THE STRUCTURAL DYNAMICS
OF A
TIDAL FLAT MOLLUSC COMMUNITY

by

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CHAPTER 6

PLANAR INTERACTIONS AMONG SPECIES

6.1 Introduction

A common approach to the study of the spatial distribution of animals is to attempt to fit theoretical models to the dispersion data. Taylor (1984) considers spatial distribution to be one of the most characteristic ecological properties of species, with each species having its own distribution pattern determined by interactions with its environment. The fundamental patterns may be further modified by intra- and interspecific interactions. Characterising a species by the parameters of a model has the advantage of allowing comparisons between species and hence the detection of general patterns common to all species.

This approach has lead to a wealth of models and indices from which to choose (Taylor 1984). Very few of these indices, however, actually examine relationships within the species. Instead, they treat the species as a unit, with the constituent individuals being subservient to that unit. Methods to examine interactions between individuals have been developed only comparatively recently (Sokal and Oden 1978 a, b). While these methods do not generate indices with which to characterise a species, they do allow a biologically more meaningful interpretation of the dispersion pattern of a species. Such methods of analysis provide a corollary to the series analysis of Chapter 5.

The serial correlation analysis reported in the previous chapter examined relationships within and between species in one dimension only, along the transect. The distances between sampling quadrats in the distribution transects was 20 m, which can be considered to be infinity relative to the body sizes of the animals. The spatial relationships detected by that analysis are effectively relationships expressed at the level of the species, along the tidal gradient. In this chapter, the scale of analysis is greatly reduced (to an order of several centimetres, rather than 20 metres) while being extended to a second dimension. The correlations detected here, therefore, can be considered to be reflections of interactions between individuals, independent of the tidal gradient.

The relationships between each species of the assemblage and the selected physical parameters were examined in the Chapter 5. Although those physical parameters undoubtedly also act at smaller scales, correlations between the physical parameters and animals at the level of the individual are not considered. Such analysis would require a quite different sampling program.

The series analysis of Chapter 5 revealed consistent relationships between species groups and also between species. The planar correlations examined here provide a test of those relationships at a much smaller scale. Caging manipulation experiments, described in Chapter 7, in turn provide a test of the interpretations derived from the correlation analysis of Chapters 5 and 6.

6.2 Methods

6.2.1 Introduction to the analysis of dispersion patterns

Sampling methods are generally of two basic types: point sampling or quadrat sampling. Point sampling is appropriate when the organisms are readily identifiable and of sufficiently low numbers to make the positioning of each, within some coordinate system, possible (see Diggle 1979, Kooijman 1979 and Warren and Batcheler 1979). When the organisms are not easily identifiable in the natural population (e.g. interstitial fauna), or are found in high numbers, quadrat sampling is the most suitable method.

Quadrats usually take the form of a common geometrical shape (e.g. rectangle, circle) but may be of any form that is suited to the habitat being sampled. The sampling process can either be random or systematic (or a combination); random sampling can be extensive while systematic sampling is generally intensive. The detection of spatial interaction between individuals is obviously best facilitated by a systematic sampling program having a scale of the same order as the size of the individuals being sampled.

A variety of methods exist to investigate the variance of the spatial pattern of a population. Two main approaches can be identified: those based on identifying the underlying probability distributions and those concerned with estimating a (usually) single parameter that characterises the spatial pattern.

The most frequently used probability model is the negative binomial distribution (Waters 1959) and this may itself be the basis for more comprehensive population models (e.g. Nachman 1981). Models can also be developed to describe spatial competition bewteen species (Cormack 1979). The biological meaning of such distribution-based models, however, is questionable. The negative binomial distribution, for example, is known to arise in at least four different ways (Thompson 1955). Also, the models make more demands on the data than aggregation indices (Taylor 1984). Nevertheless, fitting theoretical models to spatial data can be useful in many studies (see Diggle 1979).

Many aggregation indices, such as Fisher's (eg. 1970) variance/mean ratio, David and Moore's (1954) index of clumping, Morista's (1959) index and Lloyd's (1967) mean crowding index ignore the spatial location of the quadrats and so make inefficient use of the sampling effort. Also, they are based on randomly distributed quadrats and are not appropriate in the case of a systematic sampling program. Taylor (1984) presents a thorough review of these methods.

Greig-Smith (1952, 1964) developed a method suited to data collected in the form of a grid of contiguous quadrats. This method has a number of serious drawbacks, however,

which are described by Pielou (1977). Goodall (1974) proposed a more flexible method for analysing grid data, based on randomly comparing pairs of quadrats from within the grid.

Still more powerful techniques treat the grid abundance data as stationary point processes in two dimensions. Thompson (1955) discussed precise statistical techniques for detecting departures of a point process from the Poisson, or completely random, point process but further analysis and interpretation using those approaches is difficult.

Bartlett (1963, 1964) applied the methods of spectral analysis to point process, both in one (Bartlett 1963) and two (Bartlett 1964) dimensions. Spectral analysis allows the examination of small-scale periodicities, aggregation and inhibitory effects.

Similar advantages are provided by the methods of spatial autocorrelation and spatial cross-correlation, and these methods are able to use smaller data sets than spectral analysis. Like spectral analysis, these methods are particularly attractive because the examination of spatial interactions between species (cross-correlation) is an extension of the within-species (autocorrelation) technique.

The analysis of spatial autocorrelation is a technique that makes use of the location of quadrats with respect to each other. The concept and treatment of spatial autocorrelation has been described by Cliff and Ord (1973) and its potential uses in ecological and biological studies outlined by Jumars *et al* (1977) and Sokal and Oden (1978 a, b). The techniques do not demand a systematic placing of quadrats but they do require knowledge of the relative positions of the quadrats. In many ecological studies, particularly those concerned with substrate habitats, the most convenient means of identifying the relative positions of the quadrats is to conduct the sampling in a systematic manner. In the present case, a set of contiguous quadrats in the form of a square grid was selected.

Cliff and Ord (1973) describe methods for calculating indices for the autocorrelation of a variable in a plane. The methods for detecting autocorrelation can be extended to allow cross-correlation to be detected (Kooijman 1979).

6.2.2 Autocorrelation in the plane (after Cliff and Ord 1973)

Let x_i = the value of variate X in cell i of the grid where cells are numbered row by row, i.e. the grid data is stored as a vector.

Two coefficients, I (the Moran coefficient) and C (the Geary coefficient) are used to assess the degree of spatial autocorrelation, which measures the correlation between the value of a variate in a given cell and the value of that variate in neighbouring cells.

The Moran coefficient is defined as

$$I = [n/(2A)][\sum_{i=1}^{n}\sum_{j=1, i\neq j}^{n}(\partial_{ij} z_i z_j)]/[\sum_{i=1}^{n} z_i^2]$$

where $z_i = x_i - x'$, $\partial_{ij} = 1$ if cells i and j are joined, $\partial_{ij} = 0$ otherwise. Here x' is the mean of $\{x_i\}$, i.e $x' = (\sum_{i=1}^{n} x_i)/n$, n = number of cells.

The Geary coefficient is defined as

$$C = [n-1][\sum_{i=1}^{n}\sum_{j=1, i\neq j}^{n}(\partial_{ij}(x_i - x_j)^2)]/[4A\sum_{i=1}^{n} z_i^2].$$

In both definitions, $A = (1/2)(\sum_{i=1}^{n} L_i)$ where L_i = the number of cells joined to the ith cell.

In both I and C, the numerator term is a measure of the covariance among the $\{x_i\}$ and the denominator term is a measure of the variance. Both I and C are asymptotically normal as n increases.

Of the two statistics, I is less affected by the distribution of the sample abundance data and is therefore preferred in the present study.

It is possible to choose a scheme that defines neighbouring cells as being other than physically conjoined cells. The neighbourhood linkages for the grid can be defined in a weighting matrix, usually maintaining a binary weighting, with weights equal to 1 for neighbour linkages and 0 otherwise.

I (and C) can then be generalised using a generalised weighting matrix, $\mathbf{W} = \{w_{ij}\}$, instead of the simple binary weights, $\{\partial_{ij}\}$. Then,

$$I = n[\sum_{i=1}^{n}\sum_{j=1, j\neq i}^{n}(w_{ij} z_i z_j)]/[\sum_{i=1}^{n}\sum_{j=1, j\neq i}^{n} w_{ij})(\sum_{i=1}^{n} z_i^2)].$$

<u>The weighting matrix</u>

Given a grid of n cells, the weighting matrix, $\mathbf{W}=\{w_{ij}\}$, will have dimensions $n \times n$. Each element w_{ij} of the weighting matrix describes the 'neighbourliness' of cells i and j of the sampling grid, where the cells of the sampling grid are labelled row by row. For ease of computation, $\mathbf{W}$ is usually a symmetric binary matrix where $w_{ij} = 0$ or 1. Three possible weighting schemes can be likened to chess moves:

<u>rook's case</u> - tests for correlation in the vertical and horizontal directions with $w_{ij} = 1$ if j is a vertical or horizontal neighbour of i or $w_{ij} = 0$ otherwise.

<u>bishop's case</u> - tests for correlation in the diagonal direction with $w_{ij} = 1$ if

j is a diagonal neighbour of i or $w_{ij} = 0$ otherwise.

queen's case - tests for correlation in all directions with $w_{ij} = 1$ if j is a vertical, horizontal or diagonal neighbour of i or $w_{ij} = 0$ otherwise. In this case the diagonal distances are slightly greater, in a Euclidean sense, than the vertical and horizontal distances; this can be accounted for by setting weights inversely proportional to the Euclidean distances, although this removes the simplifying nature of **W**.

In each case 'neighbours' may be defined at any spacings within the constraints of the sampling grid. This allows a correlogram to be constructed, showing the changes in I with increasing interneighbour distances.

Testing the significance of I

An approximate test of significance is provided by evaluating I as a standard normal deviate (Cliff and Ord 1973). Problems may arise with sparse weighting matrices (e.g. with large interneighbour distances **W** will contain few $w_{ij} \neq 0$) and more rigid tests are available (Sokal and Oden 1978 a). For the present purposes, however, the tests are used informally as a means of reducing the number of correlations to a manageable size; rather than presenting the correlation indices themselves, only their significance (10, 5 or 1%) is provided.

The standard normal deviate can be calculated under one of two assumptions:

1) Assumption N: {xij} are the results of n independent drawings from a normal population, giving

$$E_N(I) = -(n-1)^{-1}$$

and $$E_N(I^2) = [n^2 S_1 - nS_2 + 3W^2]/[W^2(n^2-1)]$$

where $$S_1 = [\sum_{i=1}^{n}\sum_{j=1, j\neq i}^{n}(w_{ij} + w_{ji})^2]/2 ,$$

$$S_2 = \sum_{i=1}^{n}(\sum_{j=1}^{n} w_{ij} + \sum_{j=1}^{n} w_{ji})^2$$

and $$W = \sum_{i=1}^{n}\sum_{j=1, j\neq i}^{n} w_{ij} .$$

and 2) Assumption R: regardless of the underlying distribution, consider the observed value of I relative to the set of all possible values I could take if the $\{x_{ij}\}$ were repeatedly randomly permuted around the cell system (there are $n!$ such values). Then $E_R(I) = -(n-1)^{-1}$ and

$$E_R(I^2) = \frac{n[(n^2-3n+3)S_1 - nS_2 + 3W^2] - b_2[(n^2-n)S_1 - 2nS_2 + 6W^2]}{(n-1)(n-2)(n-3)W^2}$$

where

b_2 = the sample kurtosis coefficient m_4/m_2^2 where

m_k = the kth sample moment of $\{x_i\}$ about the sample mean.

6.2.3 Cross-correlation in the plane (after Kooijman 1979)

The methods of autocorrelation can be extended to the two species case, allowing the detection of cross-correlation between the species. The relationship between auto- and cross-correlation makes the latter technique preferable to other methods (e.g. Kershaw 1960; Mead 1967; Besag 1974; Besag and Moran 1975; Cormack 1979) for examining spatial interaction between species.

Kooijman (1979) describes a general equation for the Moran coefficient, I, covering both the one and two species cases.

For 2 species k and l and a weighting scheme described by the matrix **W**, the Moran statistic is defined by

$$I(k,l:\mathbf{W}) = (m_{k2}m_{l2})^{-1/2}\,\mathbf{x}_k'\,\mathbf{W}\,\mathbf{x}_l\,(\mathbf{1}'\mathbf{W}\,\mathbf{1})^{-1}$$

where

$\mathbf{x}_k$ is the (column) vector of cell contents centred so that $E(\mathbf{x}_k) = 0$ i.e. the mean of the raw cell counts is subtracted from each cell count,

1 is a (column) vector of length n equal to the length of the cell contents vectors; n = the number of cells,

and $m_{k2} = (\sum_{j=1}^{n} x_{kj}^2)/n$ is the variance of the cell contents of species k.

As before, an approximate test of the significance of I can be constructed by evaluating I as a standard normal deviate under one of two assumptions:

1. Assumption IID: the cell contents are independently and identically distributed for each species separately

and 2. Assumption R: every permutation of the cell contents, carried out for each species separately, has an equal probability of occurring.

The standard normal deviate of I, calculated under either assumption, is given by

$$[I-E(I)][E(I^2)]^{-1/2}.$$

For cell contents centred such that $E(\mathbf{x}_k) = E(\mathbf{x}_l) = 0$,

$$E(I) = 0$$

and $$E(I^2) = (m_{k2} m_{l2} w_{++}^2)^{-1} E(x_k' W x_l)^2 .$$

The second moment of $x_k' W x_l$ is given by KCR where

1. for assumption R:

$$K = \begin{bmatrix} \frac{m_{k2} m_{l2}}{(n-1)^2} & \frac{-m_{k2} m_{l2}}{(n-1)} & \frac{-m_{k2} m_{l2}}{(n-1)} & m_{k2} m_{l2} \end{bmatrix}$$

$$C = \begin{bmatrix} 1 & -1 & -1 & 1 \\ -1 & 0 & 1 & 0 \\ -1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}$$

and

$$R = \begin{bmatrix} \sum_{ij} w_{ij}^2 \\ \sum_{i} w_{+i}^2 \\ \sum_{i} w_{i+}^2 \\ w_{++}^2 \end{bmatrix}$$

while 2. for assumption IID:

$$K = \begin{bmatrix} 0 & 0 & 0 & m_{k2} m_{l2} \end{bmatrix}$$

with C and R as before.

Kooijman (1979), for reasons of generality, does not present KCR in its most concise

form and it is useful to derive the simplest form. Under assumption R,

$$\begin{aligned}KCR = {}& {}_{ij}\Sigma w_{ij}{}^2[m_{k2}m_{l2}/(n-1)^2 + m_{k2}m_{l2}/(n-1) + m_{k2}m_{l2}/(n-1) \\ & + m_{k2}m_{l2}] \\ & + {}_{i}\Sigma w_{+i}{}^2[-m_{k2}m_{l2}/(n-1)^2 - m_{k2}m_{l2}/(n-1)] \\ & + {}_{i}\Sigma w_{i+}{}^2[-m_{k2}m_{l2}/(n-1)^2 - m_{k2}m_{l2}/(n-1)] \\ & + w_{++}{}^2[m_{k2}m_{l2}/(n-1)^2]\end{aligned}$$

$$\begin{aligned}= {}& m_{k2}m_{l2}\{{}_{ij}\Sigma w_{ij}{}^2[n^2/(n-1)^2] + {}_{i}\Sigma w_{+i}{}^2[-n/(n-1)^2] \\ & + {}_{i}\Sigma w_{i+}{}^2[-n/(n-1)^2] + w_{++}{}^2[1/(n-1)^2]\}\end{aligned}$$

$$\begin{aligned}= {}& m_{k2}m_{l2}\{[n^2/(n-1)^2]\,{}_{ij}\Sigma w_{ij}{}^2 - \\ & [n/(n-1)^2][{}_{i}\Sigma w_{+i}{}^2 + {}_{i}\Sigma w_{i+}{}^2] + [1/(n-1)^2]w_{++}{}^2\}\,.\end{aligned}$$

Hence, under assumption R,

$$\begin{aligned}E(I^2) = {}& (1/w_{++}{}^2)\{[n^2/(n-1)^2]\,{}_{ij}\Sigma w_{ij}{}^2 - \\ & [n/(n-1)^2][{}_{i}\Sigma w_{+i}{}^2 + {}_{i}\Sigma w_{i+}{}^2)] + [1/(n-1)^2]w_{++}{}^2\}\,.\end{aligned}$$

Under assumption IID,

$$KCR = {}_{ij}\Sigma w_{ij}{}^2\,(m_{k2}m_{l2})$$

and so

$$E(I^2) = {}_{ij}\Sigma w_{ij}{}^2/w_{++}{}^2\,.$$

6.2.4 Analysis of Pipe Clay Lagoon data

The 28 dispersion transect grids (7 stations x 4 seasons) were subjected to analysis by the methods of both auto- and cross-correlation. As with the series analysis (Chapter 5), a thorough autocorrelation analysis was feasible but restrictions had to be placed on the cross-correlation analysis due to the large number of 2-species/group pairings possible, even with the grouped abundance data.

The autocorrelation analysis was conducted using the FORTRAN computer program ACORN and the cross-correlation analysis used WALNUT, developed and written for those purposes (described in Appendix A).

By using both the rook and bishop weighting schemes, 14 Euclidean interneighbour distances (other than zero) are possible within an 8 x 8 grid. With units of '1 cell width' (6.25 cm), these distances are 1.00, 1.41, 2.00, 2.83, 3.00, 4.00, 4.24, 5.00, 5.66, 6.00, 7.00, 7.07, 8.49 and 9.90. The integer distances are from the rook weighting scheme and the others from the bishop scheme.

As with the series analysis, autocorrelations were calculated for each size class, each grouping of size classes and the total of each species (over all possible spacings; zero spacing is meaningless with autocorrelations). The groupings are described in Chapter 5. This approach was impracticable with the cross-correlation analysis. Instead, cross-correlations were calculated only for the groupings and totals of the species. Also, the non-zero spacings were restricted to the first 4 (1.00, 1.41, 2.00, 2.83) which comprise 1 and 2 cell unit spacings in both the rook and bishop schemes; with zero, these give a total of 5 spacings.

Like the series analysis, only the significance (10, 5 and 1%) of the calculated values of I are presented. The 'correlograms' derived from the analysis, therefore, are not true correlograms but they do allow an examination of the changes in the strength and direction of spatial interactions.

6.3 Results

6.3.1 Introduction

As in Chapter 5, this chapter is concerned with both auto- and cross-correlation but here the two-dimensional (planar) case is considered.

Spatial autocorrelation correlograms are presented for each size class and also for each size group. As will be seen, much of the detail shown by the size class interactions may be lost in the size groups. The species having only one group, for example, often show relatively little interaction overall but there may be considerable interaction within the constituent size classes. Also, those species having multiple groups frequently show consistent interations within certain size classes; these cannot be discerned in the group correlograms.

Consideration of both size class and size group auto-correlograms inevitably leads to a multitude of correlograms, given that there are 16 species and a total of 28 sampling stations. The autocorrelograms, therefore, are included in Appendix B while the cross-correlograms are limited to the size groups, as they were in the previous chapter.

As with the one-dimensional correlograms, detailed descriptions of each figure are not warranted and only the general patterns of each are considered.

6.3.2 Autocorrelation analysis of dispersion patterns

Anapella

200381: Small (c. 0 - 2 mm) *Anapella* are positively autocorrelated over the shortest spacings at all stations except 600 m and 700 m. Weaker autocorrelations within these classes occur at medium/long spacings at 200 m (-ve), 300 m (+ve), 400 m (-ve) and 600 m (+ve).

The 3 mm class appears to differ from the smaller animals, particularly at 400 m and 600 m where autocorrelations are positive at short spacings and negative at long spacings.

Among the larger animals there is a general trend for the significant coefficients to be restricted to progressively larger classes at successive stations down the beach. Thus while c. 10 mm animals are positively correlated at medium spacings at 100 m and 300 m, they have non-significant correlations at other distances. Also, animals between c. 14 - 20 mm have positive correlations at 100 m (short spacings), 200 m (medium/long) and 300 m (medium/long). At 100 m and 300 m these relationships are negative at longer spacings. Larger animals ($\geq$ 20 mm) are positively associated at 300 m (short), 400 m (medium) and 500 m (short).

The 600 m station shows negligible autocorrelations among animals larger than 5 mm

while at 700 m correlations are negligible within all size classes.

270681: Autocorrelations are generally stronger in winter than in the autumn, particularly those among the small animals.

Strong short-spacing associations are evident within the small size classes at distances other than 300 m, 600 m and 700 m. Those coefficients are typically replaced by negative terms at medium/long spacings.

Again the 3 mm class differs from the smaller animals; positive autocorrelations occur at medium/long spacings at 200 m, 400 m and 600 m.

Significant correlations involving c. 10 mm animals are mainly restricted to the first 3 stations. These are generally positive at short/medium spacings and negative at medium/long spacings. At 600 m, 8-10 mm animals are negatively correlated at medium spacings.

Animals in the c. 13-15 mm classes are positively associated at medium spacings at the first 3 stations. The 15-20 mm animals are generally positively autocorrelated at 100 m (short spacings), 200 m (short), 300 m (medium) and 400 m (short). Autocorrelations among animals larger than 20 mm are found at all distances except 700 m; these occur at short spacings (300 m, 500 m, 600 m) and medium spacings (otherwise). Again, larger animals are involved at lower stations.

Correlations at 700 m are negligible.

290981: Correlations in spring are approximately the same strength as in winter.

Small animals have strong autocorrelations at short spacings between 100 m and 500 m; at 600 m and 700 m such correlations are found at medium spacings. The 3 mm class is positively autocorrelated at long spacings at 200 m but generally behaves less distinctly than in the previous seasons.

Animals in the c. 8-12 mm classes are positively associated at 100 m (medium spacing), 200 m (medium) and 300 m (short). The 15-20 mm classes generally have positive associations at 100 m (medium), 200 m (long), 300 m (long) and 400 m (short). Significant correlations involving animals ≥ 20 mm are only found at 400 m (positive, short) and 500 m (positive, medium/long).

At 600 m correlations are restricted to medium spacings and involve 0 mm and 6 - 7 mm animals. At 700 m the only strong coefficient is for 1 mm animals at medium spacings.

291281: In summer the overall correlation strength is intermediate between that of the spring and autumn.

The 0 mm class appears to behave differently to other small classes. Thus, strong

positive autocorrelations occur over short spacings at 100 m, 300 m, 400 m and 500 m. Animals close to 2 mm, in contrast, are generally negatively associated over short spacings and positively over medium spacings at 100 m, 200 m, 300 m and 500 m (long).

Positive correlations occur with c. 9-13 mm animals at 100 m (medium), 200 m (medium) and 300 m (short). Animals in the 15-20 mm classes are often positively correlated at 100 m (short), 200 m (medium), 300 m (medium/long) and 400 m (short). Between 300 m and 500 m larger animals have signifiacnt autocorrelations, usually over medium spacings but over short spacings at 400 m.

Little significant autocorrelation is evident at 600 m and 700 m, although 3 mm animals are associated at medium spacings.

Summary: Autocorrelations among the *Anapella* size classes are usually restricted to the first 500 m of the beach. Correlations weaken at 600 m and are negligible at 700 m. Overall, correlations are strongest in winter and spring.

The 0-2 mm classes typically show strong positive autocorrelations over the shorter spacings between 100 m and 500 m. In autumn and winter negative correlations occur at medium/long lags. In summer the 1-2 mm animals often exhibit negative coefficients at short/medium spacings but no associations at the shortest spacings.

The 3 mm size class often behaves uniquely. Generally, autocorrelations are most significant at 200 m, 400 m and 600 m. The positive correlations occur over short spacings in autumn and over longer spacings in subsequent seasons. In autumn there are also negative correlations at medium spacings. In summer the 3 mm class distinction is less well marked.

The remaining size classes can loosely be formed into 3 distinct superclasses: 7 - 13 mm, 14-20 mm and > 20 mm animals. Among these classes there is a general trend for correlations to become restricted to larger animals at successive stations down the beach. The first superclass generally has positive autocorrelations over medium spacings at the first 3 stations; the second has positive correlations between 100 m and 300 m over medium spacings and at 400 m over short spacings; the third has positive associations over short spacings at 400 m and medium spacings at 500 m and 600 m.

Except for the 0-2 mm classes, the above details are largely lost in the group correlograms. Group IV correlations are typically positive over short and medium spacings. In autumn and winter these correlations are restricted to the penultimate stations at either end of the beach and a midbeach station. In spring and summer, however, positive associations are evident at all but the first and last stations. Group V autocorrelations are found at most stations in all seasons, usually over medium and long

spacings. At the 400 m station these correlations are always negative and in spring and summer the 300 m coefficients are also negative. Otherwise the associations are positive.

Katelysia

200381: Correlations involving 0 mm animals are typically weak at all stations. Strong (positive) correlations only occur at 300 m (medium spacings), 500 m (medium) and 600 m (long).

Animals greater than 20 mm commonly have strong positive autocorrelations at short spacings; this is true at 300 m, 400 m, 500 m and 600 m. Exceptions occur at 300 m and 400 m when c. 25 mm animals are negatively correlated at medium and long spacings. Significant correlations involving other groups are rare, although the 8 mm class if positively autocorrelated over short spacings at 600 m.

270681: At 400 m and 500 m the 0 mm size class has weak negative autocorrelations at short spacings while at 700 m the class is positively correlated at short spacing; otherwise there are negligible autocorrelations within that class.

The 2 mm class is positively autocorrelated at 600 m (long spacings) and 700 m (medium). Animals close to 10 mm have similar correlations over medium and short spacings respectively.

The majority of remaining correlations occur within classes larger than 20 mm, usually c. 22 mm or > 25 mm. Between 300 m and 600 m the associations are positive and occur over short or medium (500 m) spacings. At 700 m the relationship is negative over medium spacings.

290981: The 0 mm class shows positive autocorrelation over short spacings at 200 m and 300 m. At 400 m and 500 m the correlations are negative and over longer spacings; at 600 m (long) and 700 m (medium) they are positive. In this season the 1 mm class also shows frequent autocorrelation and this is positive at distances other than 200 m (negligible), 500 m (negative) and 700 m (negligible).

Animals in the 3-4 mm classes are positively correlated at 500 m (short and long) and 600 m (medium) while 10 mm animals are positively associated over short and medium spacings at 600 m.

The larger animals (c. ≥ 20 mm) are less strongly autocorrelated than in the previuos seasons but positive associations occur at 300 m (short), 400 m (medium) and 600 m (medium); at 700 m the correlations are negative over medium spacings.

310382: Positive autocorrelations within the 0 mm class occur over short spacings at 300 m, 500 m and 700 m. The 1 mm class is correlated over medium spacings at 300 m (negative) and 400 m (positive) and short spacings at 700 m.

Animals in the c. 6-7 mm classes are positively autocorrelated over medium spacings at 500 m, 600 m and 700 m. Among the larger classes, those between c. 20 mm and 25 mm have positive correlations at 200 m (short), 300 m (short) and 400 m (medium/long). Still large animals are negatively correlated at 400 m (medium) and positively correlated at 500 m (medium) and 600 m (short).

Summary: In contrast to *Anapella*, the autocorrelations within large *Katelysia* size classes are frequently stronger than those within the small classes. Also, the overall interaction within *Katelysia* is markedly weaker than that within *Anapella*. This is exagerrated by the more restricted zonation of *Katelysia*. There are no obvious seasonal changes in the overall interaction strengths.

Between 300 m and 700 m the significant autocorrelations within the 0 mm class are typically positive over short spacings. In winter and spring, however, the correlations are negative at 400 m and 500 m.

Other consistent correlations involve animals close to 10 mm in size and are positive over short spacings at 600 m and 700 m in all seasons.

The larger animals (> 20 mm) are usually positively autocorrelated over short or medium spacings between 300 m and 700 m but in winter and spring the associations are negative at 700 m.

As with the group correlograms for *Anapella*, the above details are largely lost when the classes are formed into groups. Strong group III correlations are generally restricted to the 500 m and 600 m stations, where they are positive over short or medium spacings. At 600 m group IV autocorrelations are negative over short spacings in all seasons except summer, when they are positive. In winter that group also shows strong positive association at the 400 m station, over short spacings. Group V correlations are typically positive over short and medium spacings but there is considerable varitation in the seasonal transects. In autumn the associations are restricted to the 600 m station; in winter they are found between 500 m and 700 m; in spring associations occur only at 200 m and in summer they occur at all but the first and last stations.

