposed and sheltered transects, and it is consistent with this hypothesis. Moreover, it was a general field observation that the lower shrub boundary was more abrupt on the exposed shore than in the sheltered bay.

Observations 4 and 5 also correspond with this hypothesis. Upper and lower boundaries tend to co-occur because the upper limit of many shoreline species (and aquatics) is determined by the depth to which terrestrial species (particularly shrubs) can grow. As exposure forces the terrestrial species (particularly shrubs) up the gradient, the shoreline and aquatic species move up into the available habitat. Thus the terrestrial-aquatic interface (from a botanical perspective) changes with exposure.

We might then interpret observation 6 to mean that in the absence of repeated environmental disturbance, biotic interactions produce several discontinuities in the distributions of species along the gradient. Each cluster of boundaries might represent the end or beginning of a competitive dominant. With increasing physical disturbance, however, these biotic interactions are overwhelmed by exposure effects which leave only one competitive dominant, the shrubs. Since the lower boundaries of most species are unaffected by the shrubs, it follows that (observation 7) lower boundaries are less sensitive to changes in exposure.

Thus, Terborgh's models must be applied to plant communities with caution. The role of dominance in plant communities may make it difficult to separate the effects of ecotones from those of competition. A physical factor, may, for example, affect only one or two dominants (e.g., *Myrica gale*), and then those dominants may competitively induce all other species to respond at the same point on the gradient. Thus the physical factor may have both direct and indirect effects upon species distributions. This could easily be tested by removing the proposed dominant and observing how the distributions of the remaining species adjust.

Other studies on zonation patterns have suggested that generalizations can be drawn regarding factors affecting species' boundaries. Connell (1961) proposed that for intertidal species, the landward limit was determined by physical factors (desiccation), and the seaward limit was determined by competition. Recent experimental work has confirmed that the lower limits of intertidal organisms are usually determined by biological interactions (Connell 1972, Lubchenco 1980), although Rabinowitz (1978) has shown that mangrove zonation is apparently determined by tidal sorting based on propagule sizes. Pielou and Routledge (1976) hypothesized that for vascular plants in salt marshes the landward limit was determined by competition, and the seaward limit was determined by physical factors such as salinity. Such generalizations are not easily applied to lakeshores, where aquatic, shoreline, and terrestrial species all interact.

TABLE 2. Kendall rank correlation coefficients relating characteristics of zonation patterns to both exposure and species richness. The last column gives partial rank correlation coefficients relating richness to zonation patterns with effects of exposure removed.

	Independent variable		
Zonation characteristic	Exposure	Richness	Richness · Exposure*
	Kendall's τ		
Boundary clustering			
Lower	.04	−.04	−.03
Upper	−.46***	.23	.05
Mean niche width			
Shoreline species	−.19	.14	.08
All species	−.01	−.18	−.21

* No significance values are given since the distribution of Kendall's partial rank correlation is unknown.

*** $P < .001$.

Species richness and zonation patterns

The bitonic relationships between species richness and exposure has already been noted. There was, however, an independent (orthogonal) monotonic negative correlation between richness and exposure ($\tau = -.42$, $P < .01$). Exposed shores have fewer species than either intermediate or low exposures (Fig. 4). Thus the observed changes in zonation patterns with respect to exposure may reflect the monotonic component of changes in species richness. Kendall partial rank correlation coefficients (Siegel 1956) may assist in determining whether richness has any effect on zonation patterns once exposure is held constant. Upper boundary clustering appears marginally related to richness ($\tau = .23$, $P = .11$), until the effect of exposure is partialed out (Table 2). Thus, the variation in boundary clustering is clearly an exposure effect. Mean niche width is not significantly correlated with either exposure or richness, although removing the effects of exposure marginally increases the correlation of niche width with richness.

CONCLUSION

Exposure has a marked effect on lakeshore vegetation in Axe Lake. Species composition changed dramatically. Large leafy species on sheltered shores tended to be replaced by small creeping or rosette species on exposed shores. In spite of these marked changes, mean niche width was unaffected by exposure. Exposed shores did, however, have more generalists, aquatic species which extended well above the waterline. I hypothesize that this reflects decreased competition from large leafy plants above the waterline on the exposed shorelines. Species richness was significantly correlated with exposure, with a peak at intermediate exposure levels.

Boundary clustering data showed that at least two discrete groups of species occur on the shoreline, separated by a narrow discontinuity. The discreteness of the species zones (clustering of upper boundaries) increased with exposure. The position of the discontinuity shifted upward with increasing exposure. Thus, while exposure did not change the mean niche widths of shoreline species, it did change their arrangement along the water depth gradient. These changes may directly reflect changes in the physical attributes of the shoreline, such as ice damage, nutrient status, organic content, or aeration. They may also indirectly reflect these physical factors acting on a few competitive dominants, which in turn affect the remaining shoreline flora. Since the discontinuity corresponds to the lower limit of shrubs on the shoreline, it may be that physical factors which control the lower limit of shrubs (perhaps ice damage or wave action) indirectly control the rest of the shoreline assemblage.

Thus, both water depth and wave energy affect the within-lake distribution of lakeshore plants, thereby determining the species composition of shoreline vegetation. Many other strongly correlated physical factors would be expected to vary along these two gradients. Field measurements of these physical factors, and experimental manipulation, will be necessary to provide convincing explanations for many of the phenomena observed.

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