Wallucina

Wallucina exhibits fundamentally similar patterns in each season. Correlations are typically restricted to stations other than 100 m and 200 m and the 600 m correlations are always weak. Negligible autocorrelations also occur at 300 m in autumn, 500 m in spring and at 400 m and 600 m in summer.

The smaller and larger size classes do not exhibit strong autocorelations and most associations occur in the 3-6 mm classes. There is a general trend for small animals to

be positively associated over short spacings and larger animals to be associated over medium or long spacings. In autumn and winter negative correlations occur at 700 m, within medium sized classes.

Soletellina

The relatively low numbers of *Soletellina* undoubtedly contribute to the poorly structured correlograms. Some trends are evident, however. Small (0-1 mm) animals often have positive autocorrelation at medium spacings below the 400 m station. Animals near 2 mm in size have negative associations over long spacings below c. 500 m except in autumn.

Hydrococcus

200381: Overall correlations are strongest at 100 m and 300 m. The 0 mm (and often 1 mm) size class is positively autocorrelated at the shortest spacings except at 300 m and 400 m. At 100 m this is also true for 2 mm and 3 mm animals. At 500 m and 700 m those small classes show negative correlations over medium or long spacings. The 0 mm class has positive autocorrelations at 200 m and 600 m over medium spacings. Larger animals (3 mm and 4 mm) show positive correlations at medium or long spacings at 100 m, 300 m and 400 m. Total *Hydrococcus* shows positive correlations over short, and negative over long, spacings at 100 m, 300 m and 700 m.

270681: Overall correlations are strongest at 200 m. At all distances except 300 m and 500 m, the 0-2 mm animals are typically positively autocorrelated over short spacings and often negatively associated at medium or long spacings. The small animals have positive autocorrelations at 300 m and 500 m over medium spacings. Larger animals are positively associated over medium spacings at 100 m and 200 m. Total *Hydrococcus* shows positive correlations over short, and negative over long, spacings at 100 m, 200 m, 400 m and 700 m. There is a general trend for the interactions to extend over larger spacings with larger animals.

290981: Autocorrelations are comparatively weak at a number of sampling stations but are strongest at 200 m. Only at 600 m and 700 m does the 0 mm class show positive associations over short spacings. Instead, between 200 m and 400 m the small classes are negatively autocorrelated over medium and long spacings. Significant correlations involving larger animals are relatively rare but at 600 m the 3 mm class shows positive autocorrelation over long spacings. Only at 400 m is the pattern of positive/short and negative/long correlations among total numbers evident.

291281: Associations are strongest at 600 m but are also strong at 100 m and 200 m. At those distances (only) the small classes show positive autocorrelations at short

spacings. At all distances but 100 m and 300 m the small classes are also associated at longer spacings. These associations are positive at 200 m and 700 m and negative at other distances. Autocorrelations among larger animals occur at 200 m, 400 m, 500 m and 700 m, usually over medium spacings. Those coefficients are positive except at 500 m.

Only at 500 m is the pattern of positive/short and negative/long correlations among total numbers evident.

Summary

Overall interactions are strongest in winter. Small animals frequently show positive associations over short spacings. In autumn and winter this is true over most of the transect except at 300 m and 400/500 m. The spring associations are restricted to below 500 m and the summer pattern is intermediate. In spring those animals are negatively associated at longer spacings between 200 m and 400 m. In other seasons the animals are often positively autocorrelated over longer spacings either side of the mid-beach zone.

Larger animals frequently show interactions at medium spacings. In autumn and winter this occurs at the top end of the beach while in spring it occurs towards the lower end; summer is intermediate.

There is often a general trend for total *Hydrococcus* numbers to exhibit positive interactions at short spacings and negative interactions at longer spacings. This is particularly so in winter, less so in autumn and least so in the other seasons. This reflects the overall interaction strengths of each season.

Zeacumantus

200381: Interactions are mainly restricted to the first 4 sampling stations and are strongest overall at 300 m. There is a general trend for positive autocorrelations to occur over progressively larger spacings with increasing size of animals. Often there is a similar pattern of negative correlations at larger lags. These trends are reflected in the total interaction which, at least high on the beach, is positive at short spacings and negative at medium or long spacings. Significant interactions extend over greater spacings in *Zeacumantus*, in comparison to the previously described species. Most size classes show correlations; interactions are not confined to a narrow range of sizes as in previous species (although at 400 m correlations are negligible in animals over 5 mm).

270681: Overall correlations are strongest in this season, particularly at 100 m and 200 m and extend down to the 500 m station. The correlograms are fundamentally similar to those of the previous season although the trends are more well defined. Again, correlations at 400 m are negligible in large animals while at 500 m significant

associations only occur in the 0 mm and 1 mm classes.

290981: The trends described above are less marked in spring. At 100 m and 200 m, for example, there are minimal autocorrelations at short spacings although the medium spacing interactions persist. Significant associations are largely restricted to stations between 100 m and 400 m (300 m is strongest overall) but there is little restriction among the size classes.

291281: This season shows the least interaction and correlations are found mainly in the first 300 m and are strongest at 100 m. The general trend common to all seasons is evident but is only loosely defined below 200 m.

Summary

Zeacumantus shows a trend that was hinted at in *Hydrococcus* , and to a lesser extent *Anapella* : animals of increasing size consistently show interactions over increasing spacings. This is true in all seasons but is strongest in winter and weakest in summer. There are generally 2 levels of interaction, with positive associations at shorter lags being replaced by negative associations at longer lags. Significant autocorrelations are found in most classes above 400 m but are restricted to the small classes lower on the beach.

Because of the amalgamation of size classes, this trend is less evident in the group correlograms.

Salinator

The size class correlograms are always poorly structured and difficult to interpret. The group correlograms show only slightly more structure.

200381: Group I is positively autocorrelated over short and longer spacings at 300 m and 400 m. Group II has negative associations, usually over medium spacings, at 100 m and 200 m and at 600 m and 700 m.

270681: Between 100 m and 500 m group I is positively correlated at short spacings. Positive associations within this group also occur at longer spacings at 200 m, 300 m and 500 m. At 600 m and 700 m the group is associated at medium spacings only and the correlations are negative at 600 m and positive at 700 m. Group II has negative coefficients at 100 m (long spacing) and 400 m (short) and positive terms at 300 m (short) and 600 m (medium).

290981: Autocorrelations within group I occur over short spacings at 100 m (-ve), 200 m (+ve) and 700 m (-ve). At 100 m and 200 m positive correlations also occur at long spacings. Group II correlations are positive at 200 m, 400 m and 500 m over progressively longer spacings.

291281: Group I autocorrelations occur between 100 m and 600 m and are mainly over long spacings; the coefficients are negative at 200 m and 600 m but positive elsewhere. At 100 m group II is positively autocorrelated over short spacings while at 200 m and 300 m similar associations occur at longer spacings. At 500 m and 600 m the group shows negative associations at long spacings.

Summary

There is comparatively little consistency in *Salinator* associations within either the size classes or groups. There are trends in the overall interaction strengths, however. Correlations are strong at 100 m in all seasons but autumn. From winter to summer there is an extension of strong interactions down the beach to the 300 m station. In autumn strong associations occur at 400 m while in winter and spring they are also evident at 500 m.

Cylichnina

200381: Small animals are positively associated over long spacings at 400 m and short spacings at 600 m and 700 m but 1 mm animals have negative autocorrelation at 700 m.

270681: In winter most correlations involve 2 mm animals which are typically positively correlated over medium or long spacings. The 0 mm class, however, is positively associated over short and long spacings at 700 m. Significant correlations are found at stations other than 100 m, 300 m and 600 m in this season.

290981: Correlations are relatively weak at all stations except 700 m where all classes are positively autocorrelated at medium spacings (the 2 mm class also shows positive association over medium spacings at 400 m as do total numbers at 600 m).

291281: The strongest associations occur at 400 m when the 1 mm and 2 mm classes are positively autocorrelated at medium spacings; similar associations occur within the 0 mm class at 300 m. At 400 m, 600 m and 700 m, 0 mm animals are correlated over a range of spacings.

Summary

Cylichnina shows little autocorrelation at stations above 300 m. Correlations in winter and spring usually involve larger animals over medium spacings although at 700 m, 0 mm animals are also autocorrelated. In summer and autumn, the 0 mm class frequently shows association and this is usually positive in autumn and negative in summer.

Rissopsis

200381: At 400 m and 500 m, 0 mm animals are positively correlated over medium/long spacings while at 700 m the 1 mm class is similarly associated over short

spacings. Correlations are negligible above 400 m.

270681: Autocorrelations occur at all stations except 500 m. Usually 0 mm animals are positively correlated over medium or long spacings but at 300 m the relationship is negative. At either end of the beach the 1 mm class is positively correlated over short spacings.

290981: As in the previous season, correlations are evident at most stations but in spring strong associations also occur at 500 m. Small animals are positively related over short and long spacings at either end of the transect and over medium and long spacings at 500 m.

291281: Associations are relatively weak in this season. Only at 100 m (total over long spacings) and 400 m (1 mm over long spacings) do strong (positive) autocorrelations occur. Corelations are negligible below 400 m.

Summary

Overall correlations are strongest in winter and spring and in these seasons they occur over most of the dispersion transect. In autumn correlations are restricted to the bottom half of the beach while in summer they are confined to the top half. The most common autocorrelations involve small animals over medium and long spacings.

Microdiscula

Correlations are strongest in winter and weakest in autumn and summer. The general pattern is for positive associations high on the beach but in winter negative associations occur in the lower half of the transect. From winter to summer there is a decrease in the interaction spacings.

Nassarius

Most significant autocorrelations occur in the upper half of the beach and involve large animals (> 10 mm). In autumn and winter the associations are over short spacings and in spring they occur over longer spacings. In summer negative asociations are evident over longer spacings high on the beach.

Agatha

Autocorrelations are negligible.

Bembicium

Autocorrelations are negligible.

Austrocochlea

Autocorrelations are negligible.

Notoacmea

Autocorrelations are negligible.

Anthopleura

200381: Strong autocorrelations are evident among animals larger than 1 mm between 200 m and 500 m. The associations are typically positive and act over short and medium distances. The strongest interactions overall occur at 200 m. At that station the interactions tend to occur over shorter distances (from medium to short) with increasing animal size. At 300 m small and large animals are negatively autocorrelated over medium spacings.

270681: Overall interactions are weaker than in the previous season, except at 100 m; most involve animals less than 5 mm in size, over short spacings.

290981: Autocorrelations are relatively weak at stations other than 100 m, 300 m and 500 m. At 100 m small animals show negative associations over long spacings. Strong negative associations also occur among 5 mm and 8 mm animals at 500 m. At 300 m autocorrelations are strong among 3-10 mm animals and they act over spacings which decrease in length with increasing animal size (this trend moves from long to medium spacings).

291281: Strong autocorrelations are evident among animals larger than 1 mm between 200 m and 500 m. The associations are typically positive and act over short and long distances. The strongest interactions overall occur at 500 m. At that station the interactions tend to occur over shorter distances (from medium/long to short/medium) with increasing animal size.

Summary

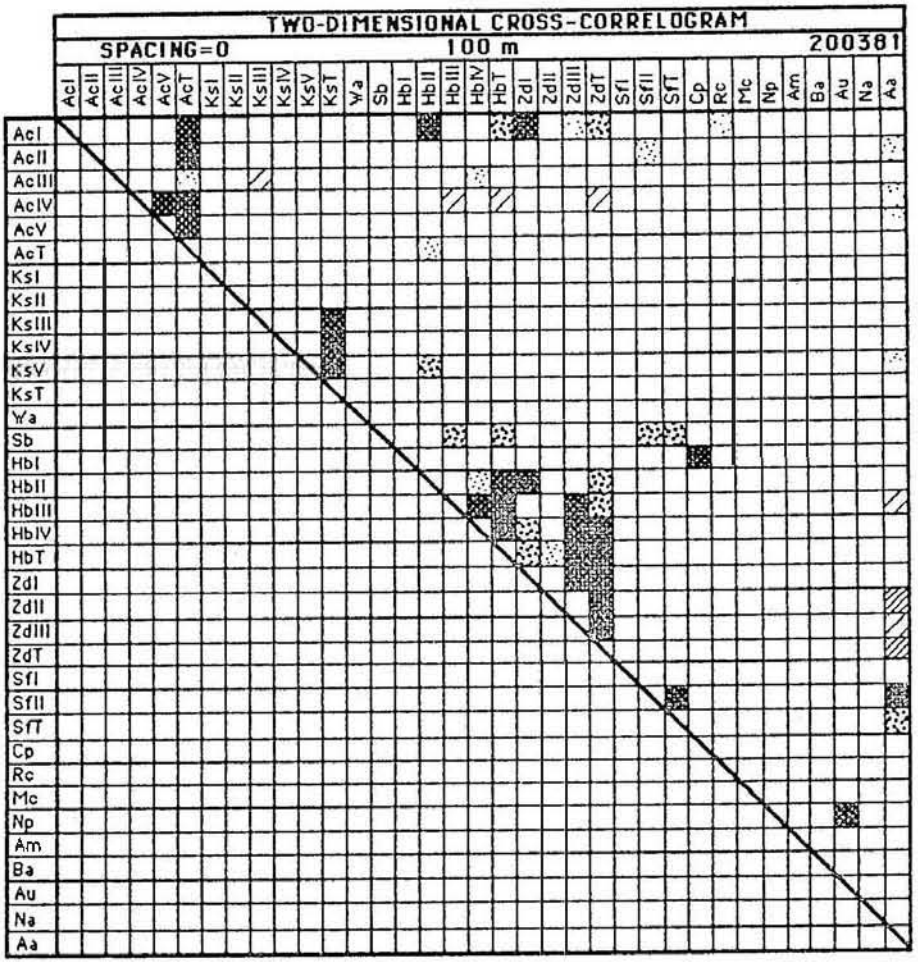
Significant autocorrelations usually involve a range of animals between 1 mm and 10 mm but in winter they are restricted to groups less than 5 mm. Autumn and summer show the strongest relationships. In each season other than winter, the strongest interactions are associated with a trend for shorter spacings with larger animals. In spring the spacings decrease from long to medium, in autumn from medium to short and in summer the changes occur over intermediate spacings.

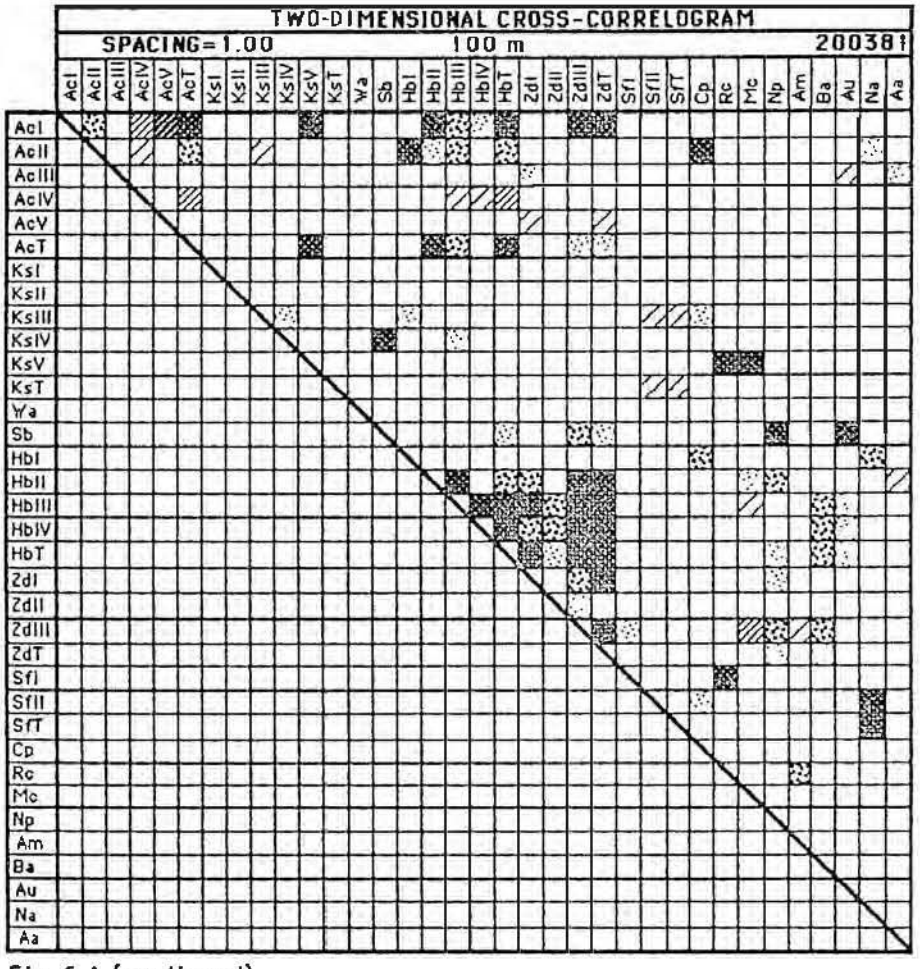
6.3.3 Cross-correlation analysis of dispersion patterns (Fig. 6.1)

6.3.2.1 Within species analysis

As with the series analysis (Chapter 5), the primary indicator of interaction between groups/species is the zero spacing correlogram. The correlograms of non-zero spacings show how interaction varies with distance between animals. Again, correlations between a species total and its constituent groups lack independence and are therefore unreliable

Fig. 6.1 Planar cross-correlation analysis of species groupings. Correlograms are calculated over spacings of 0 to 2.83 cell units (0 to 17.69 cm) for all stations in the dispersion transects. Species abbreviations as defined in Table 5.1. Shadings indicate sign of correlation and level of significance as defined in Table 5.2.





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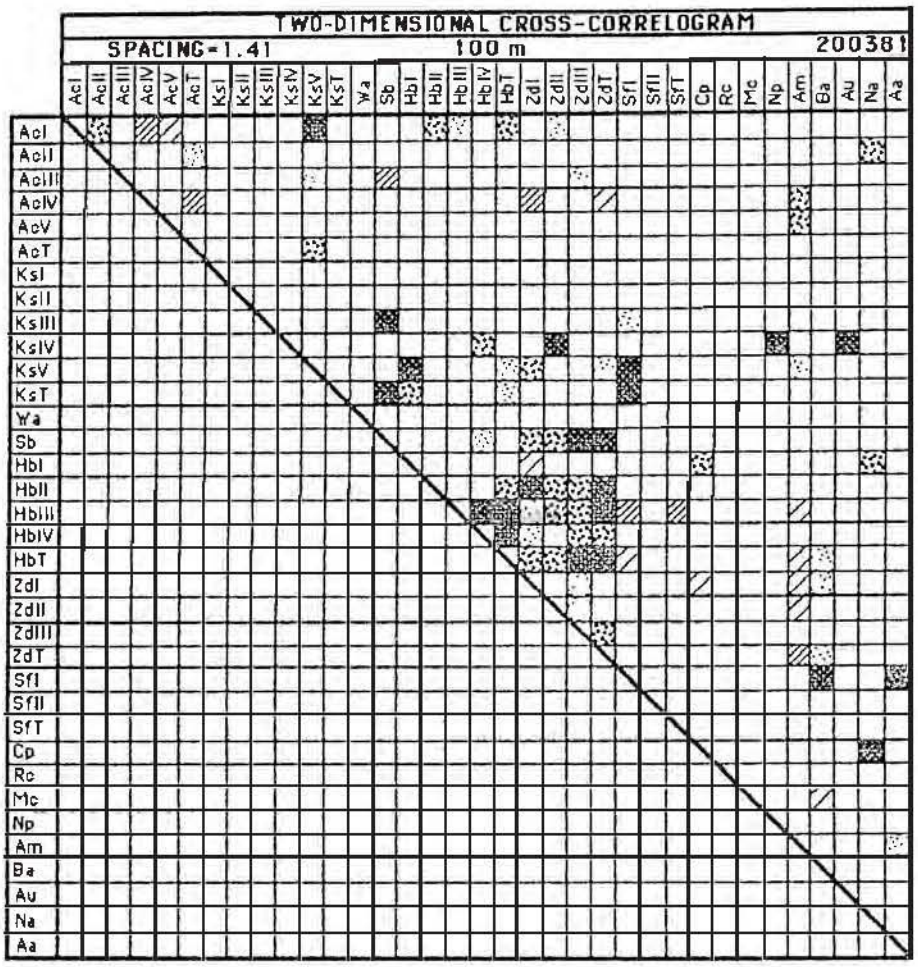

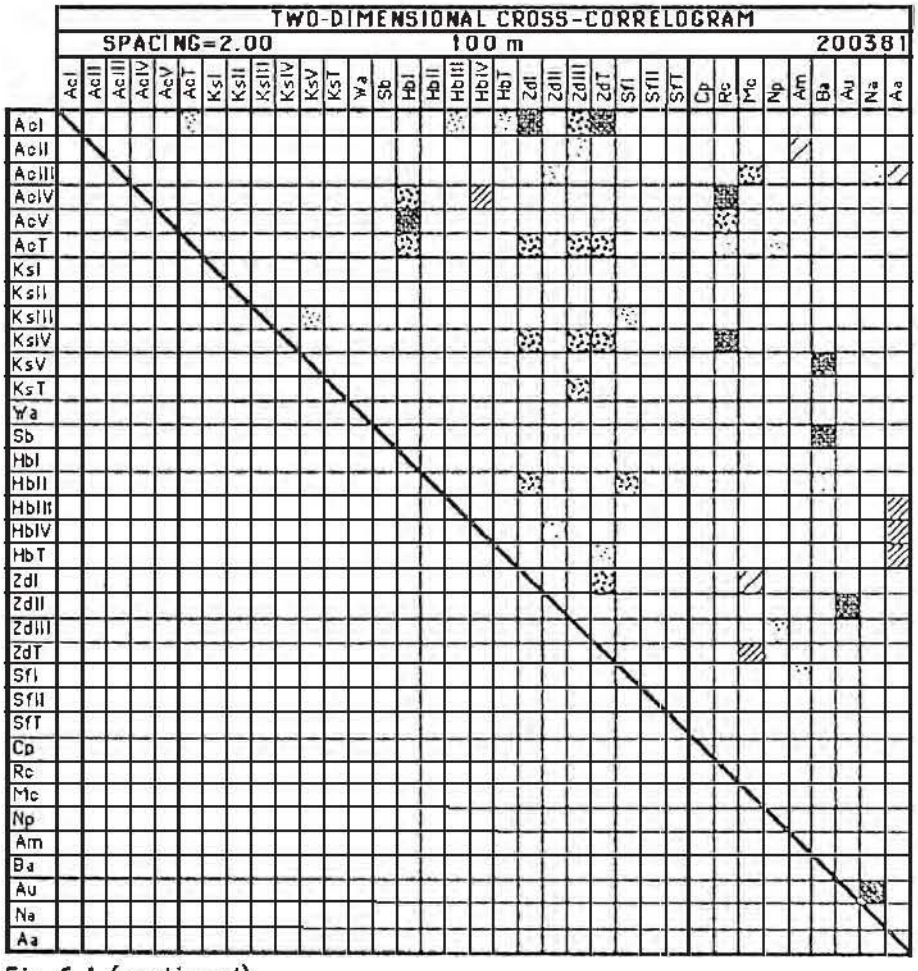

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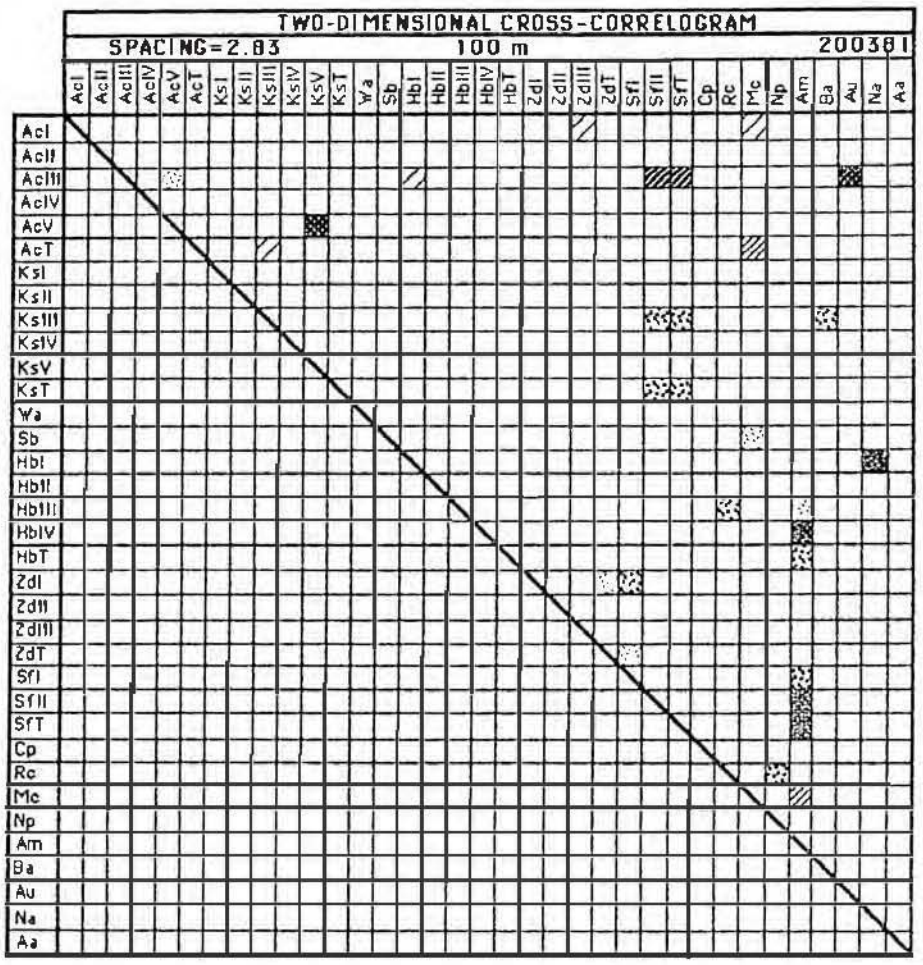

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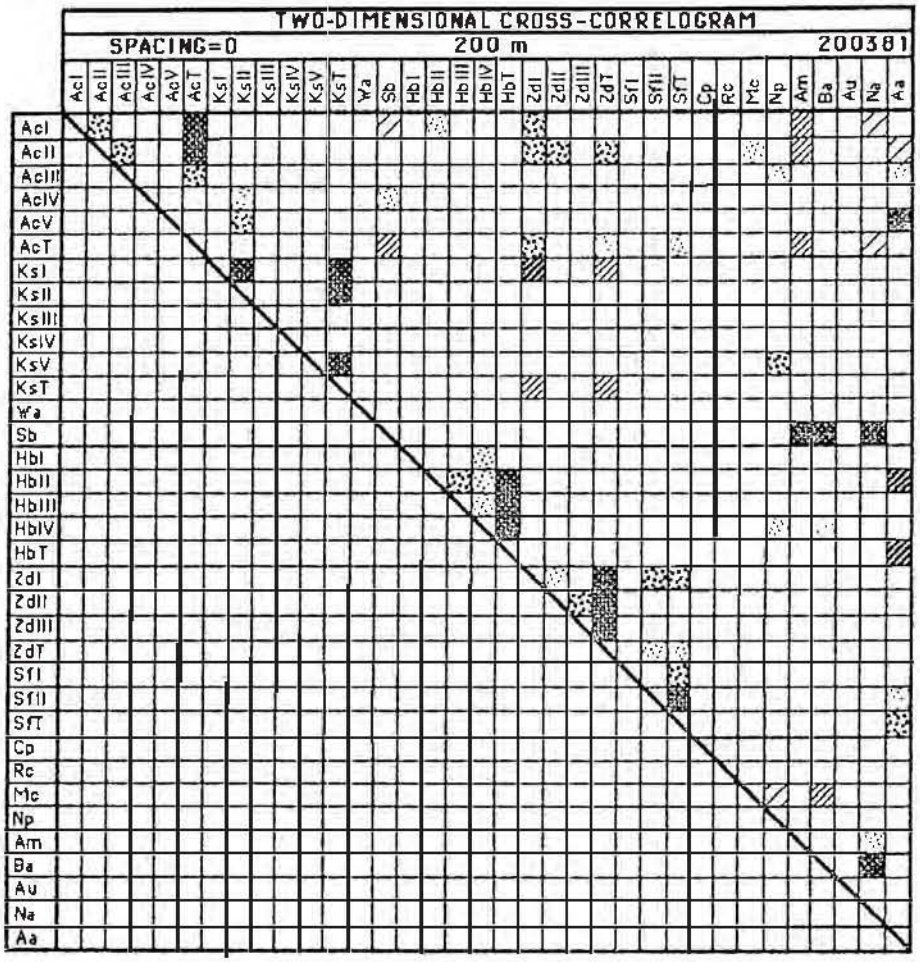

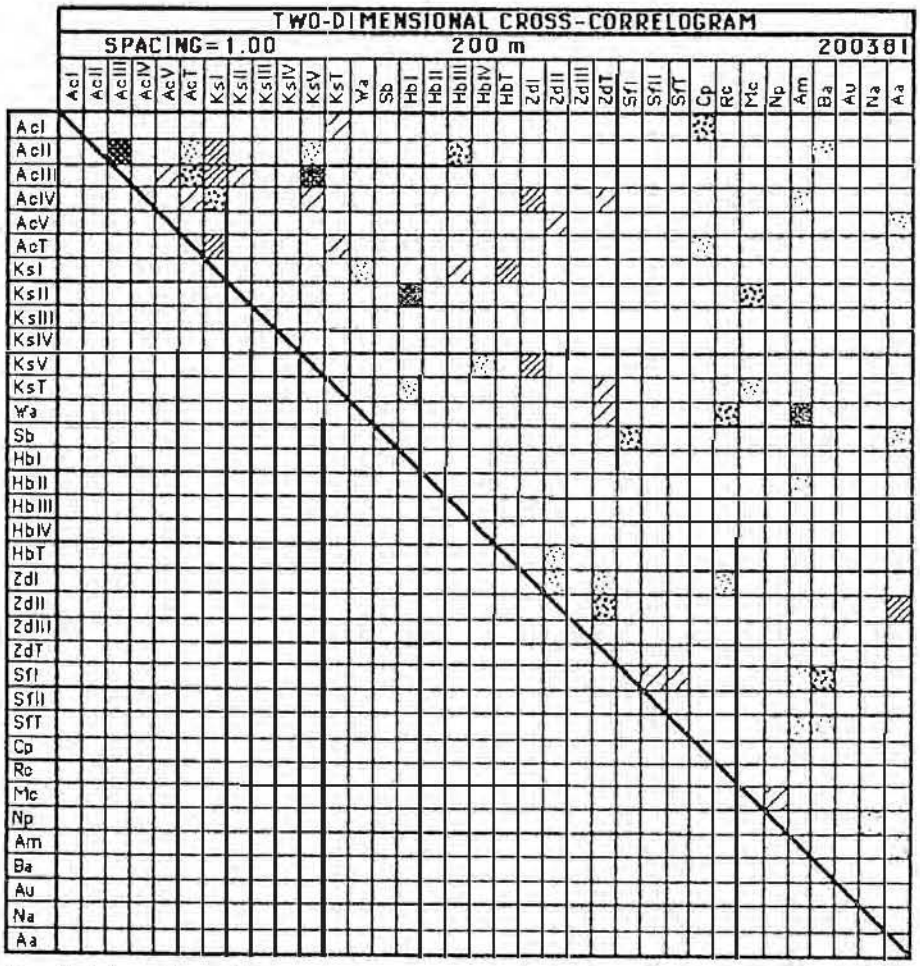

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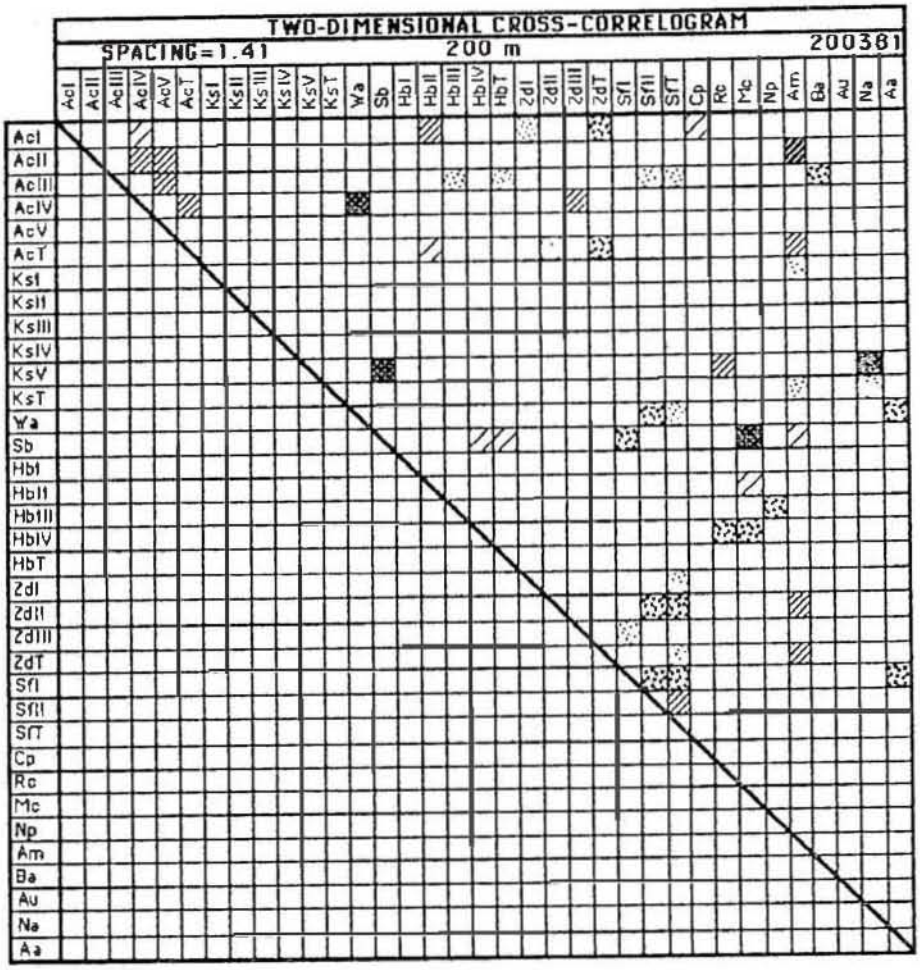

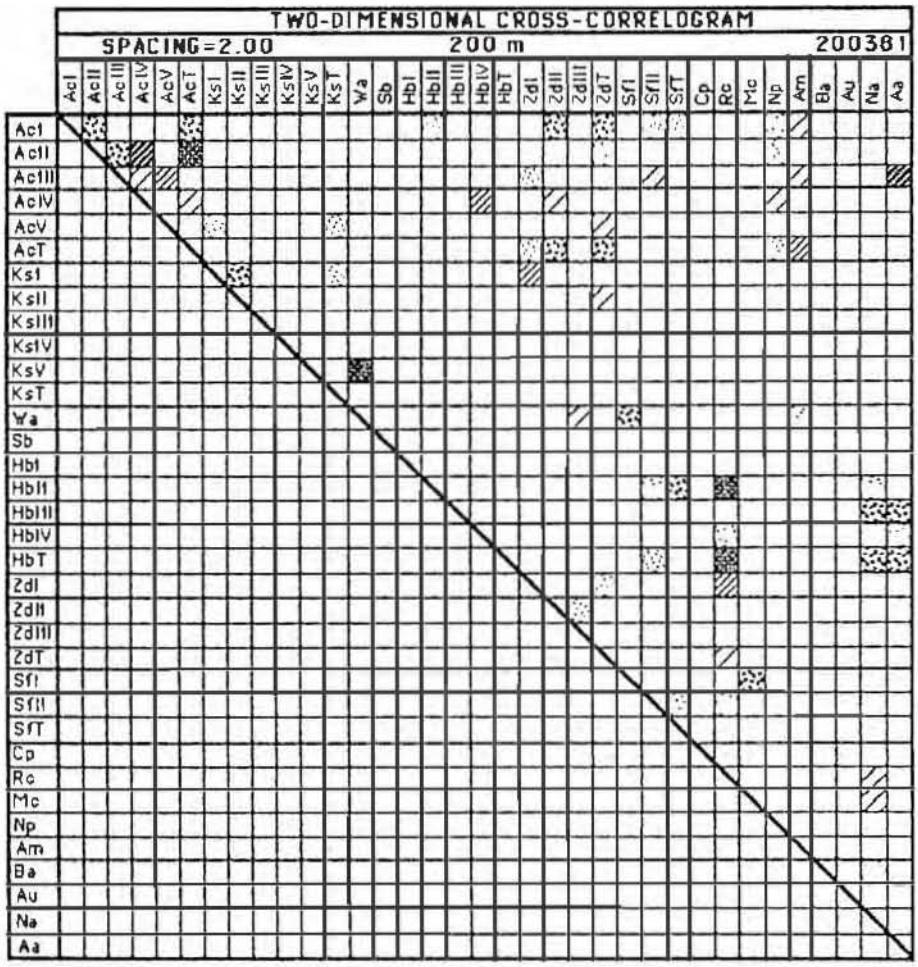

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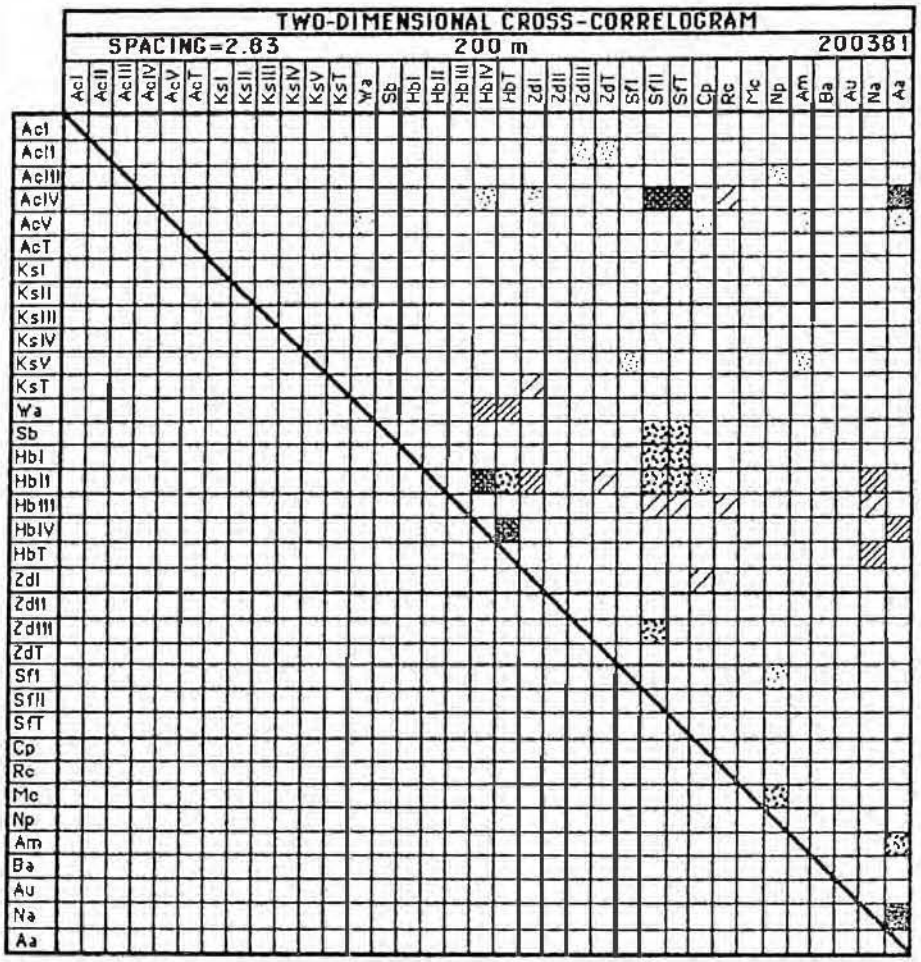

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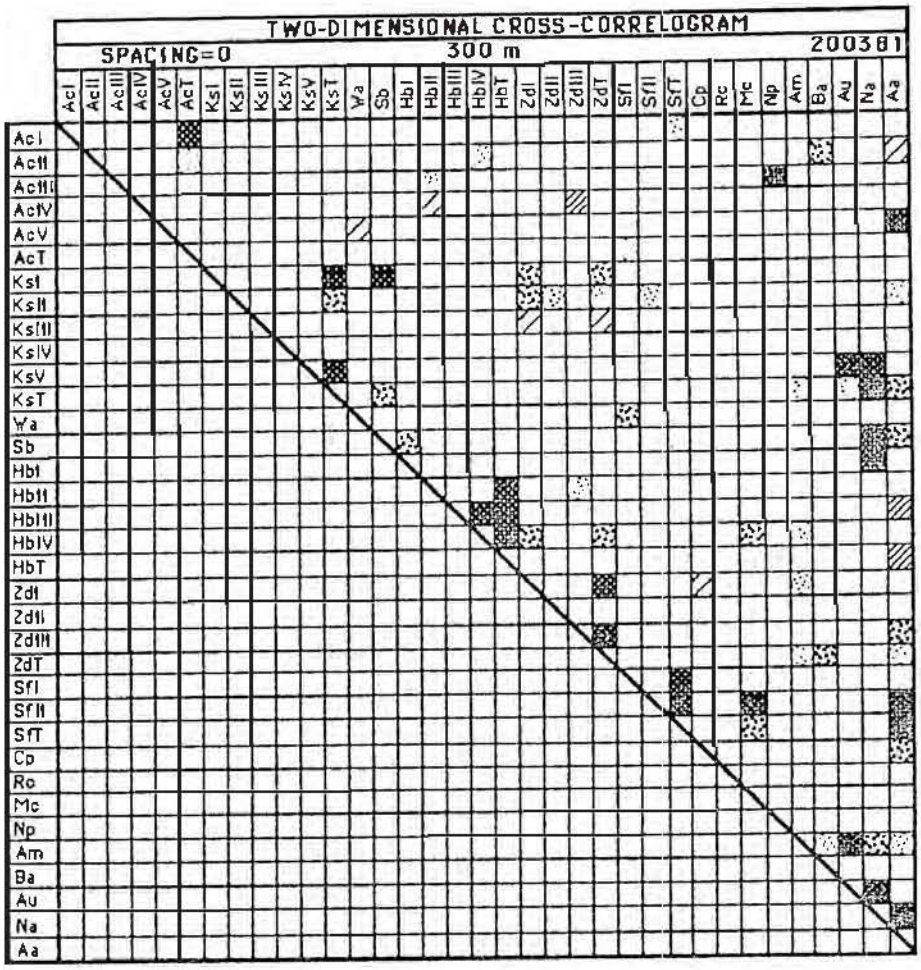

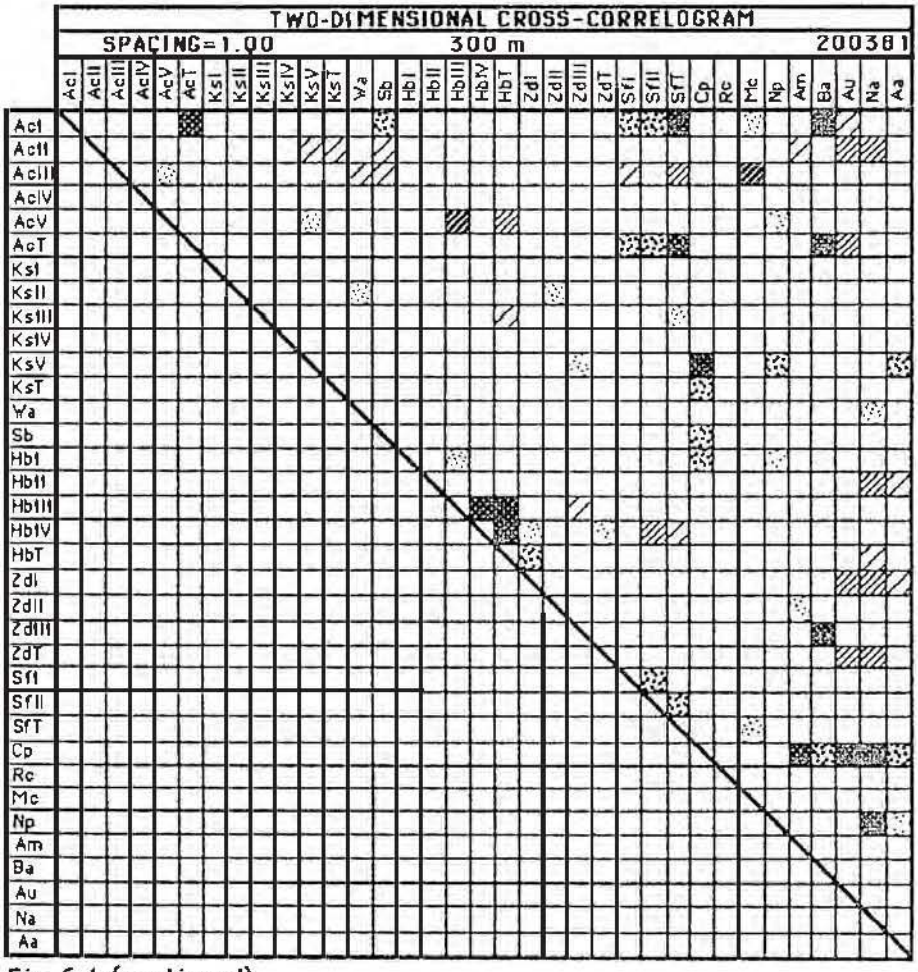

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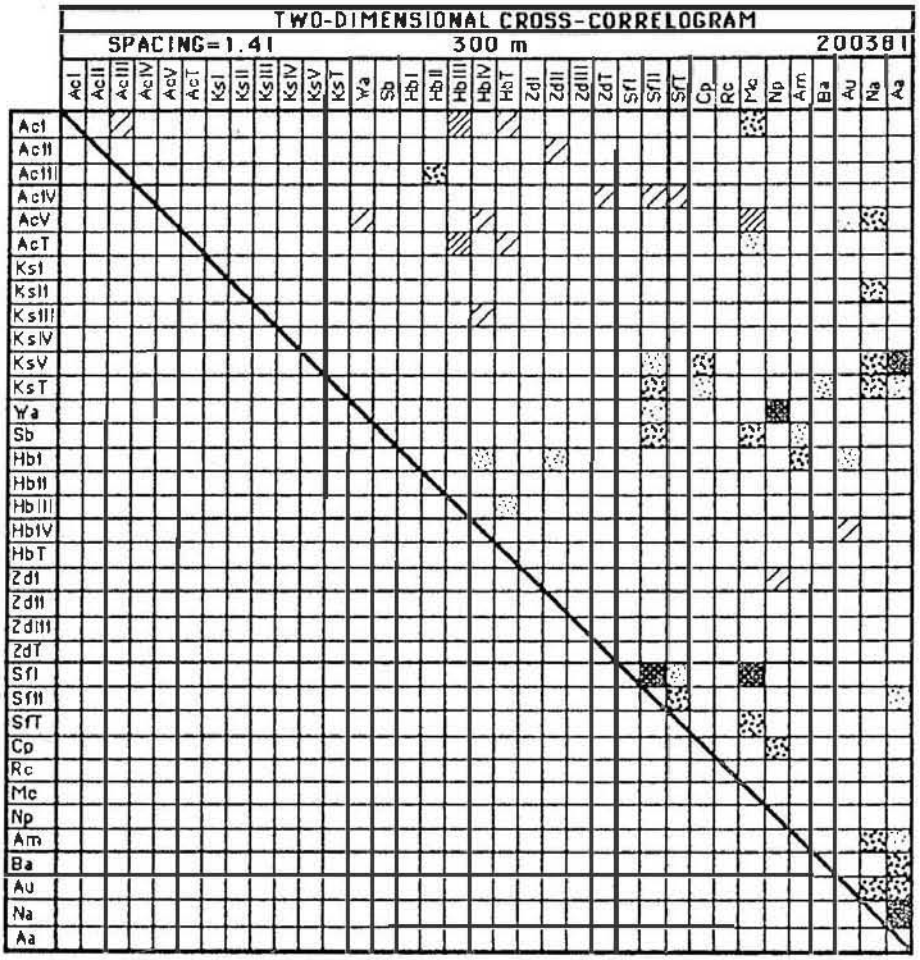

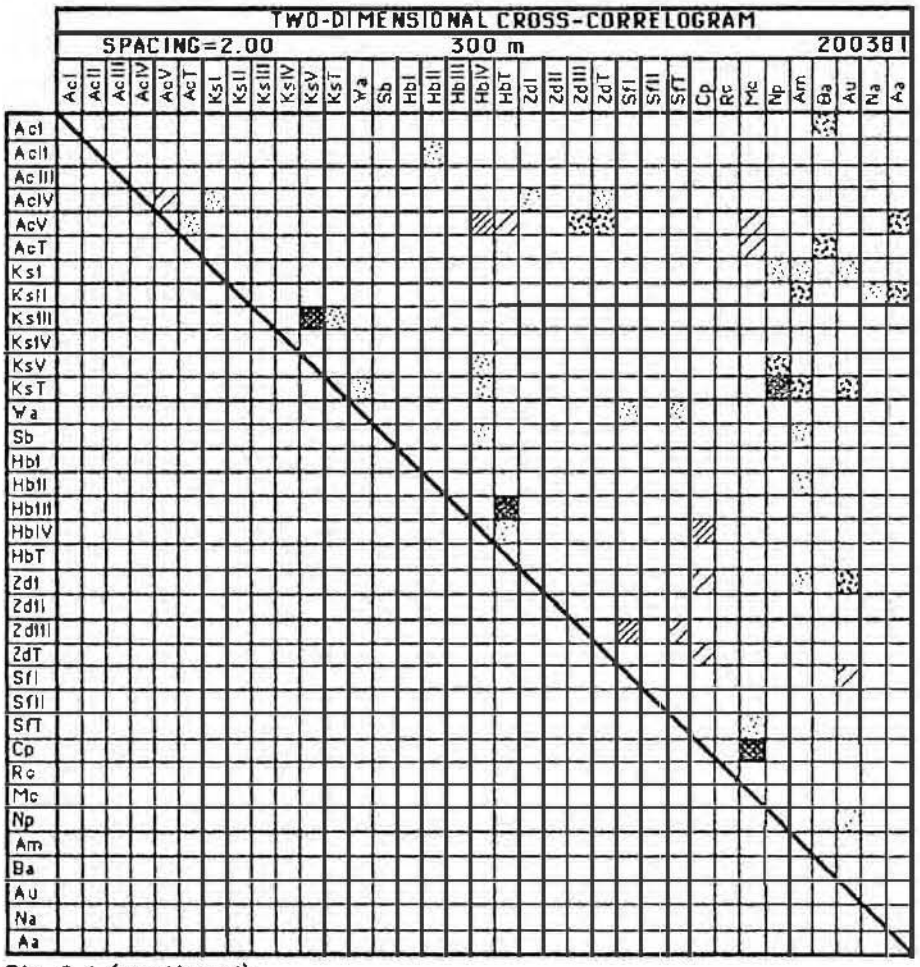

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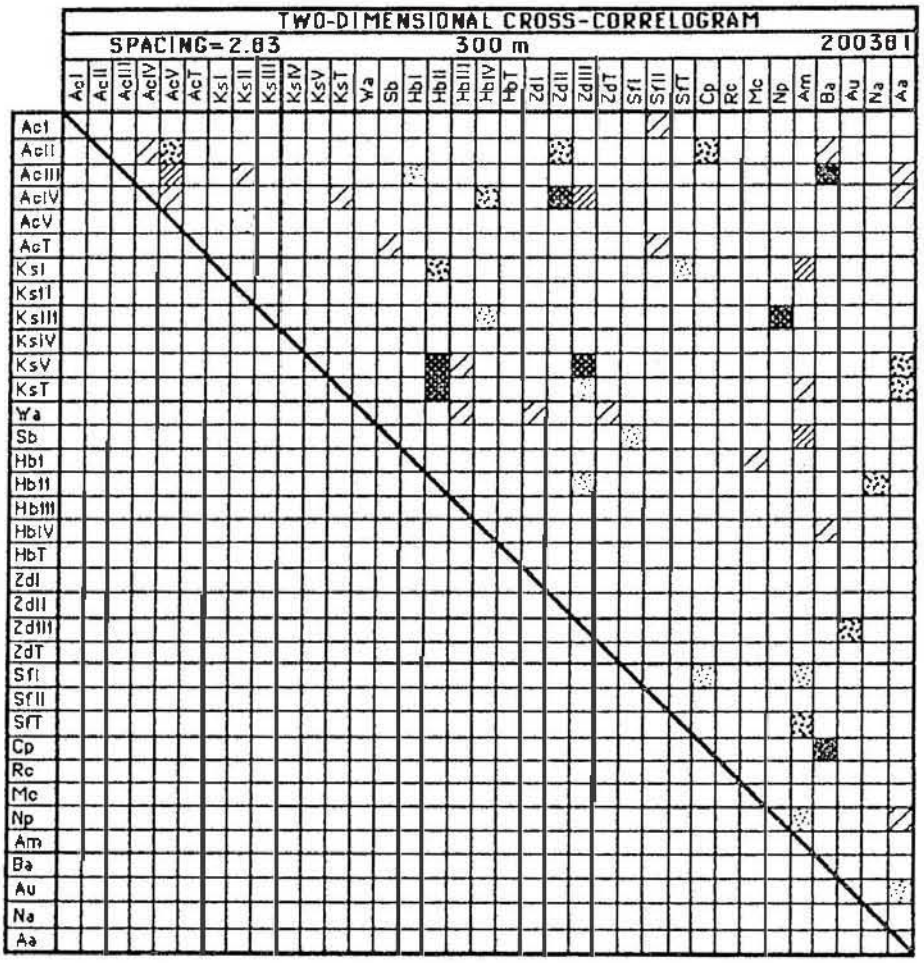

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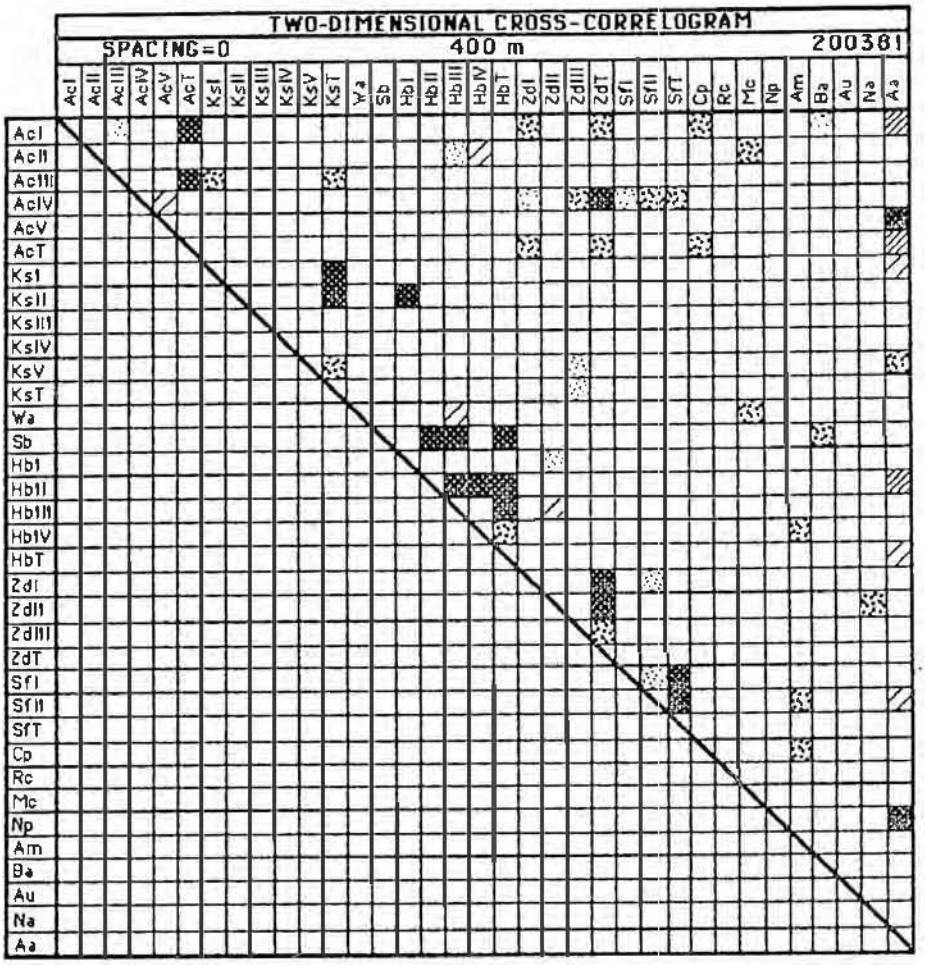

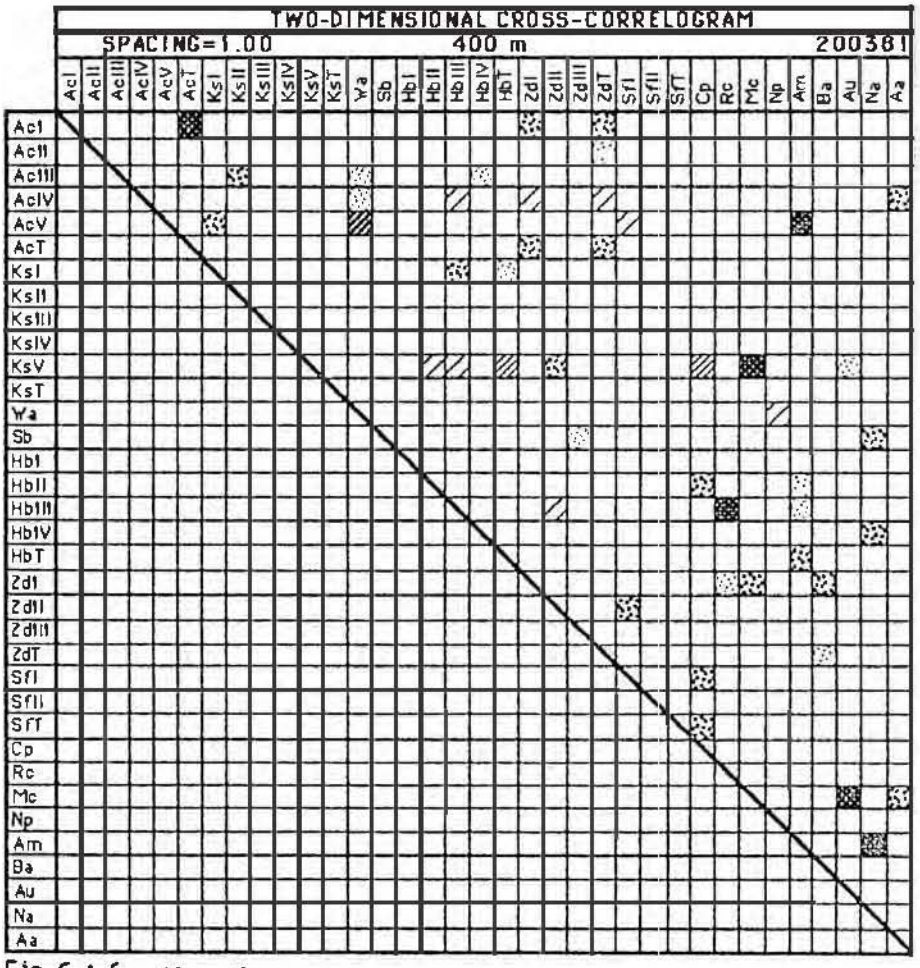

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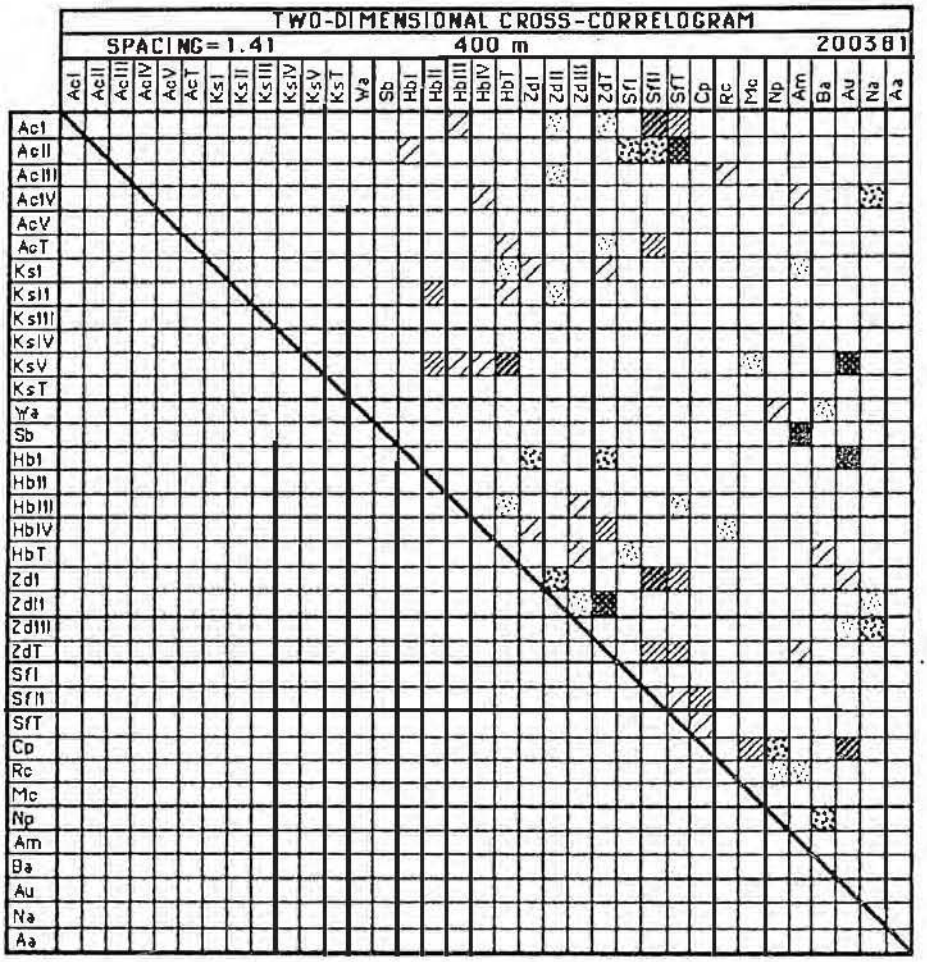

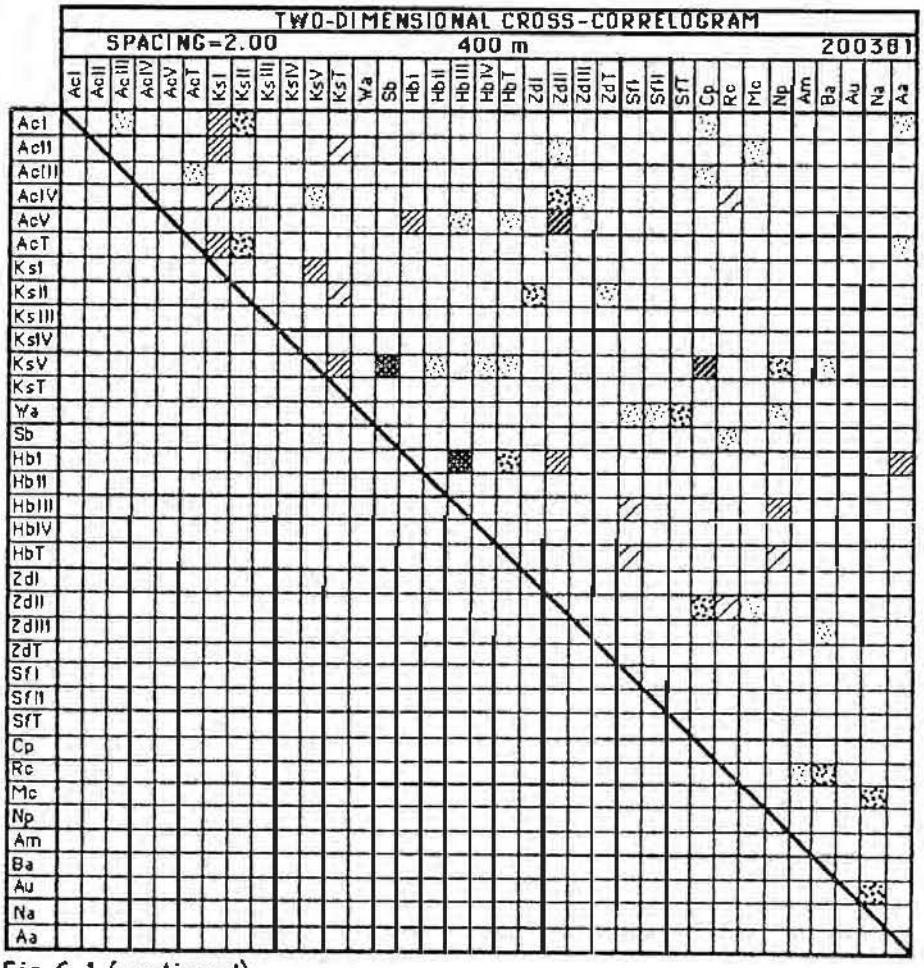

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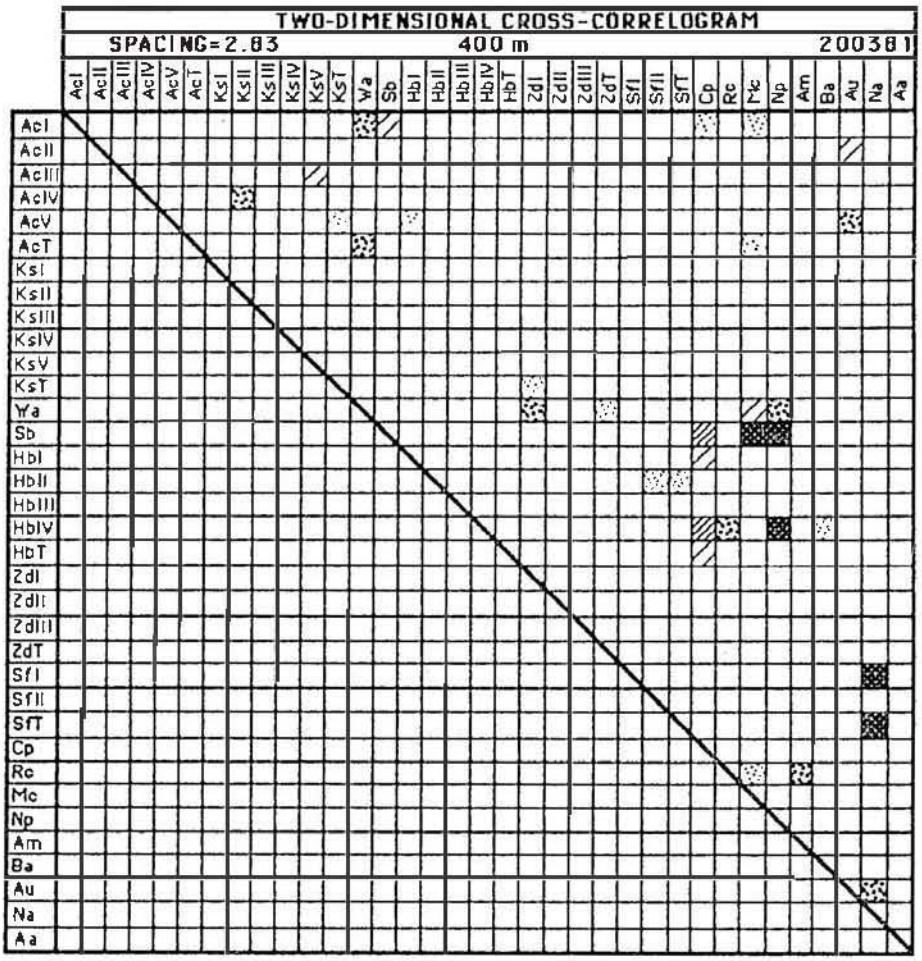

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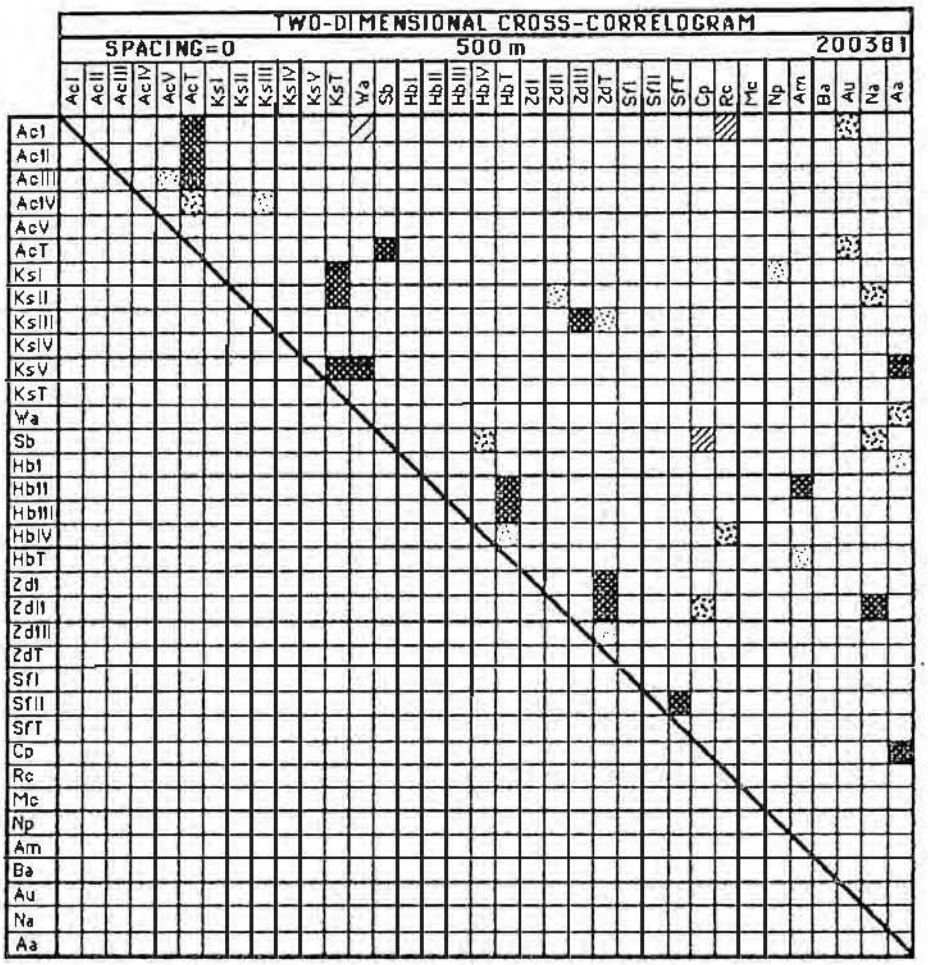

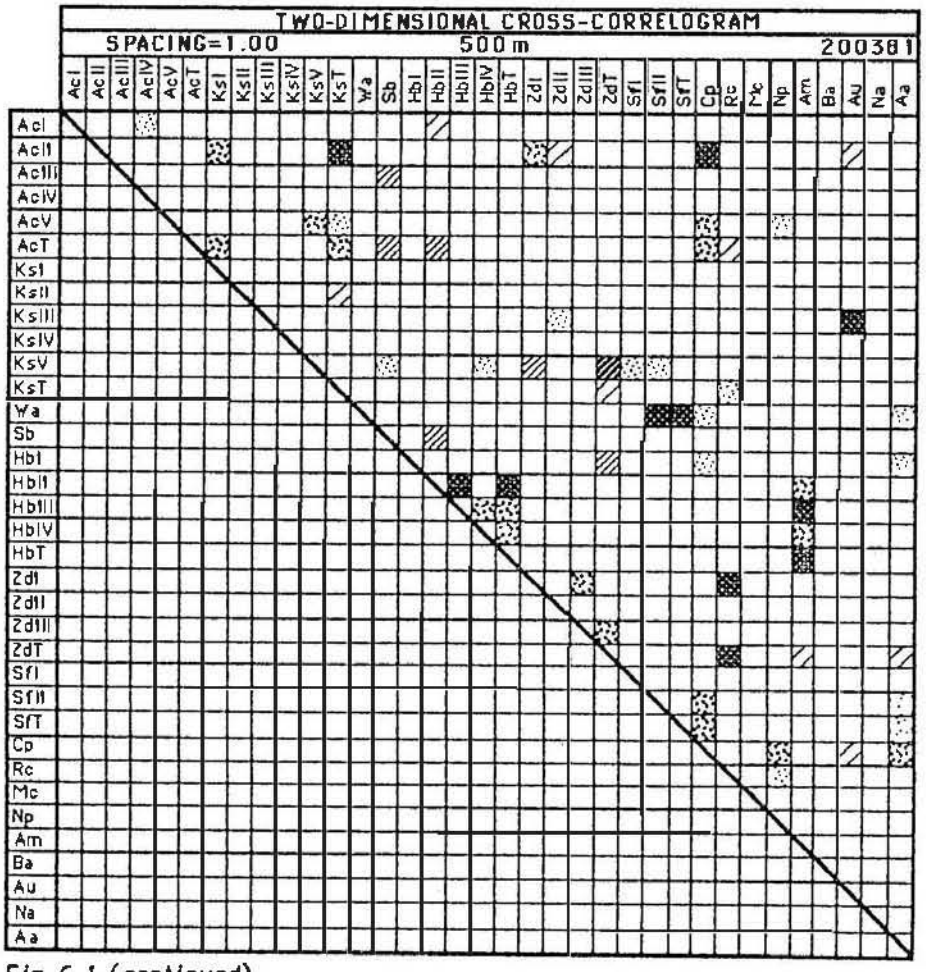

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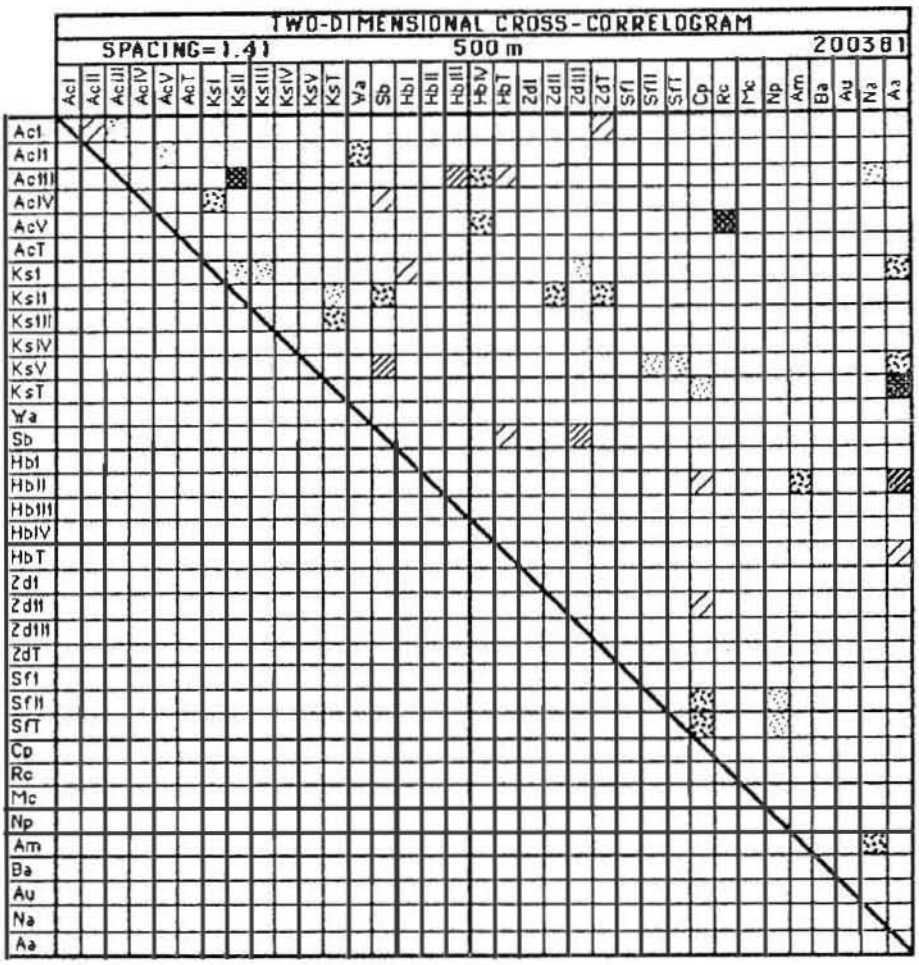

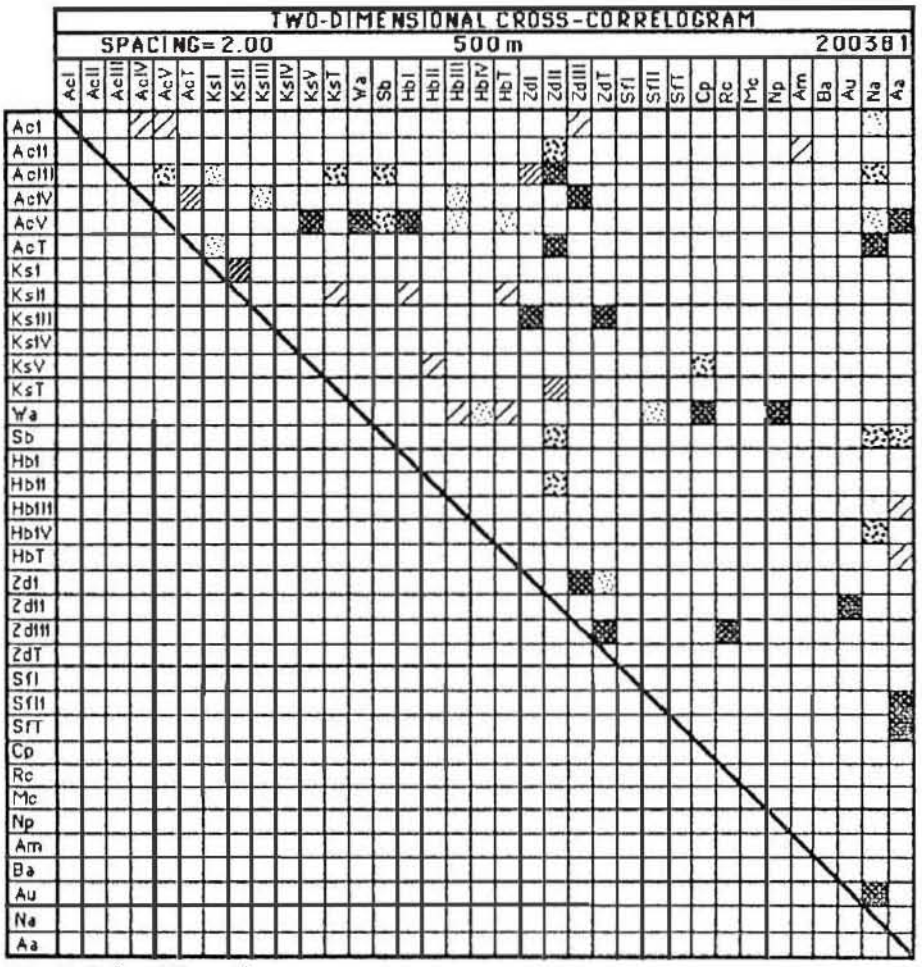

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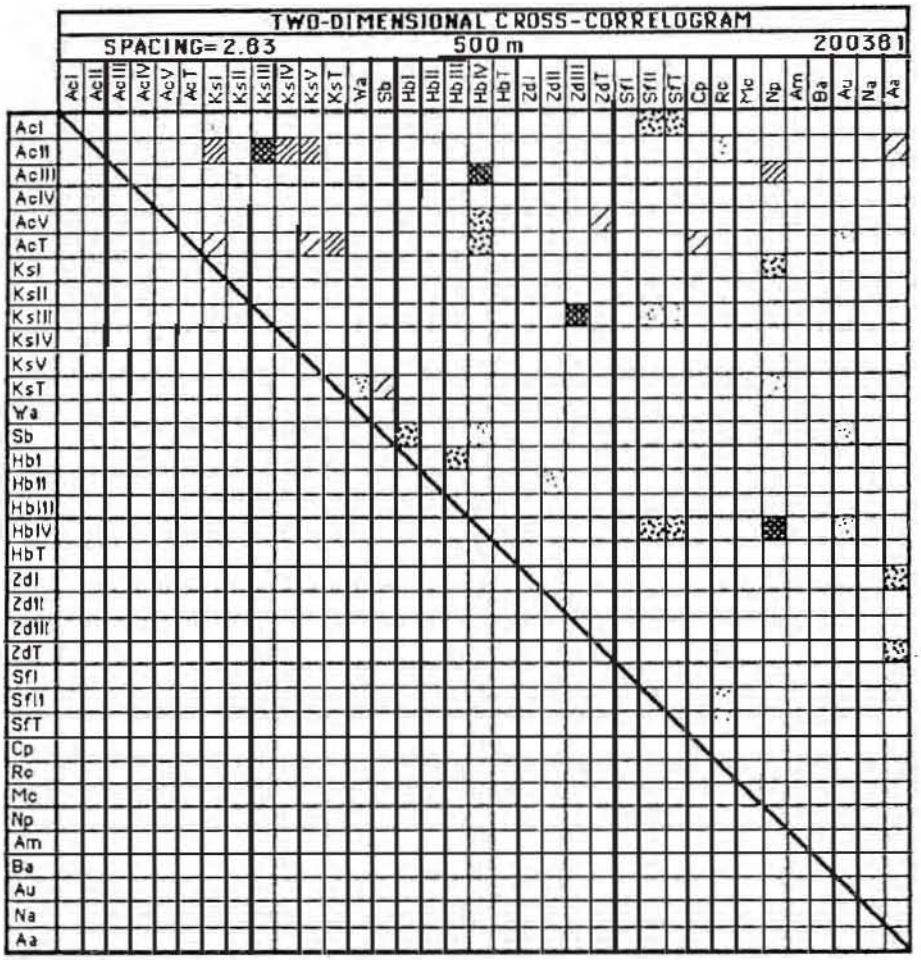

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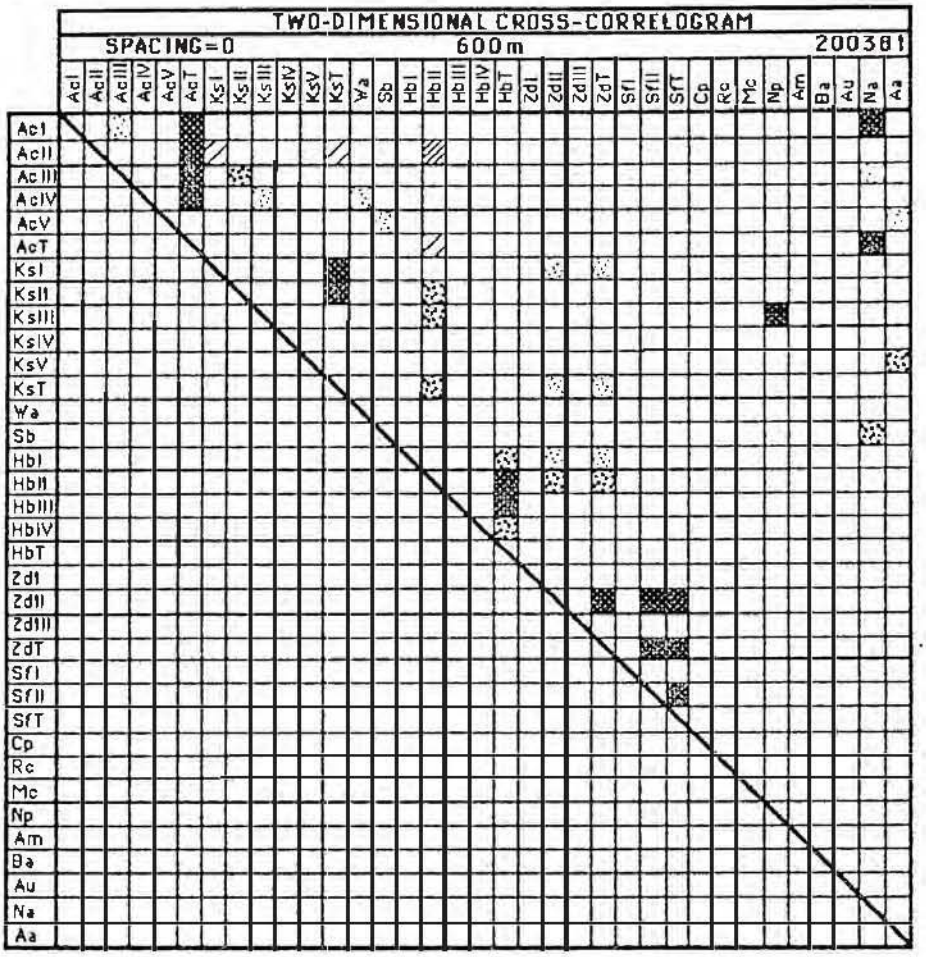

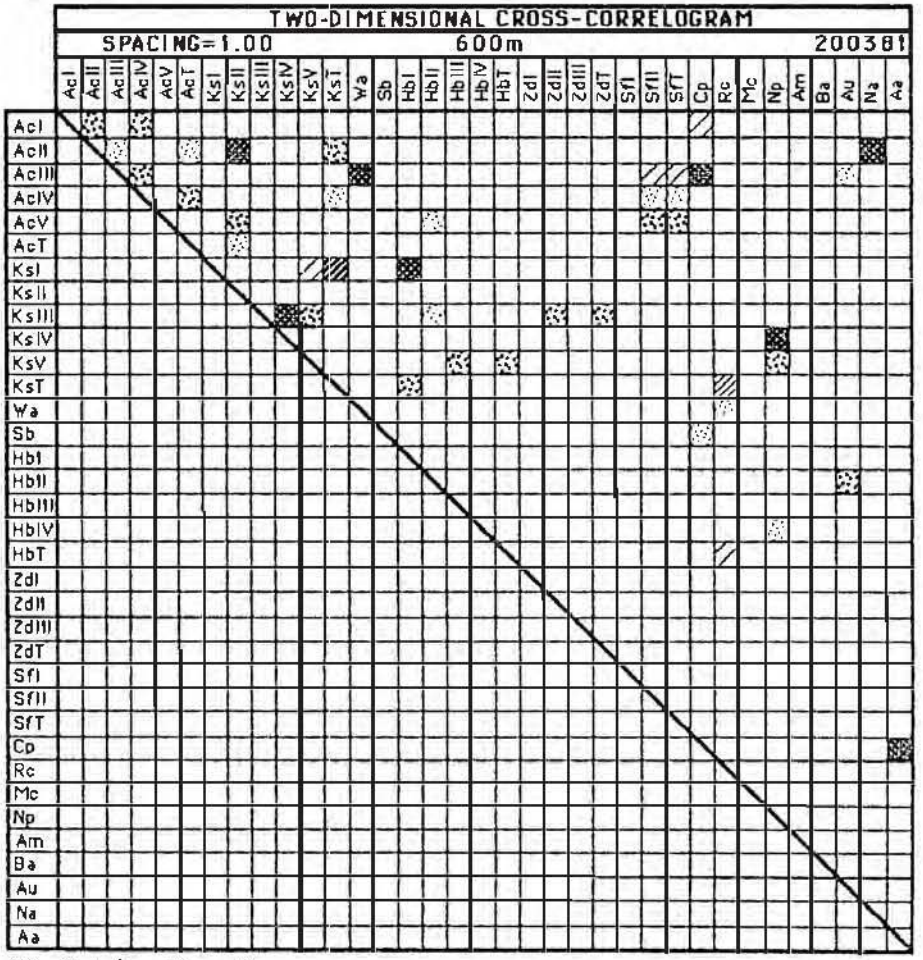

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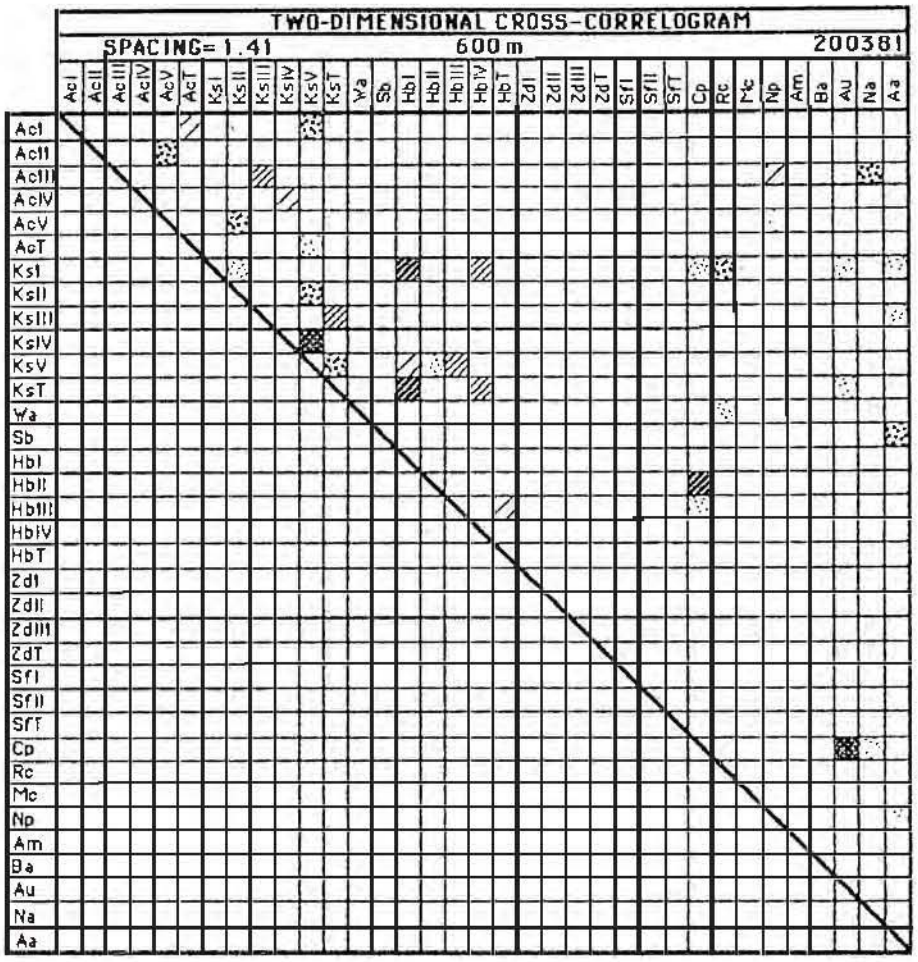

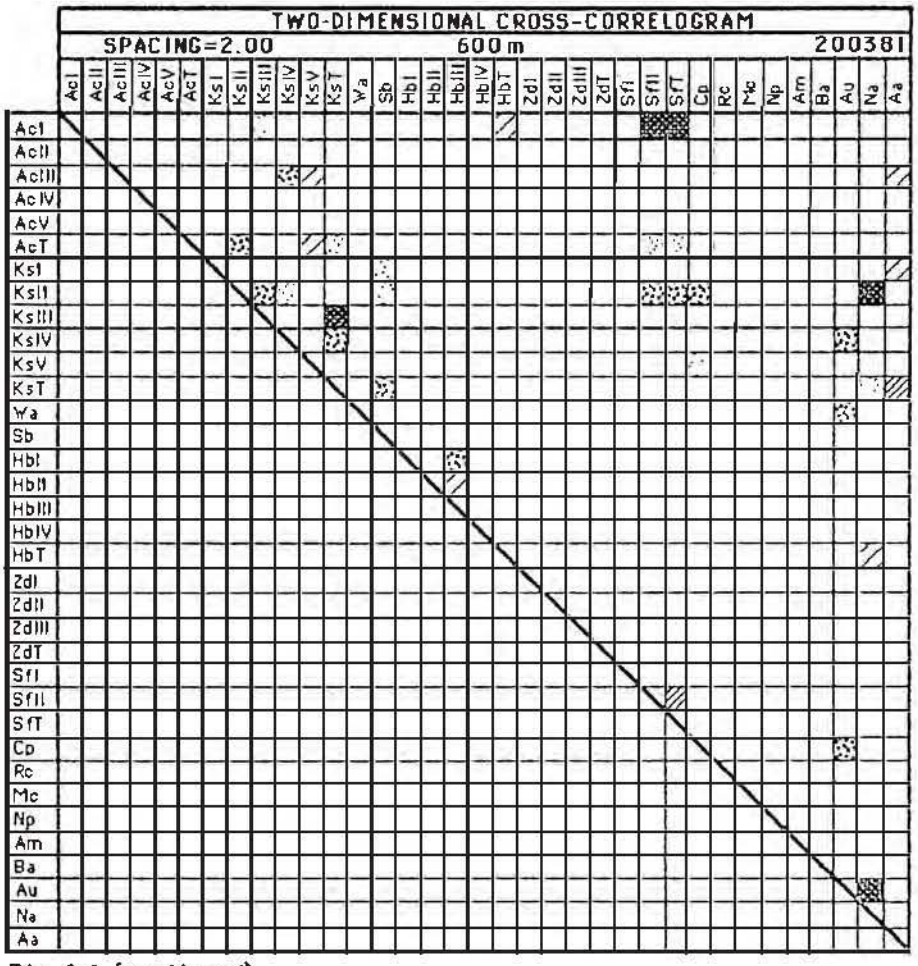

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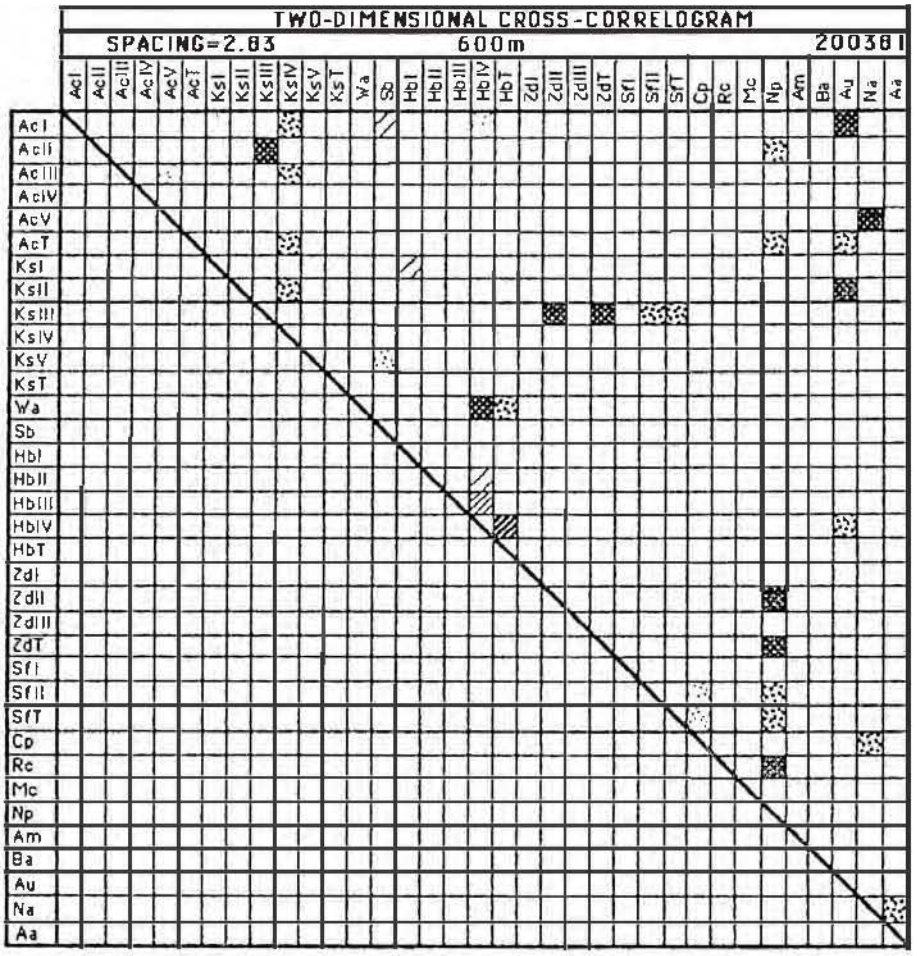

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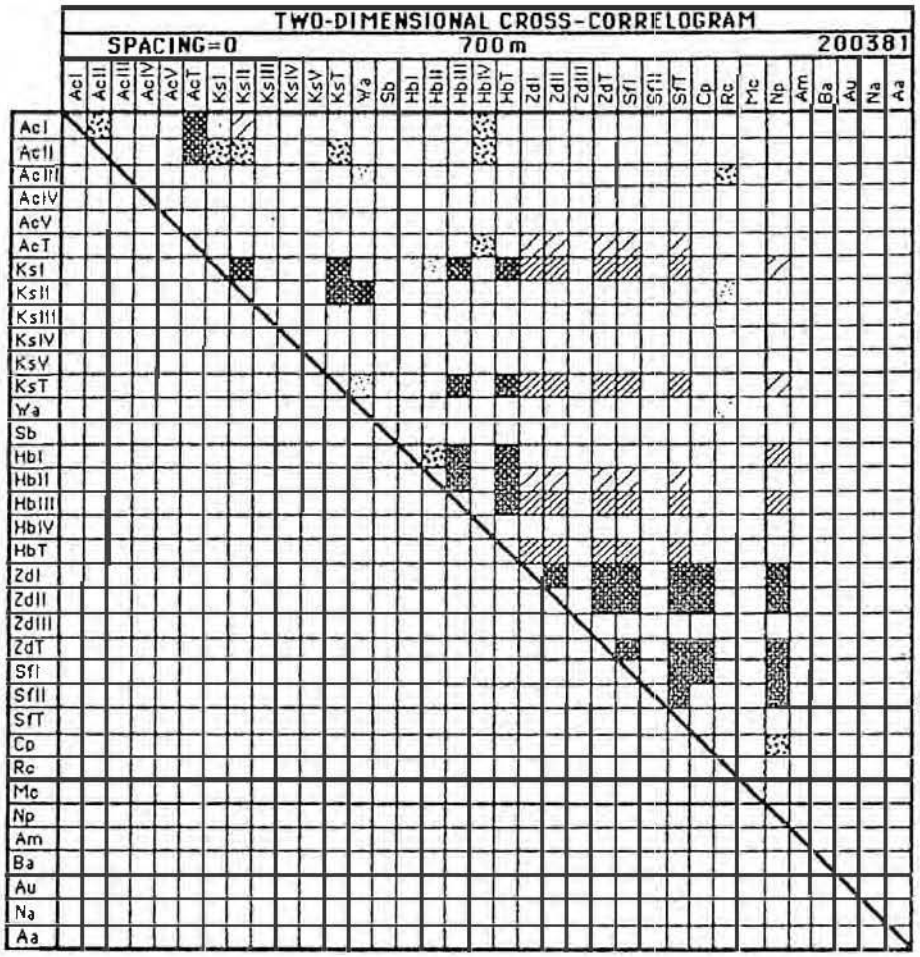

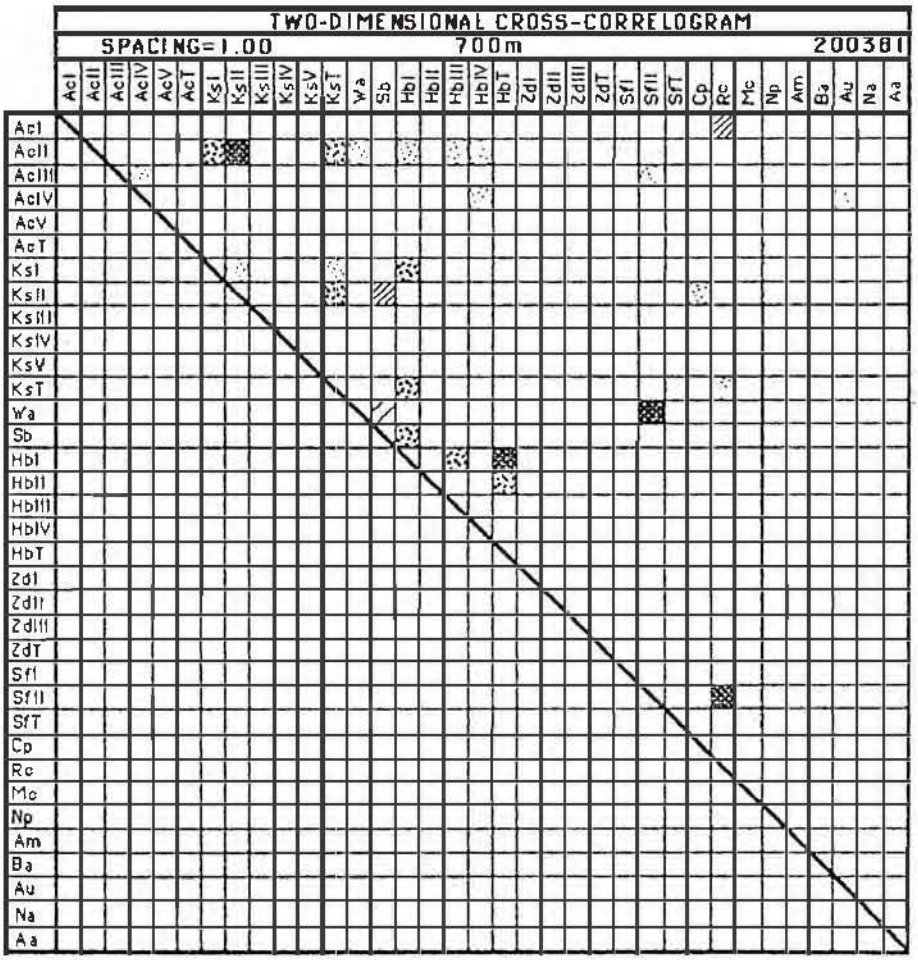

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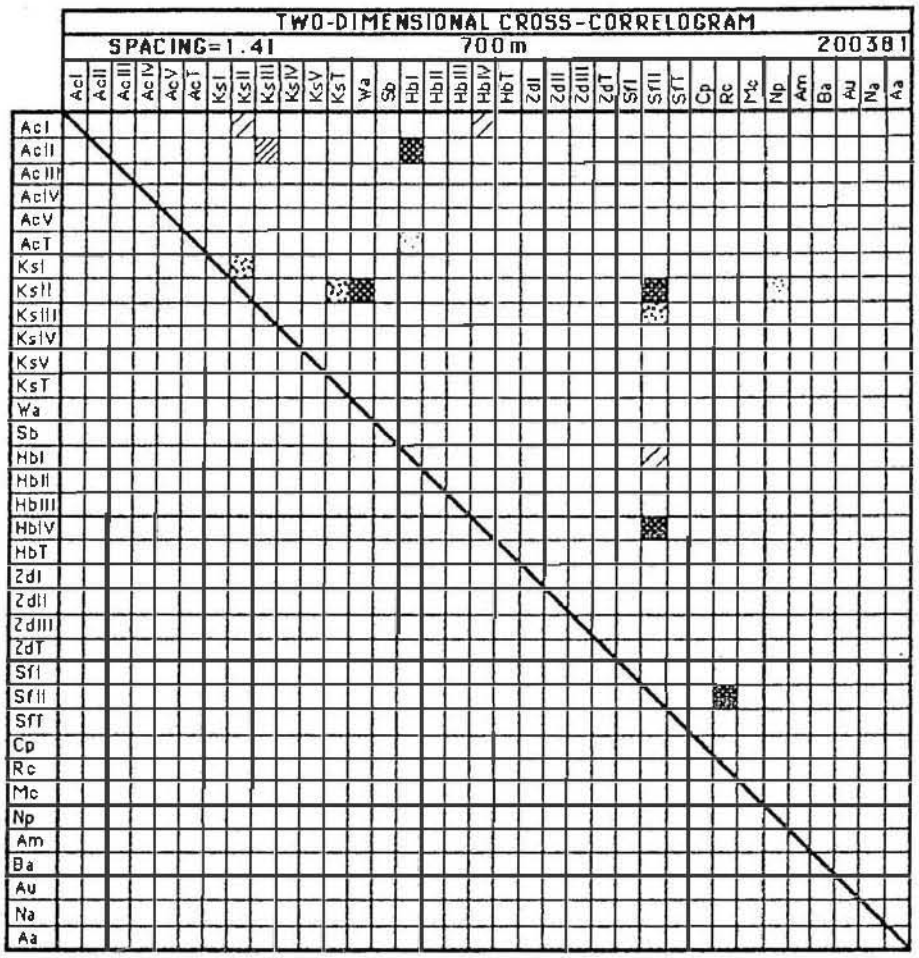

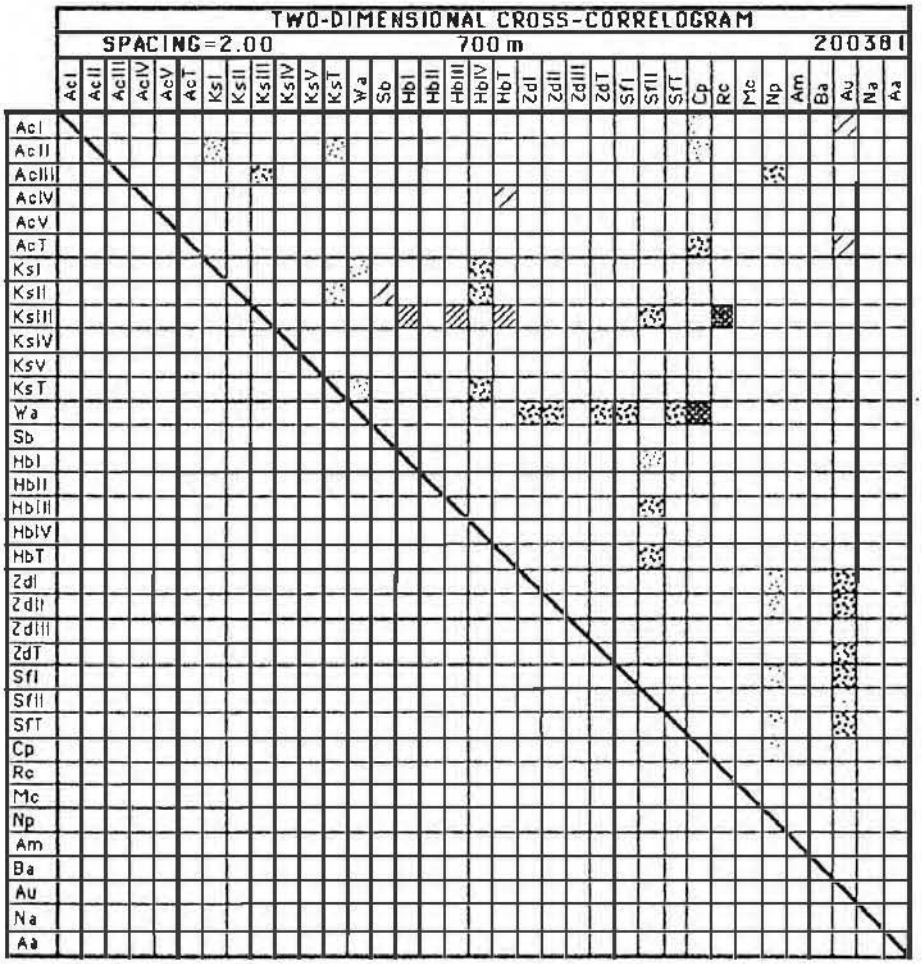

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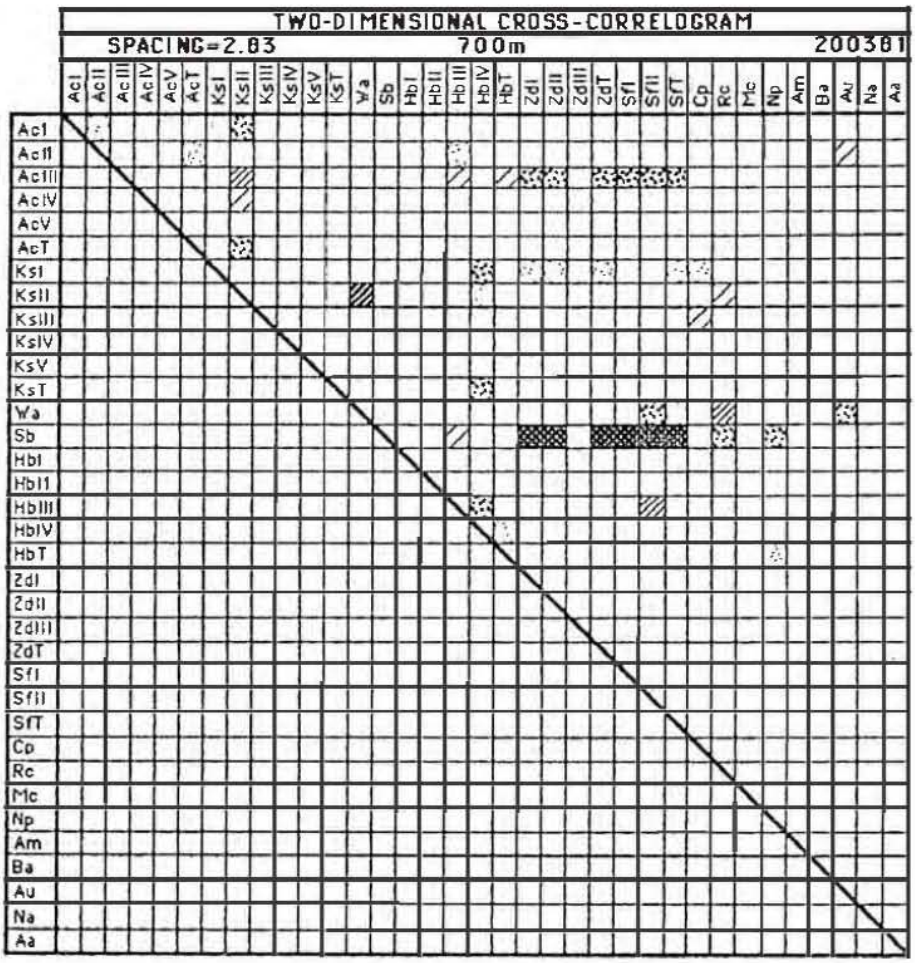

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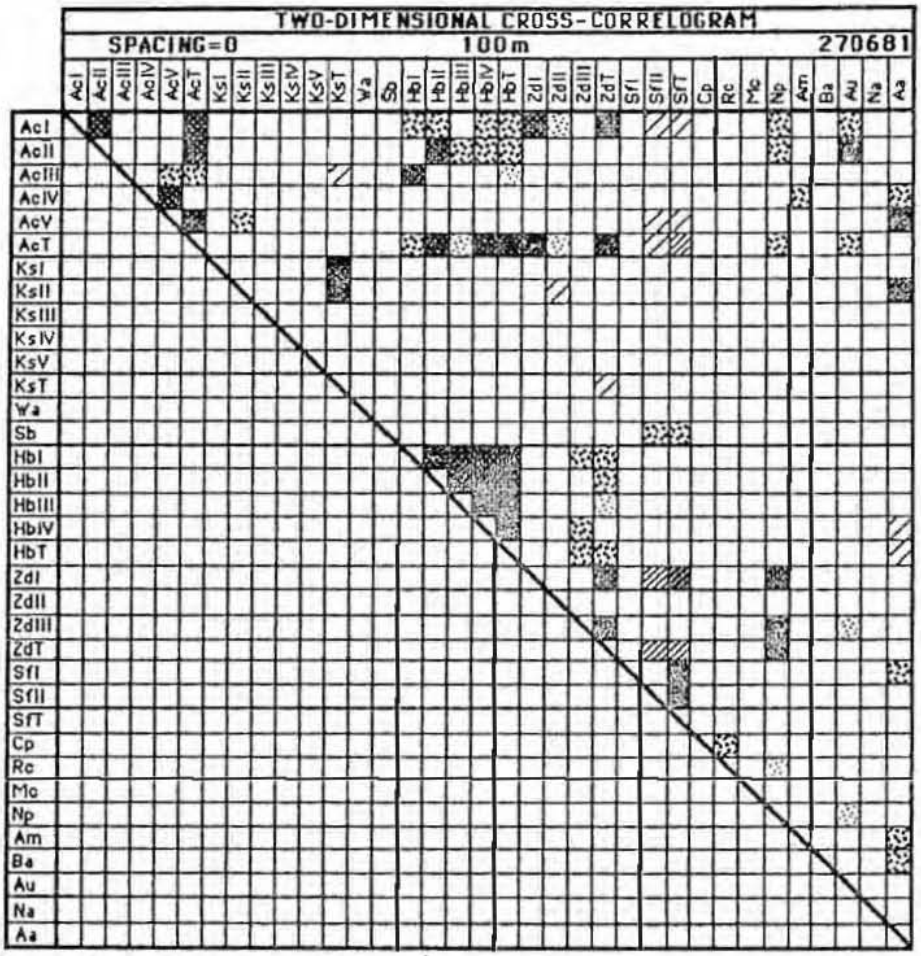

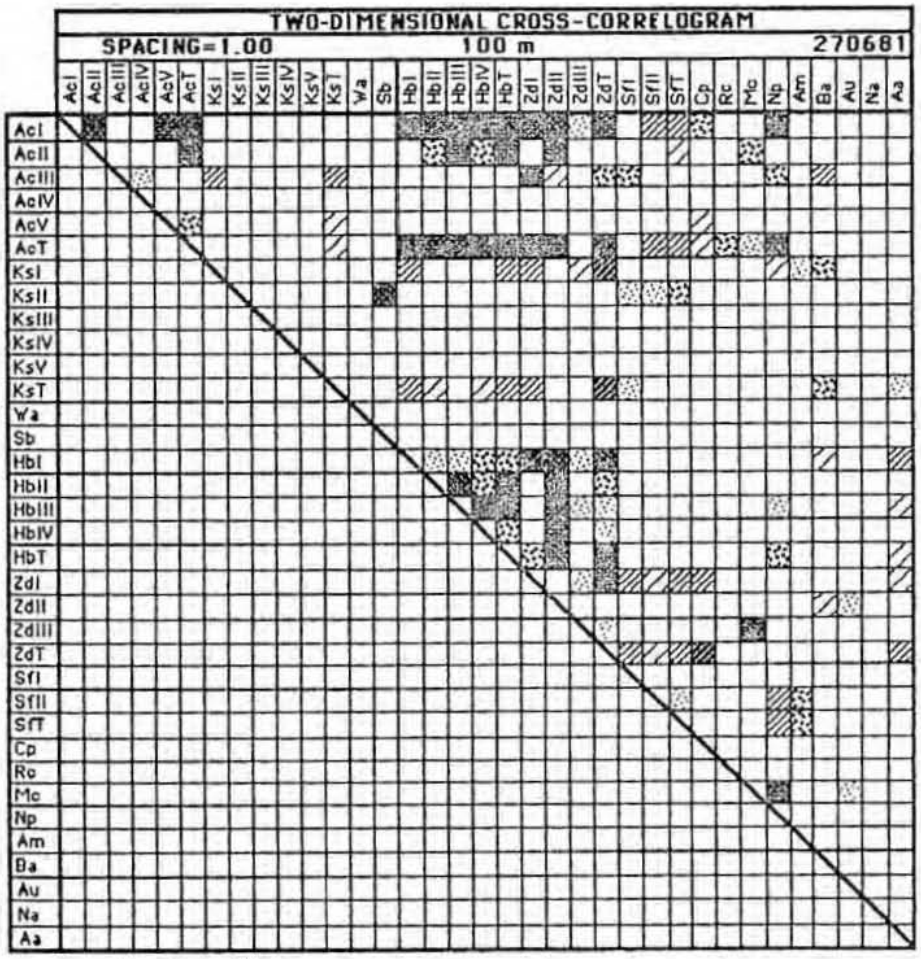

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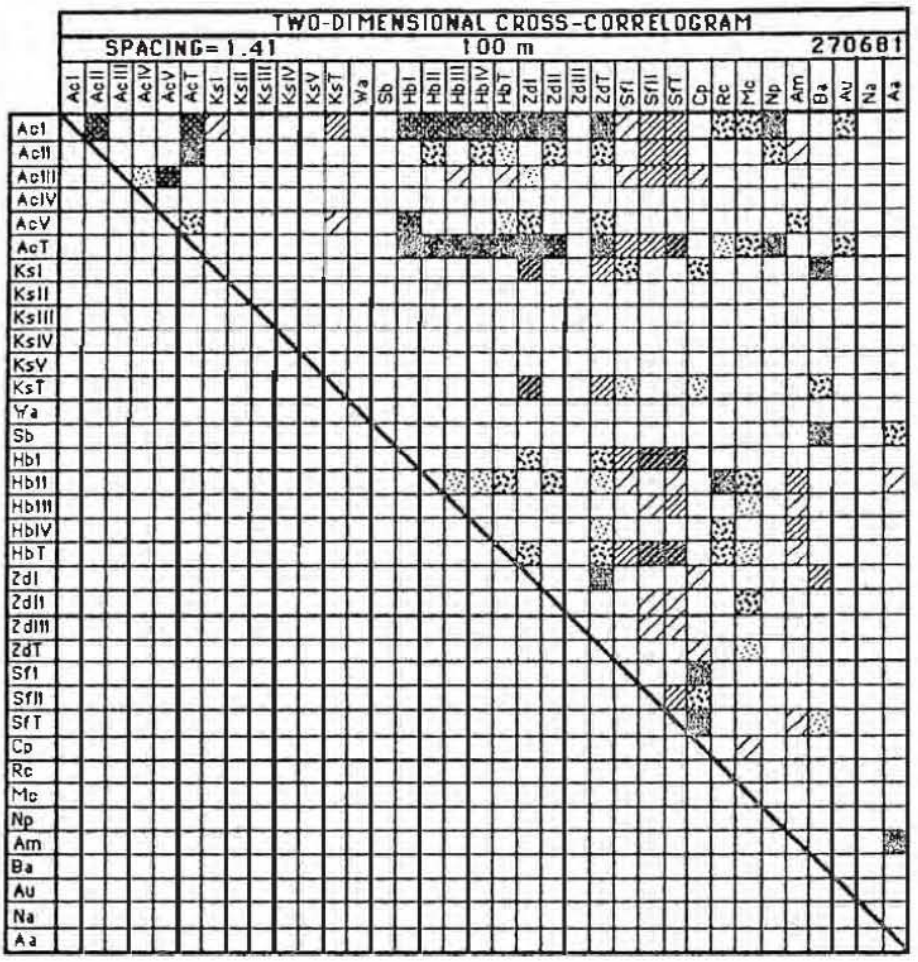

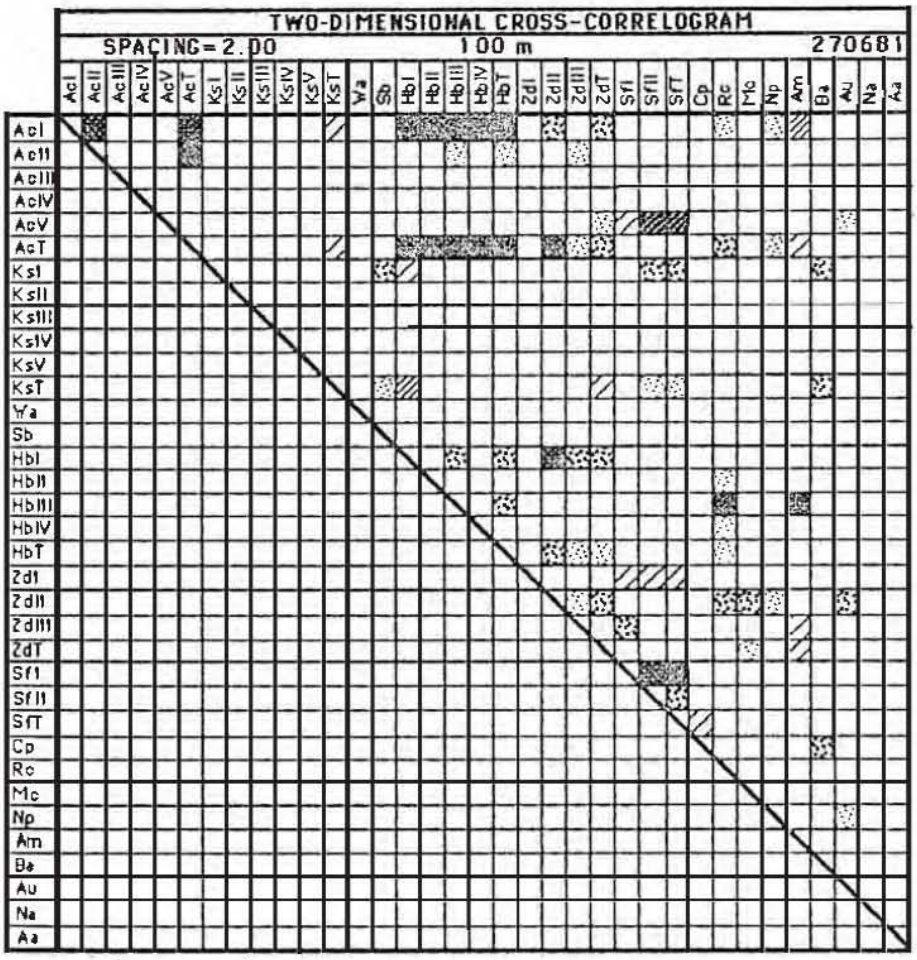

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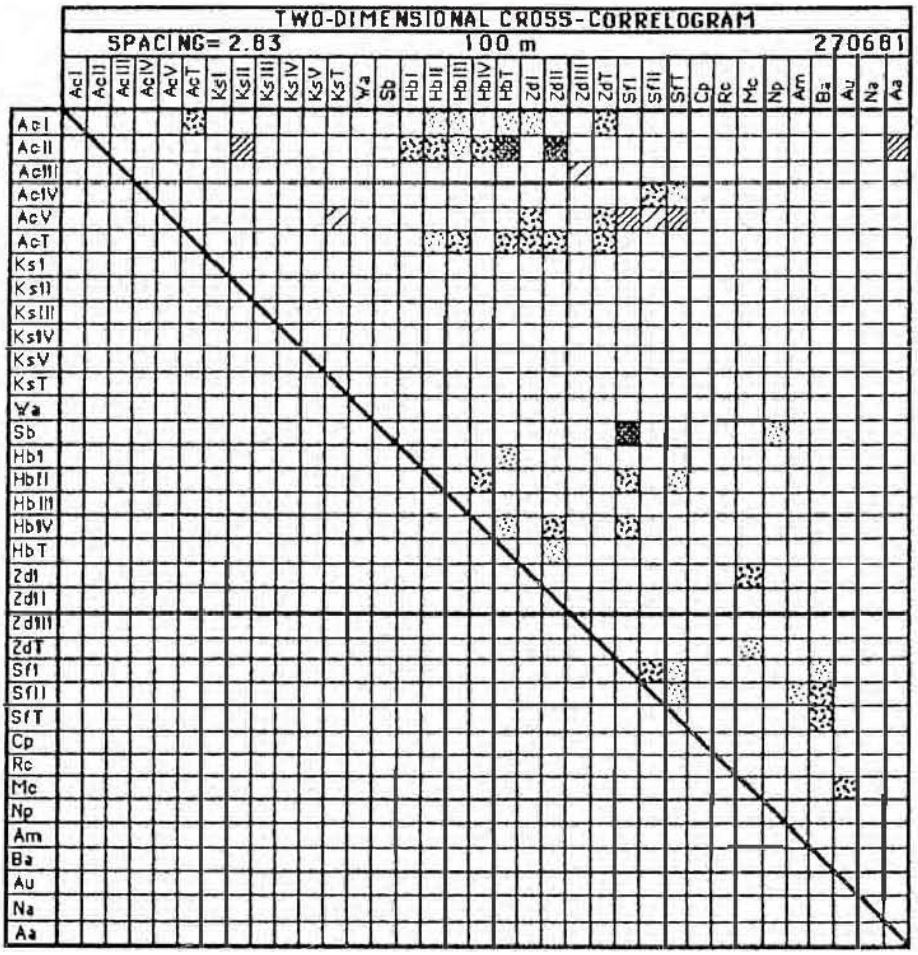

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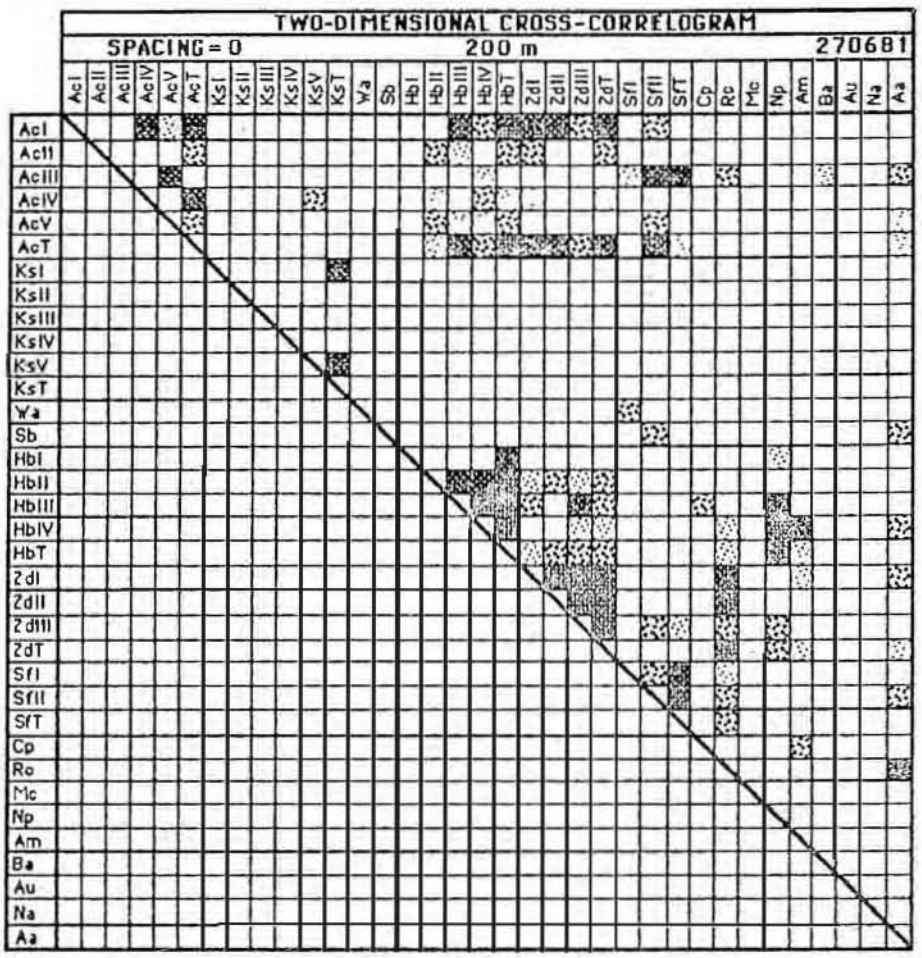

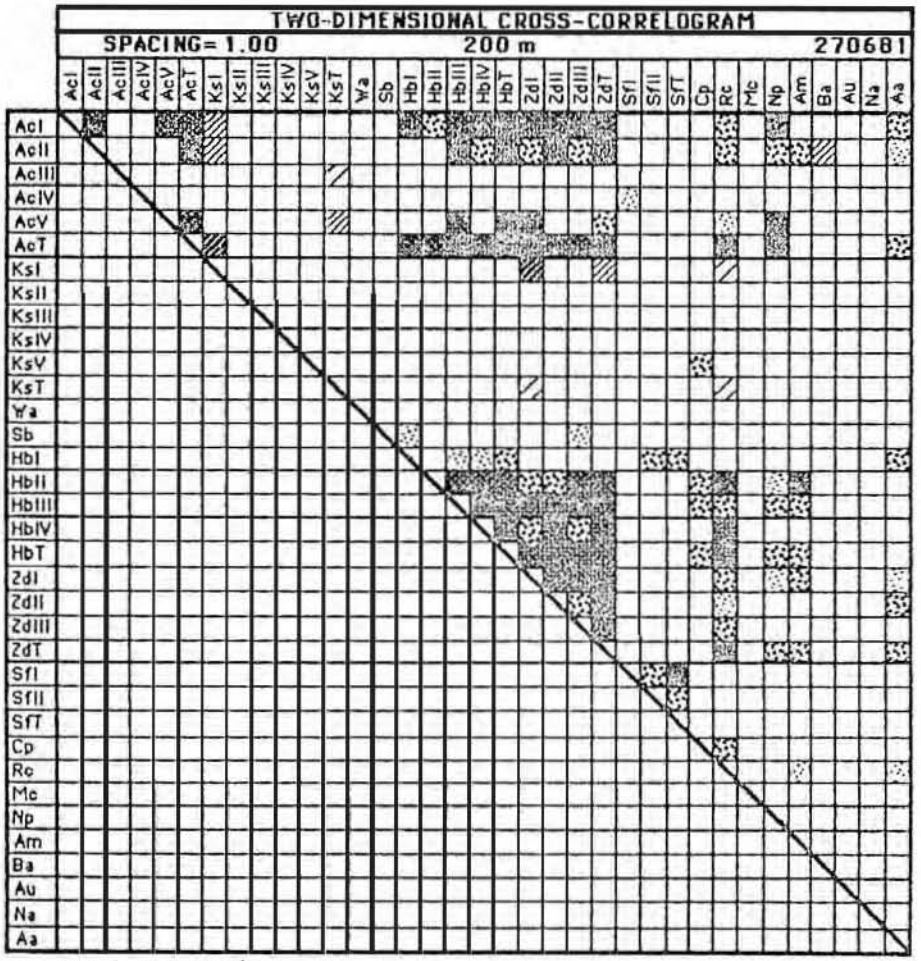

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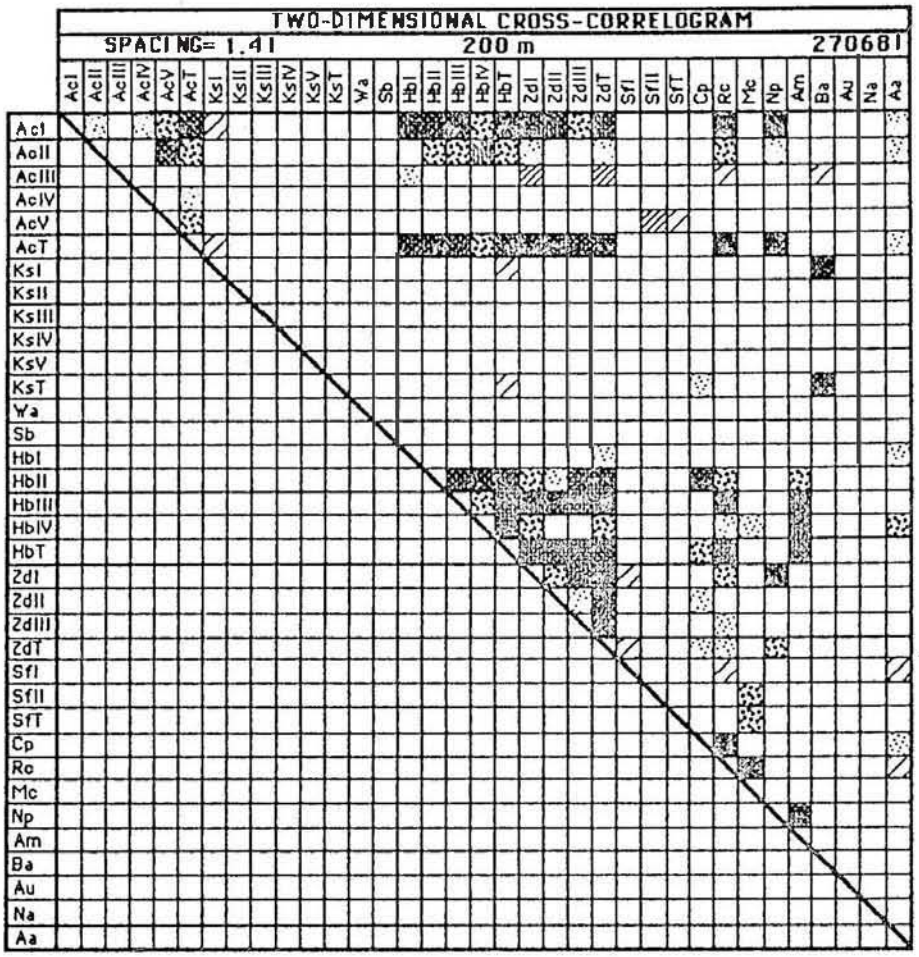

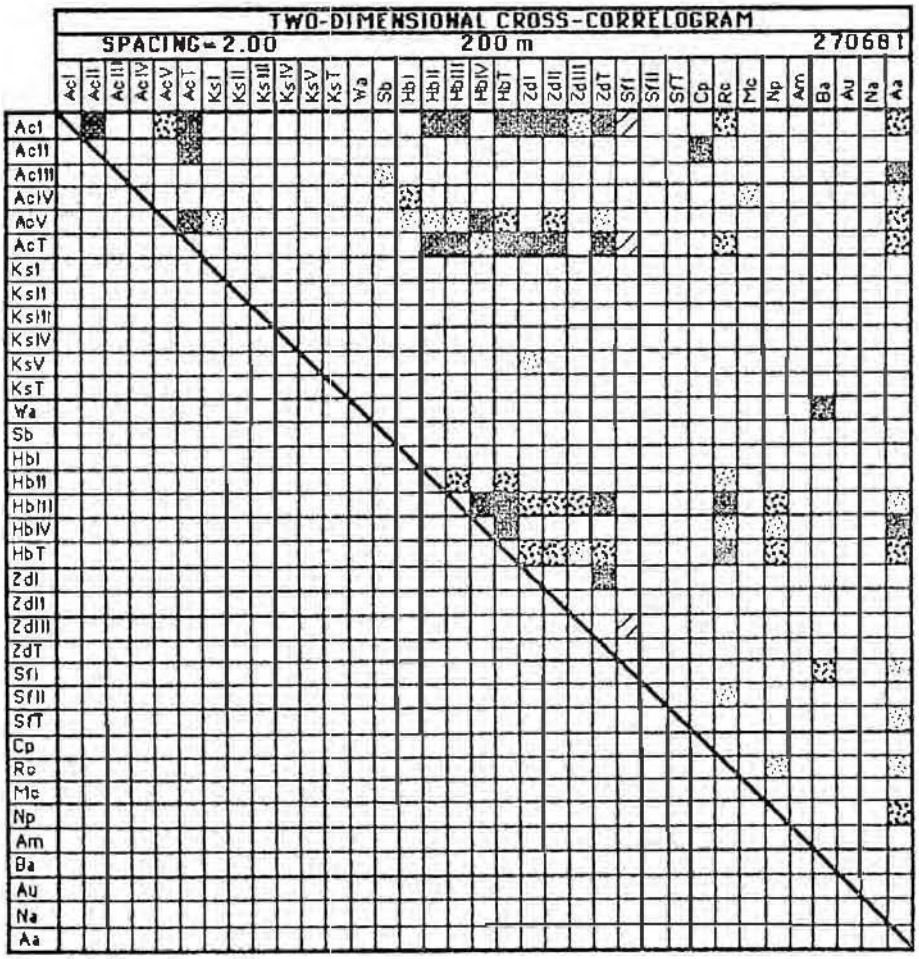

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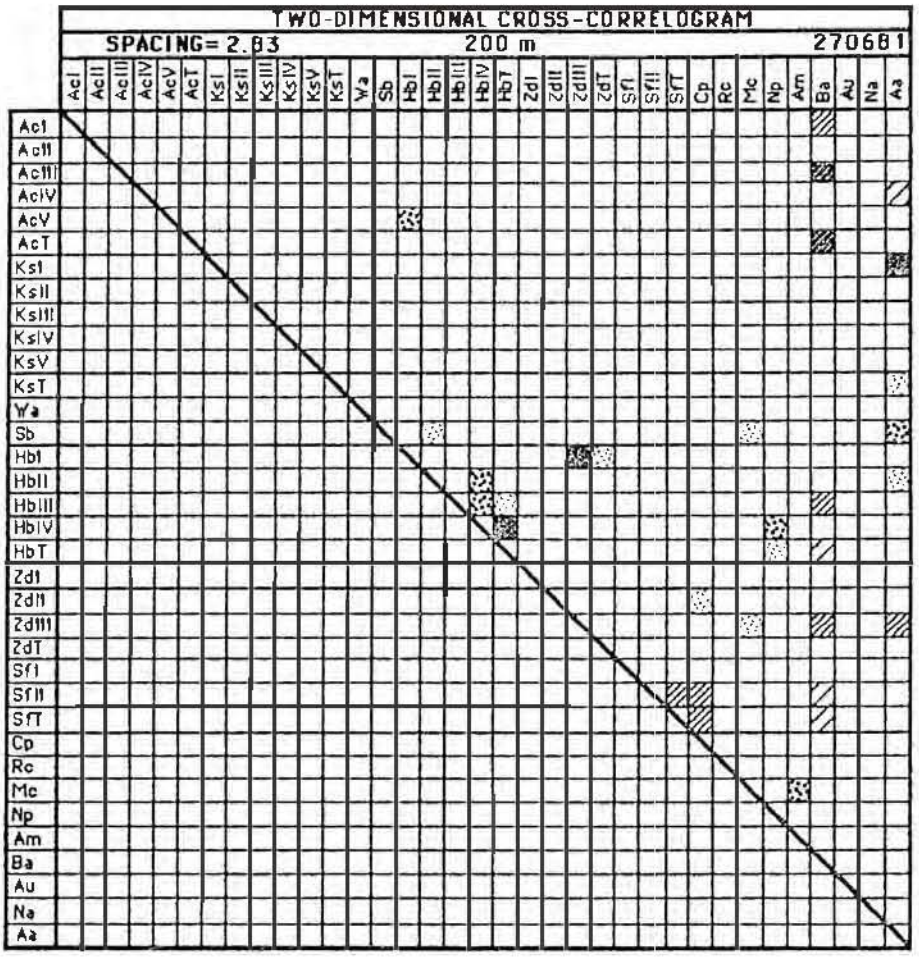

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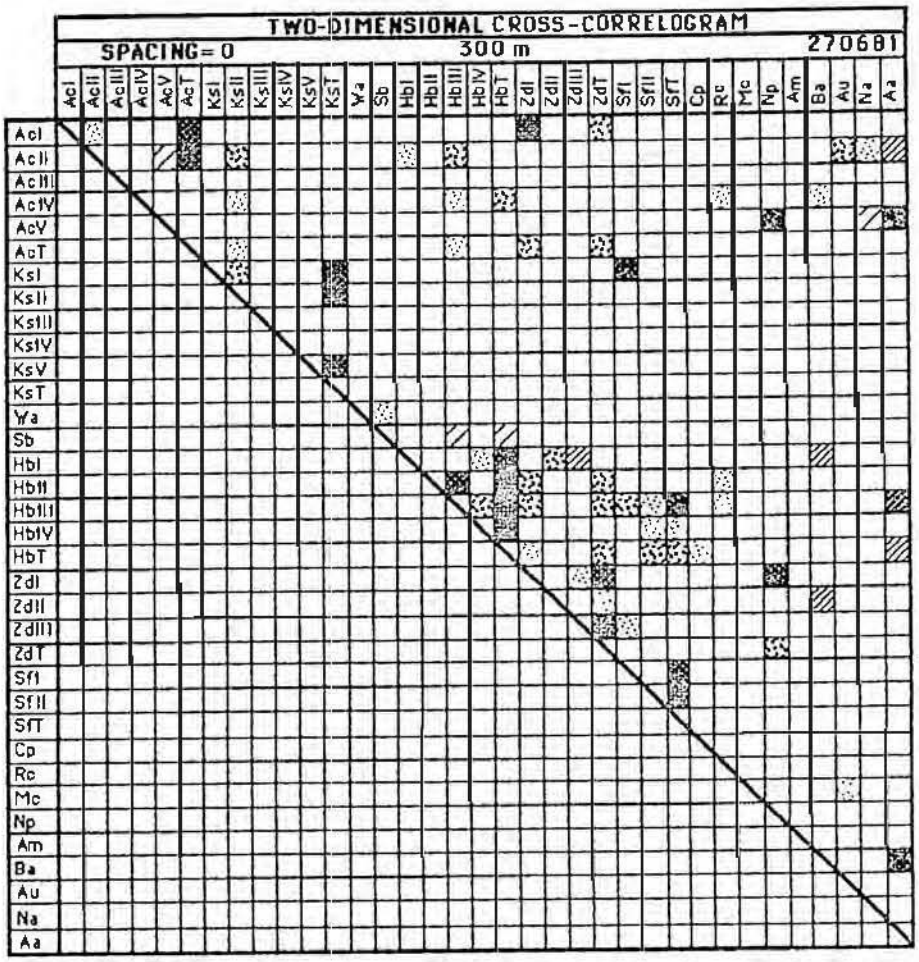

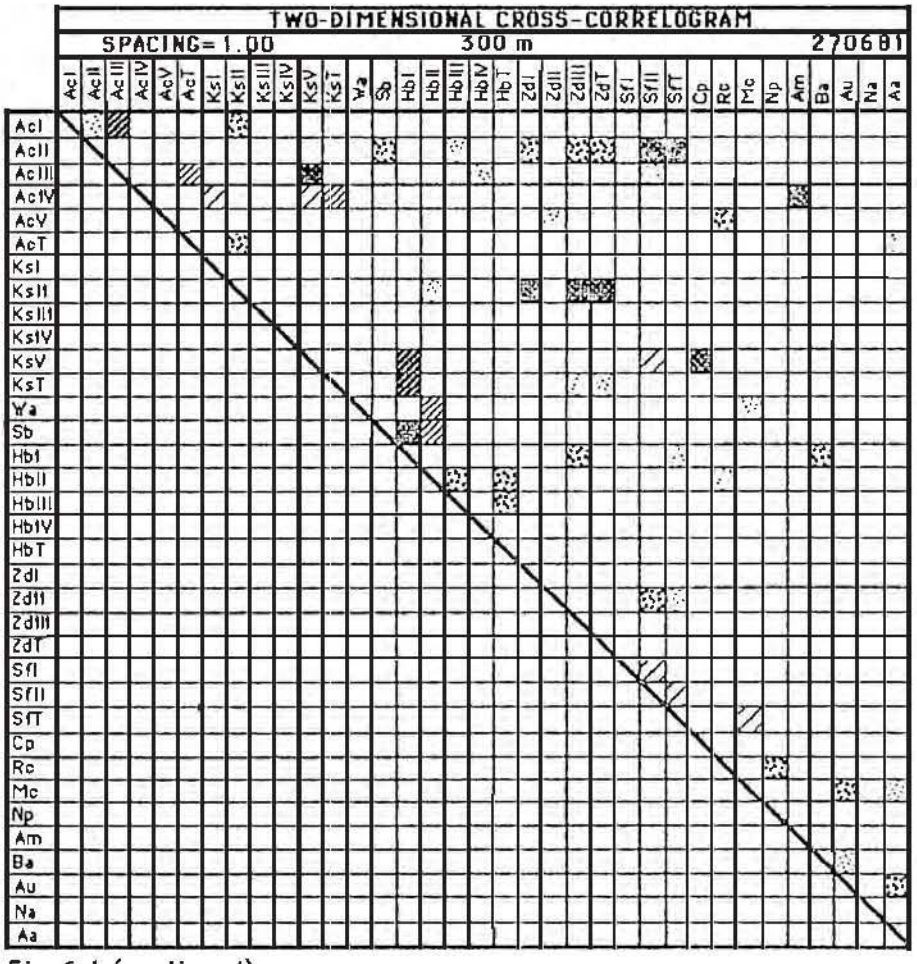

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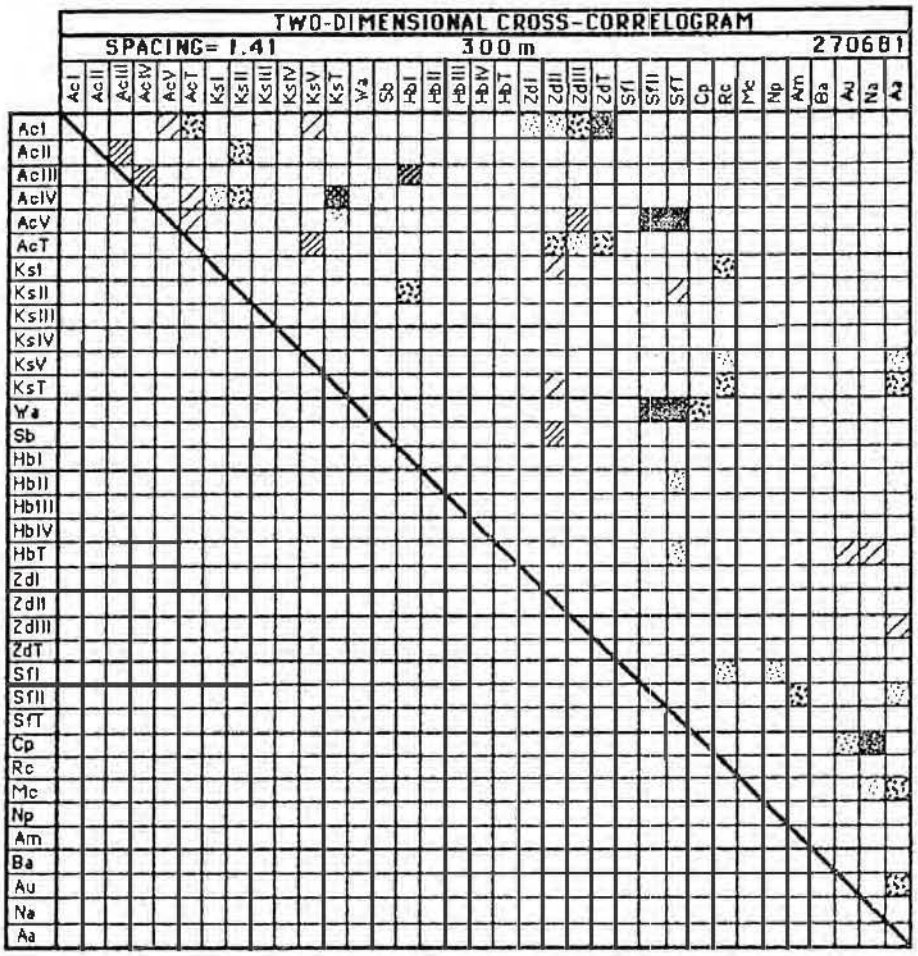

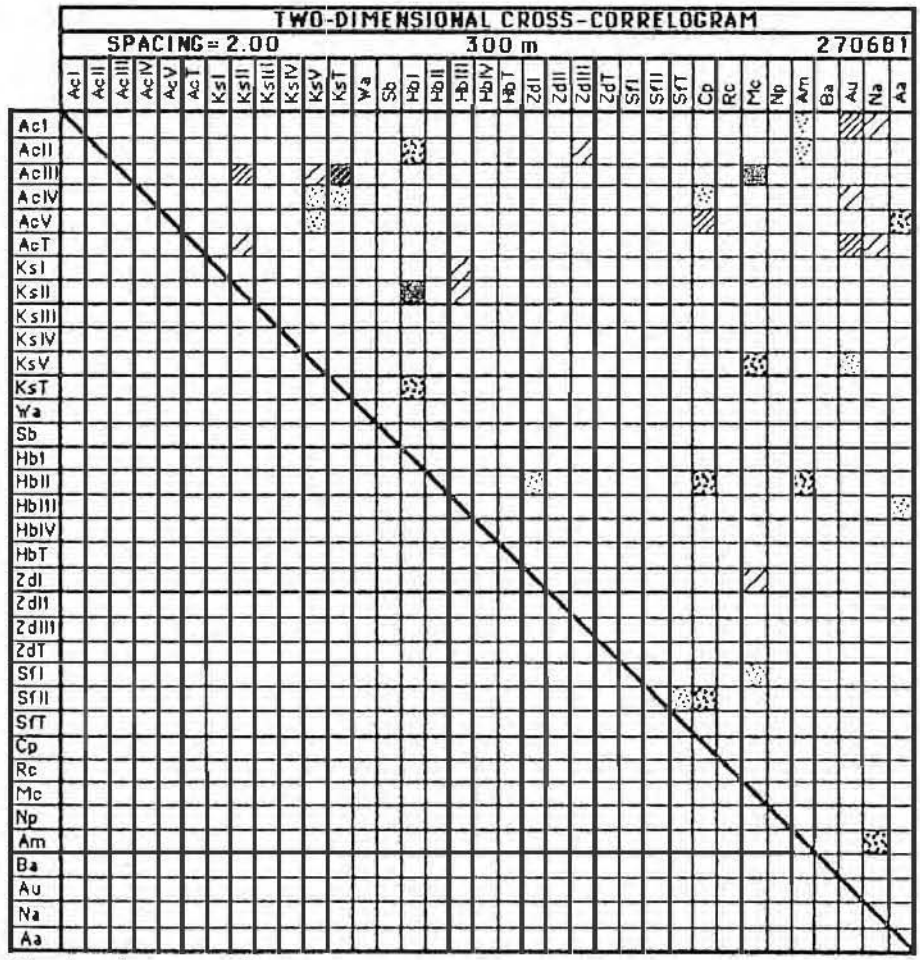

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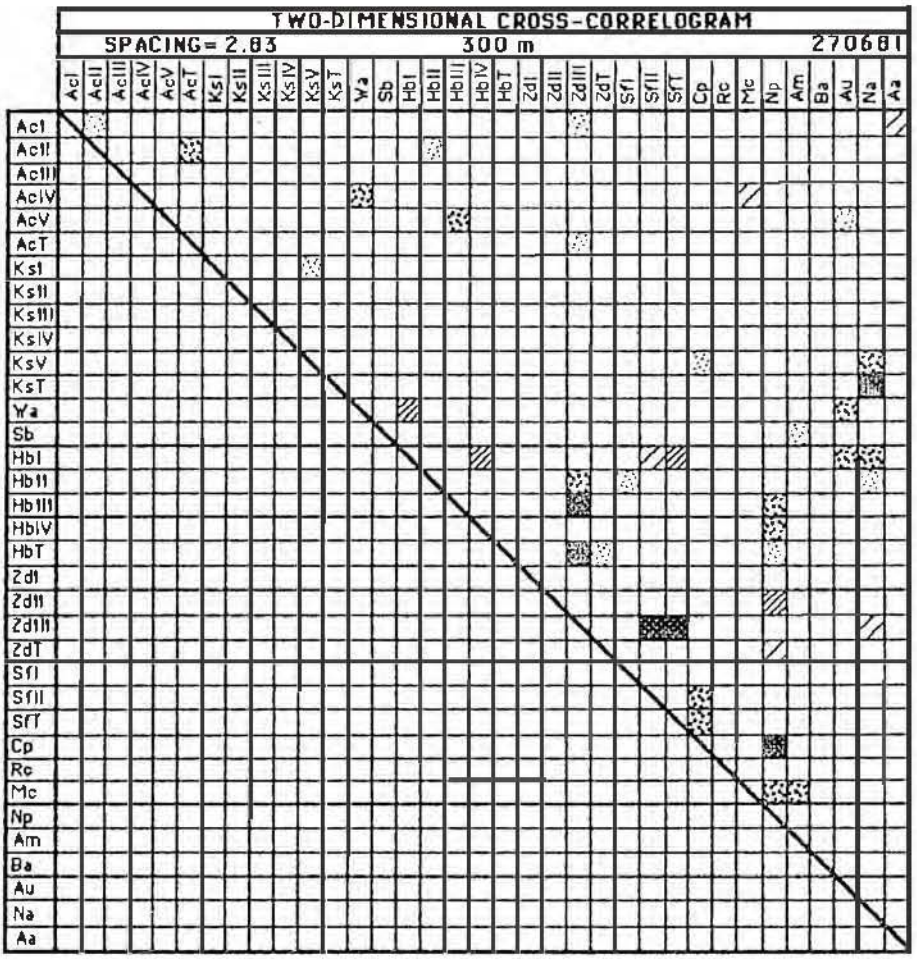

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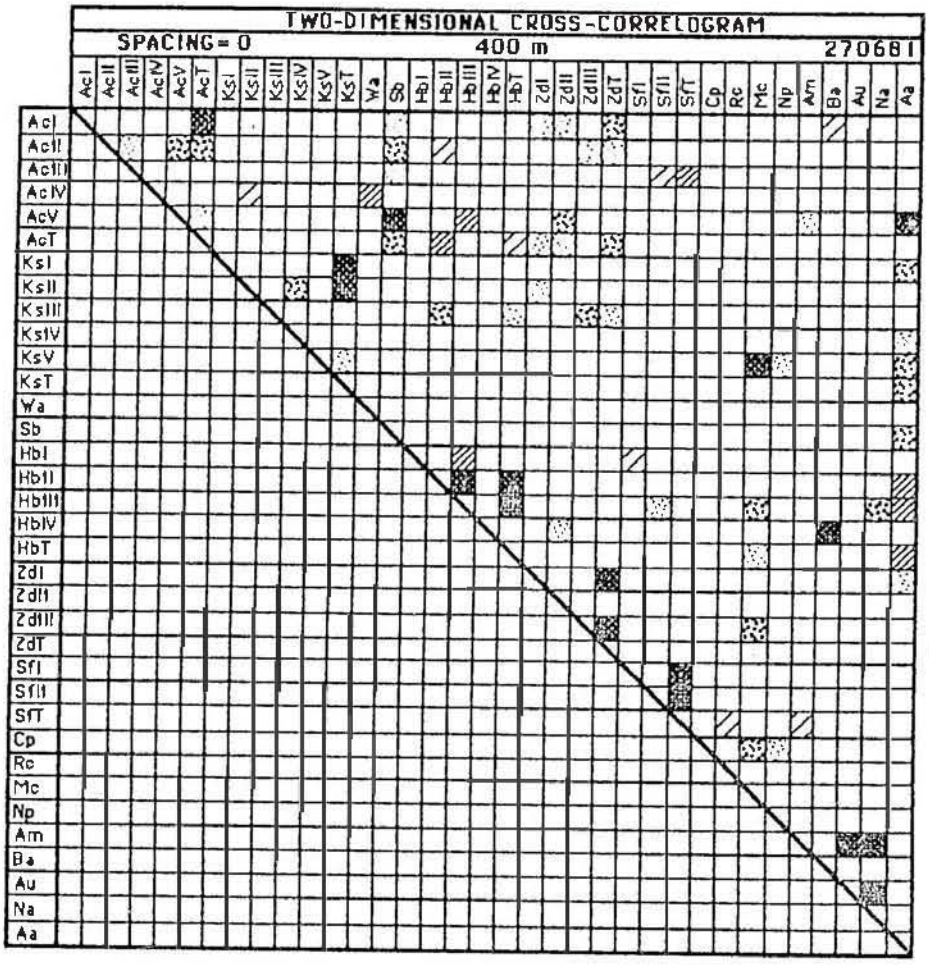

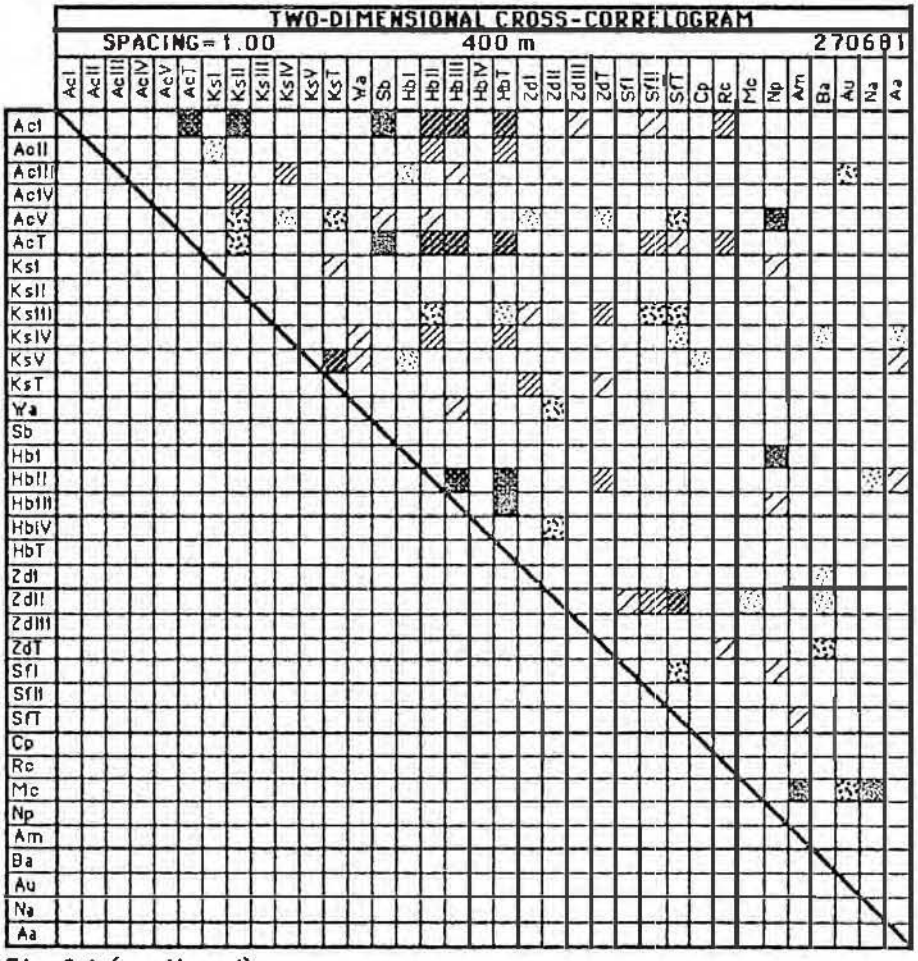

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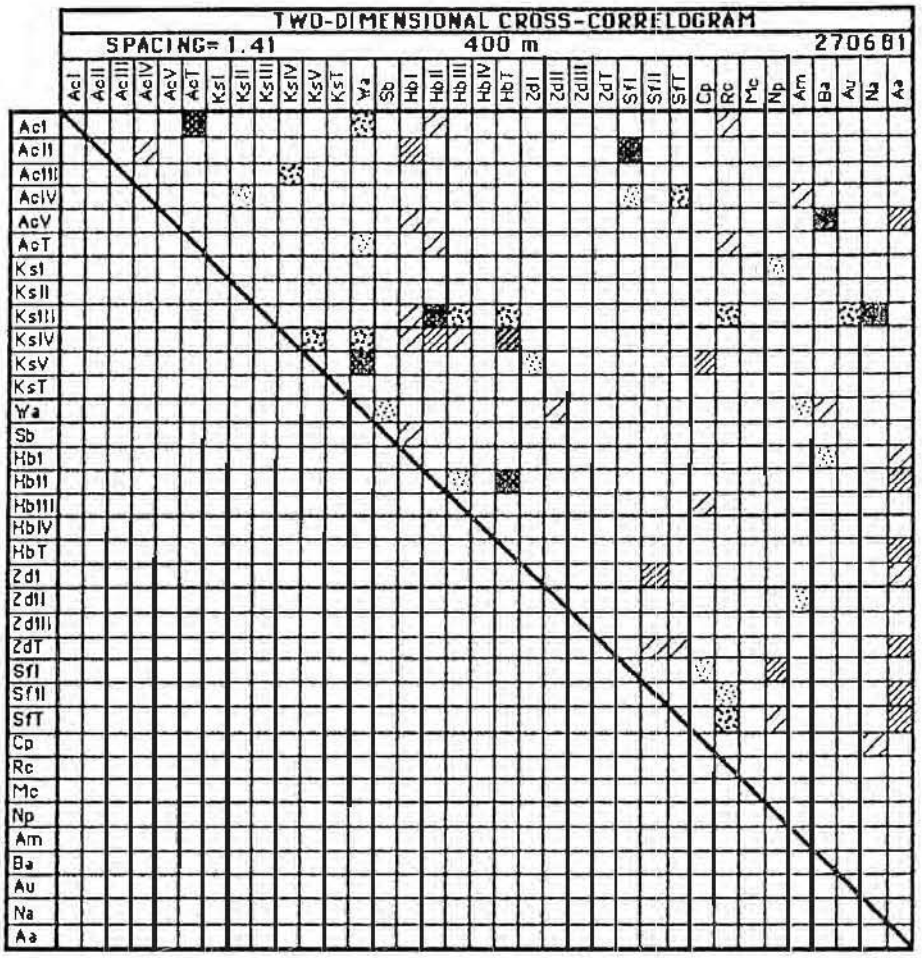

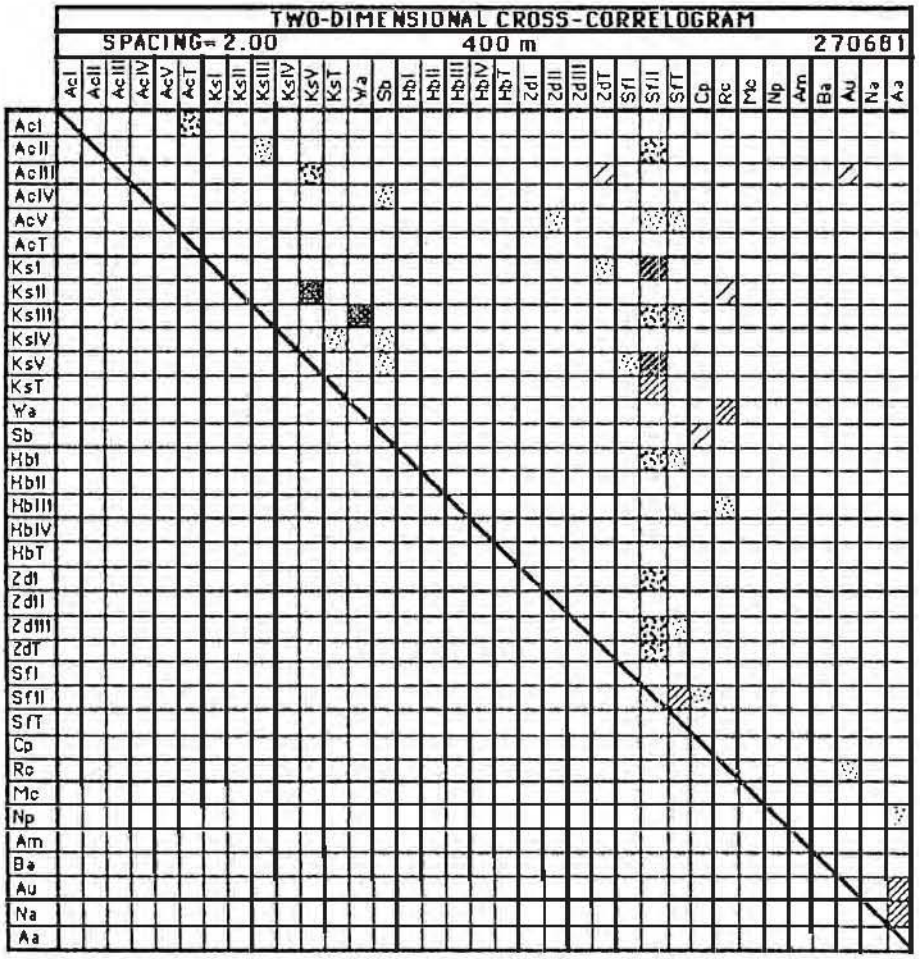

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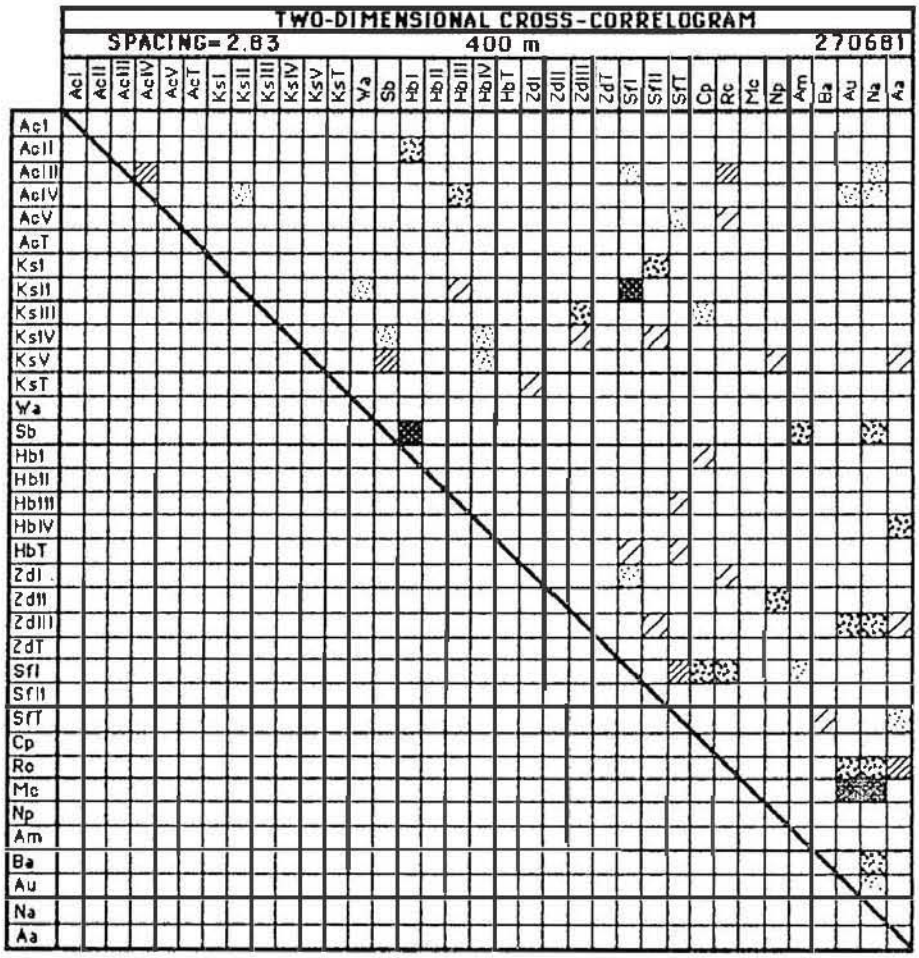

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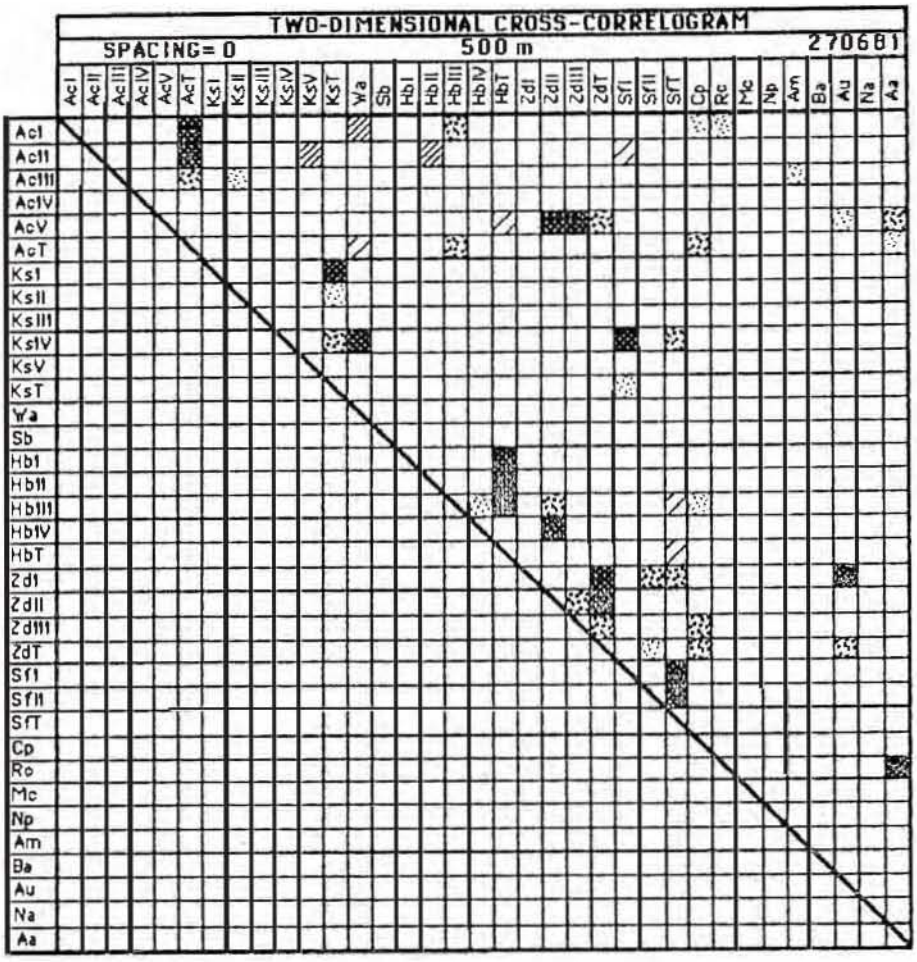

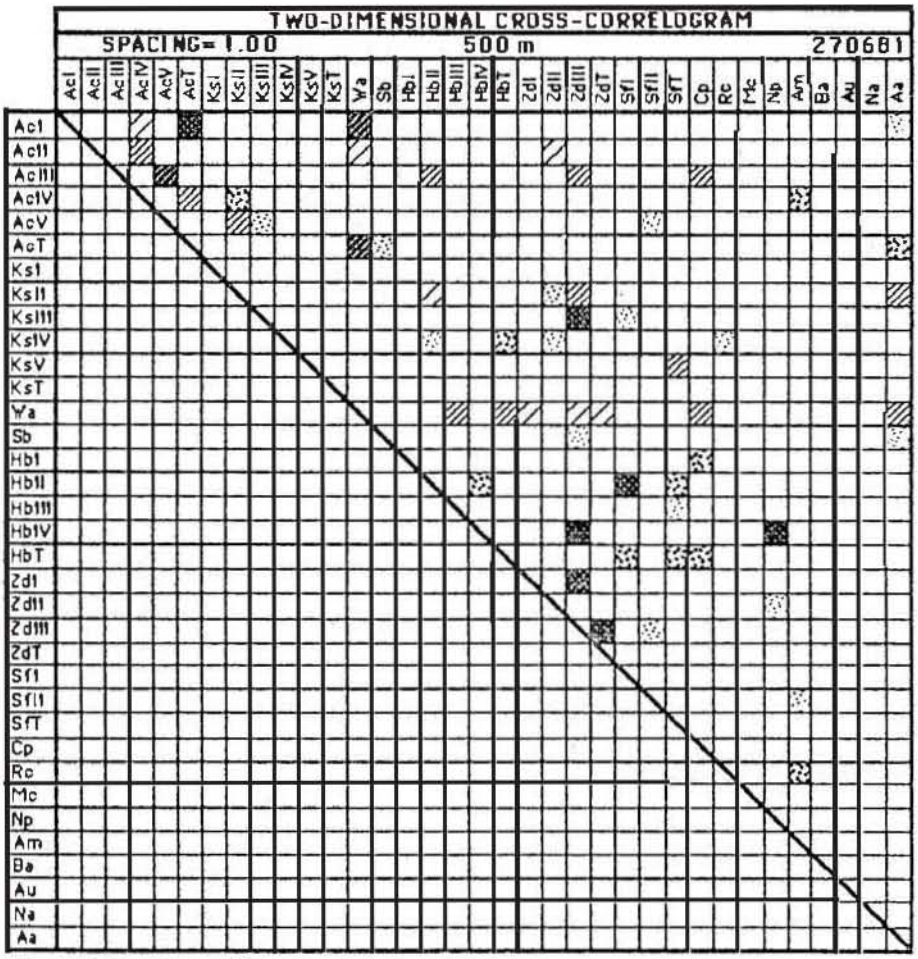

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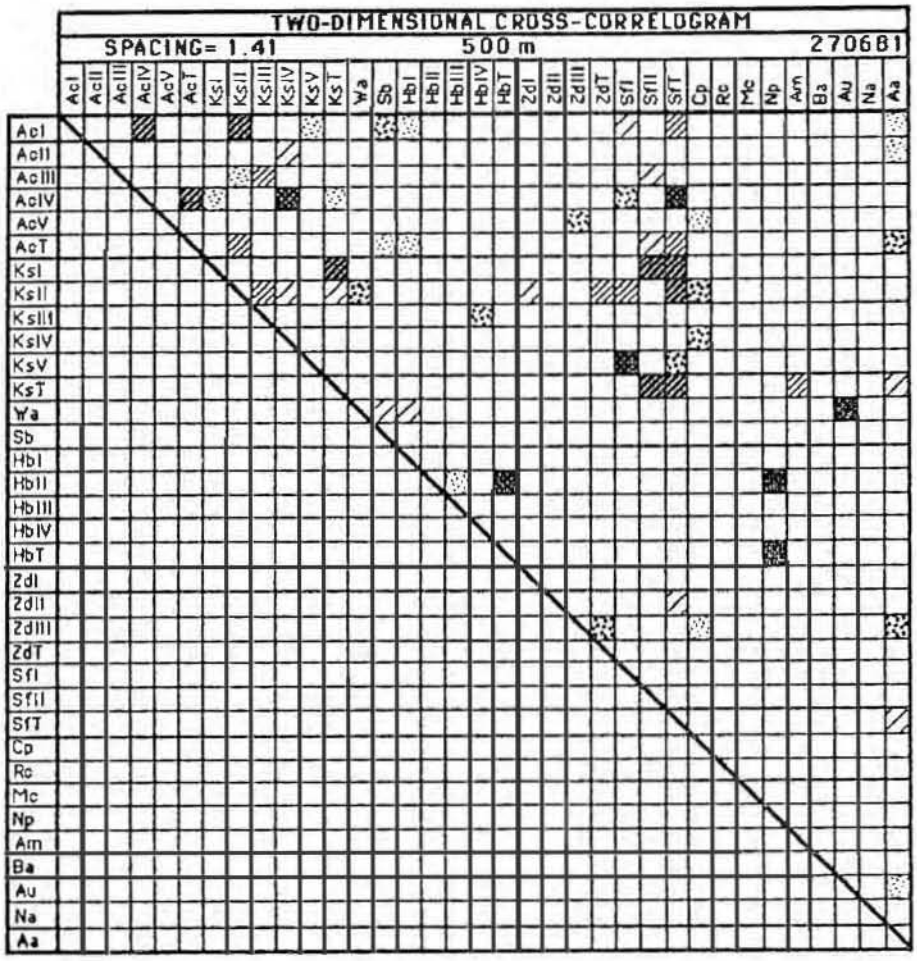

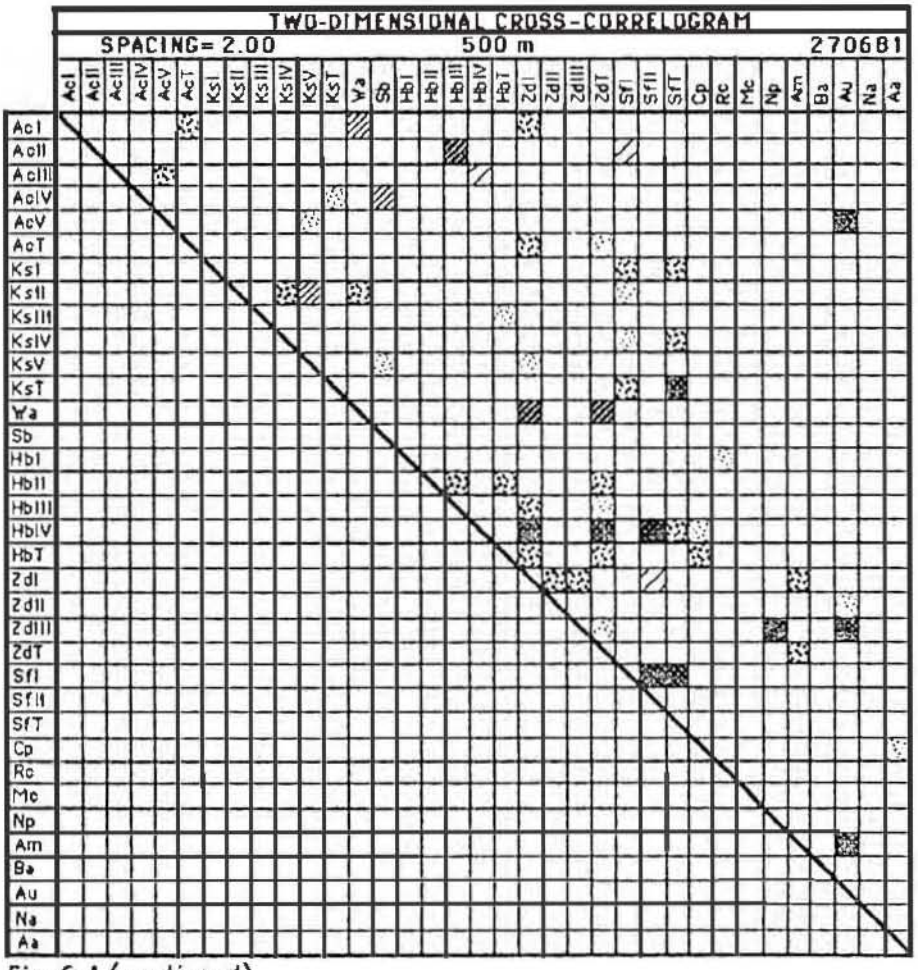

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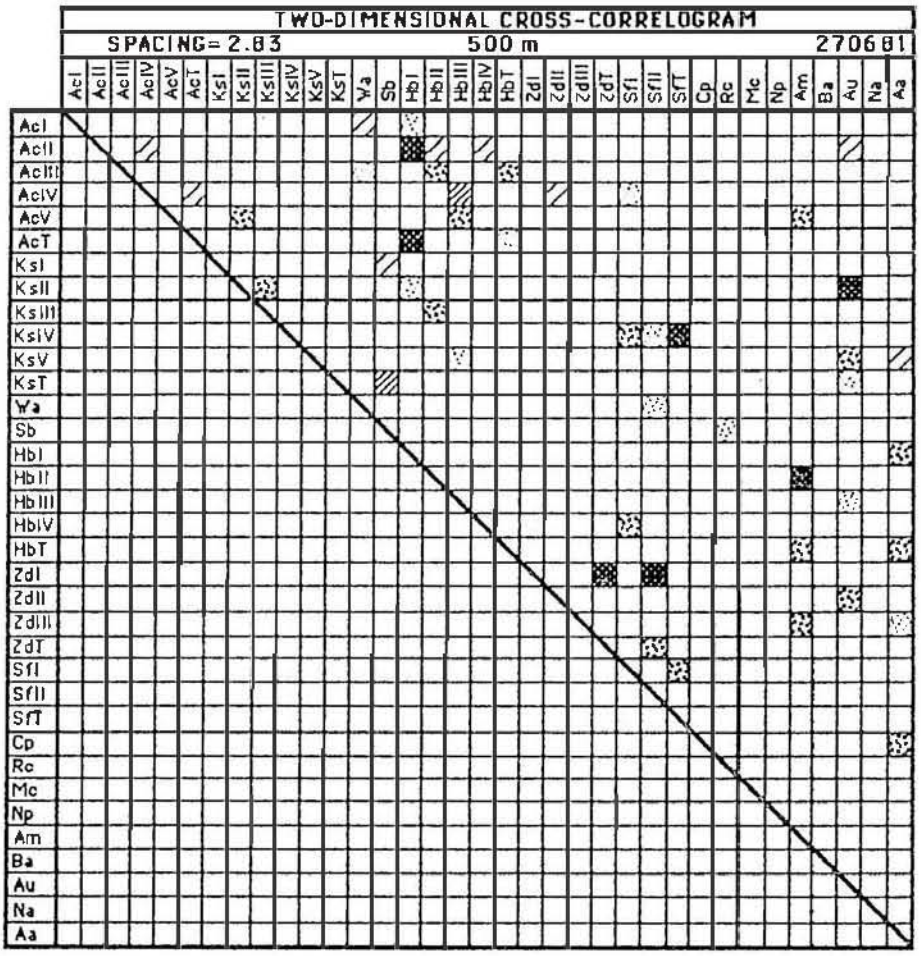

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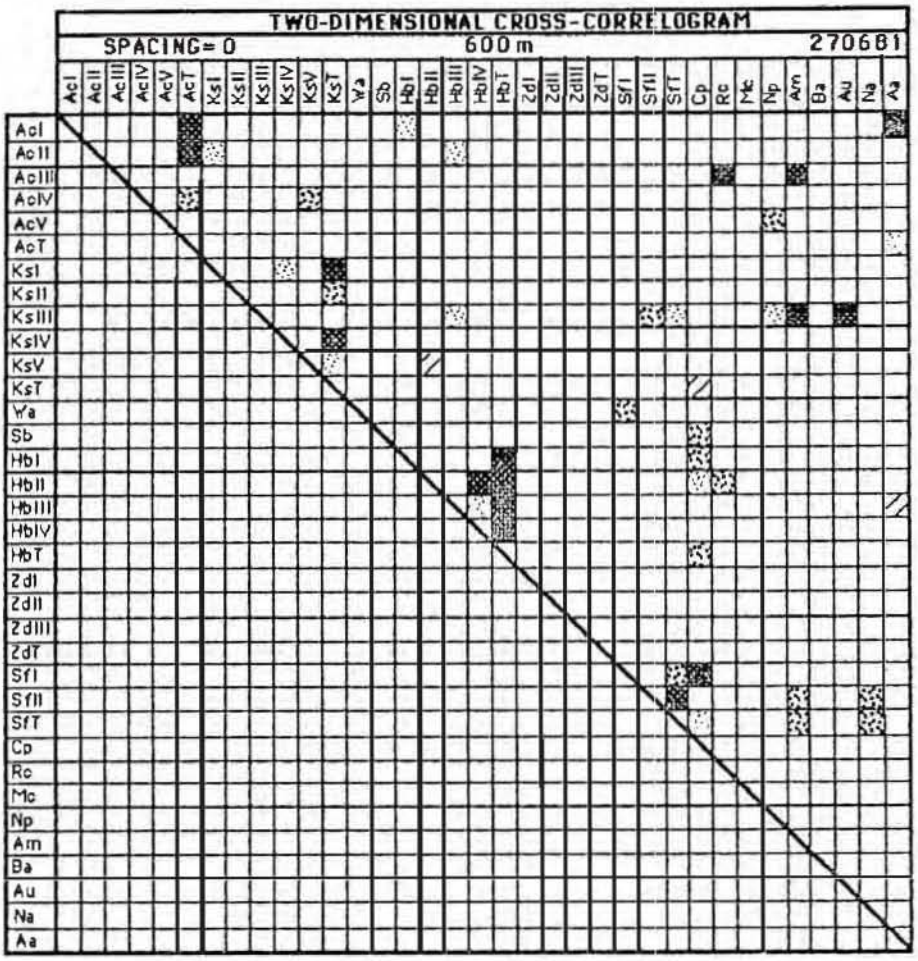

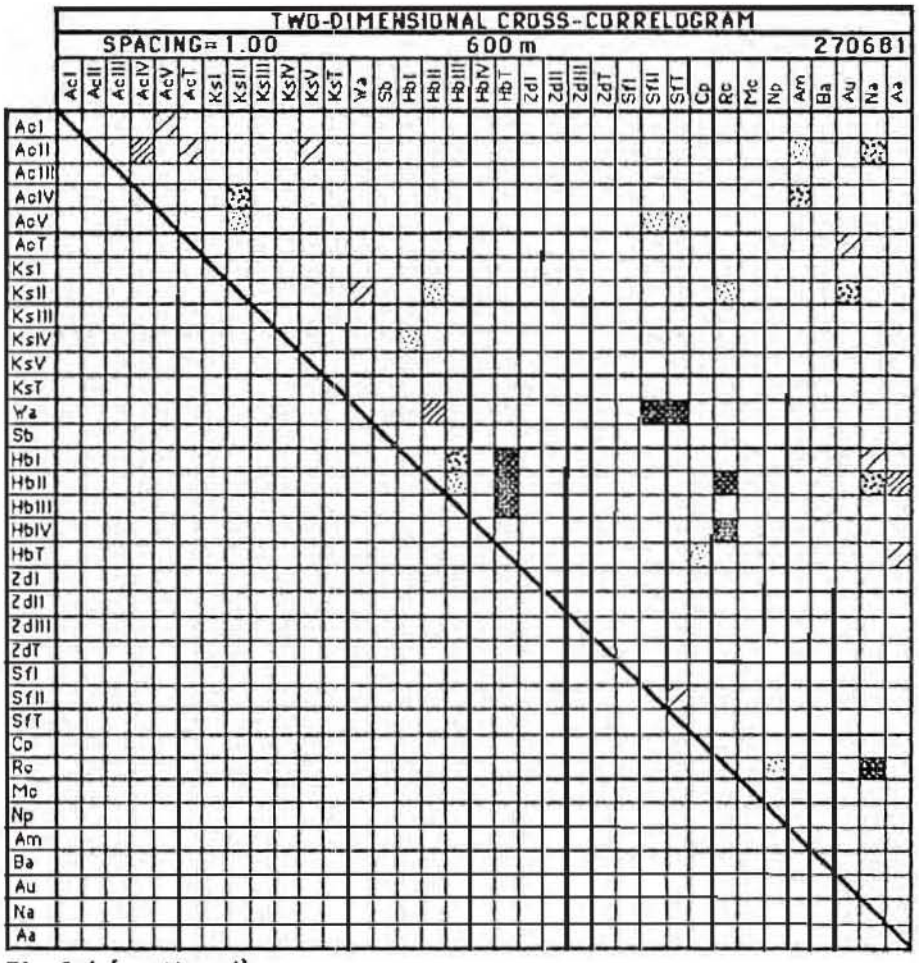

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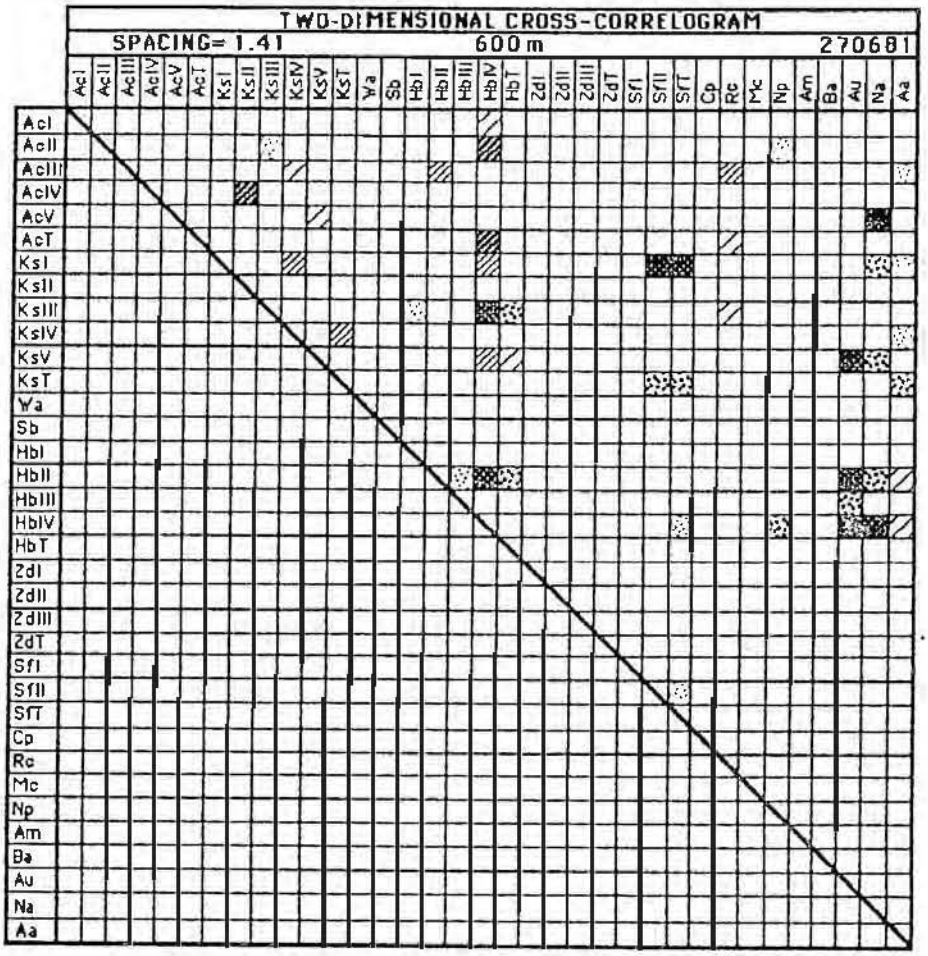

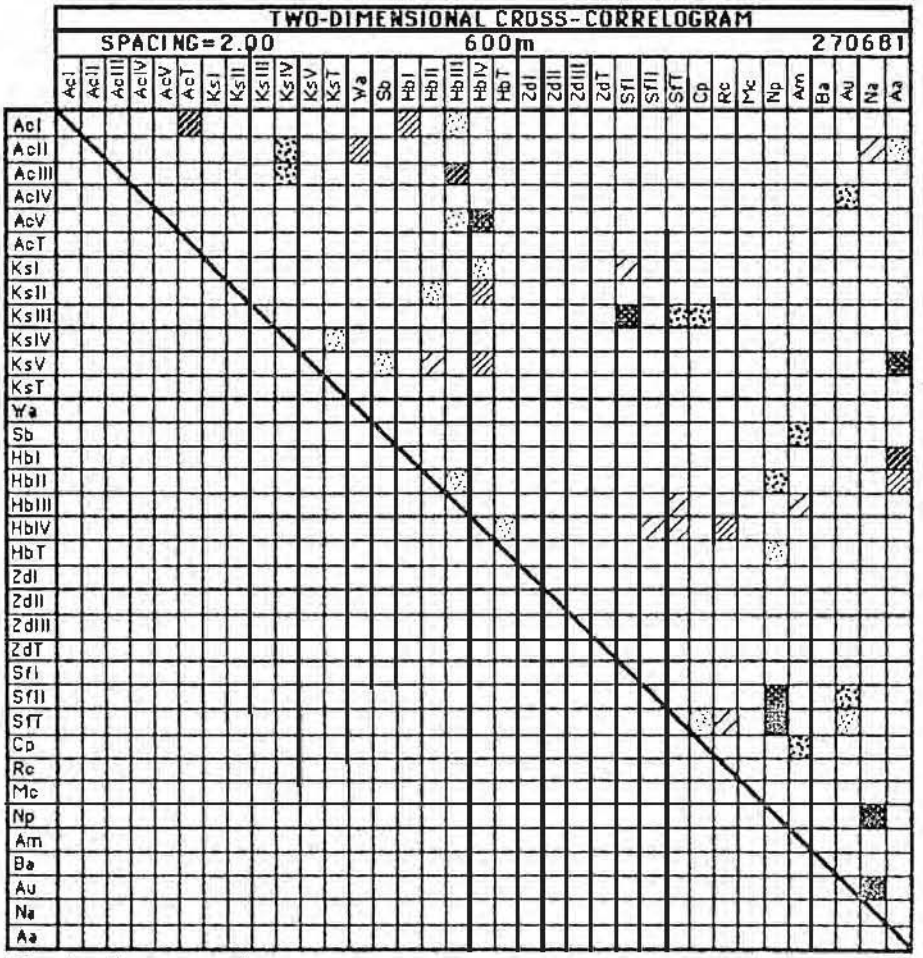

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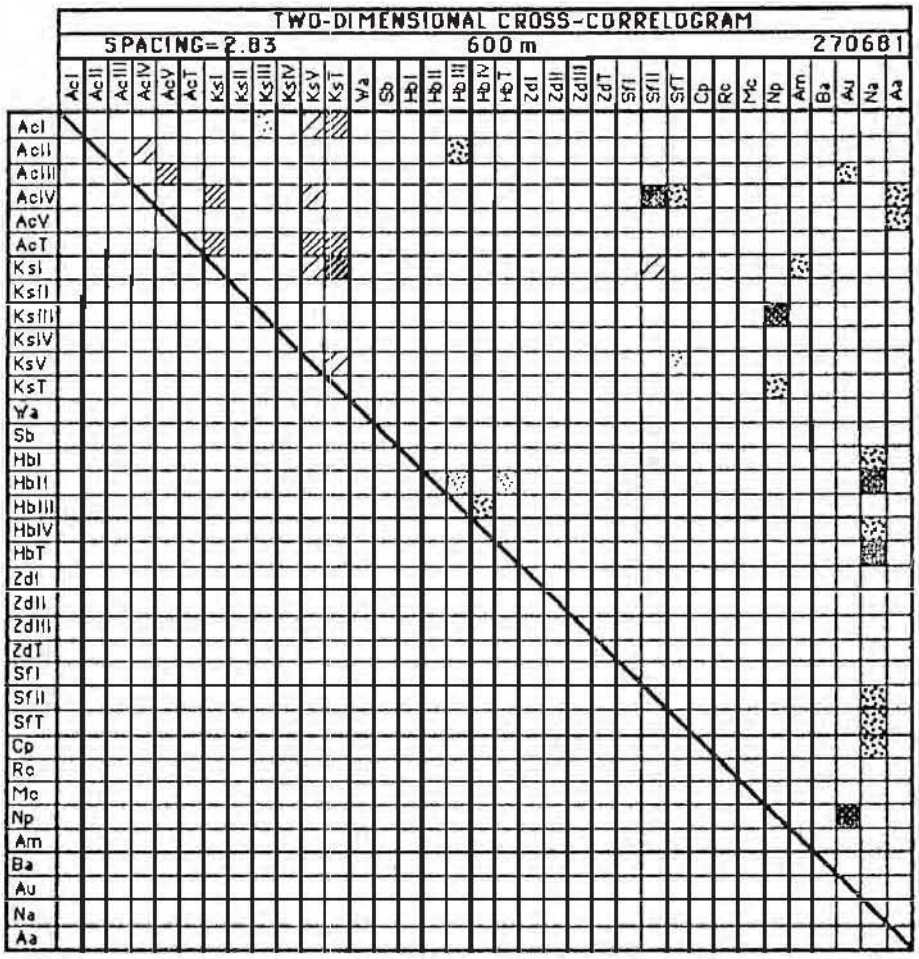

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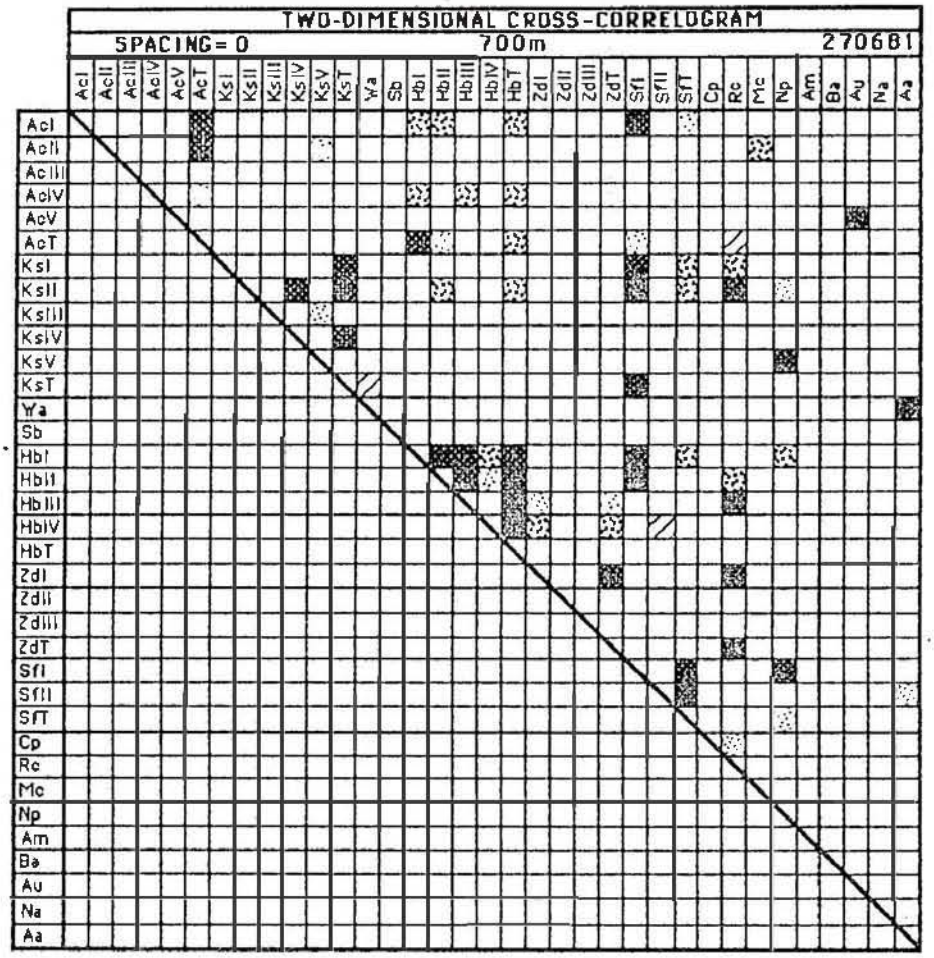

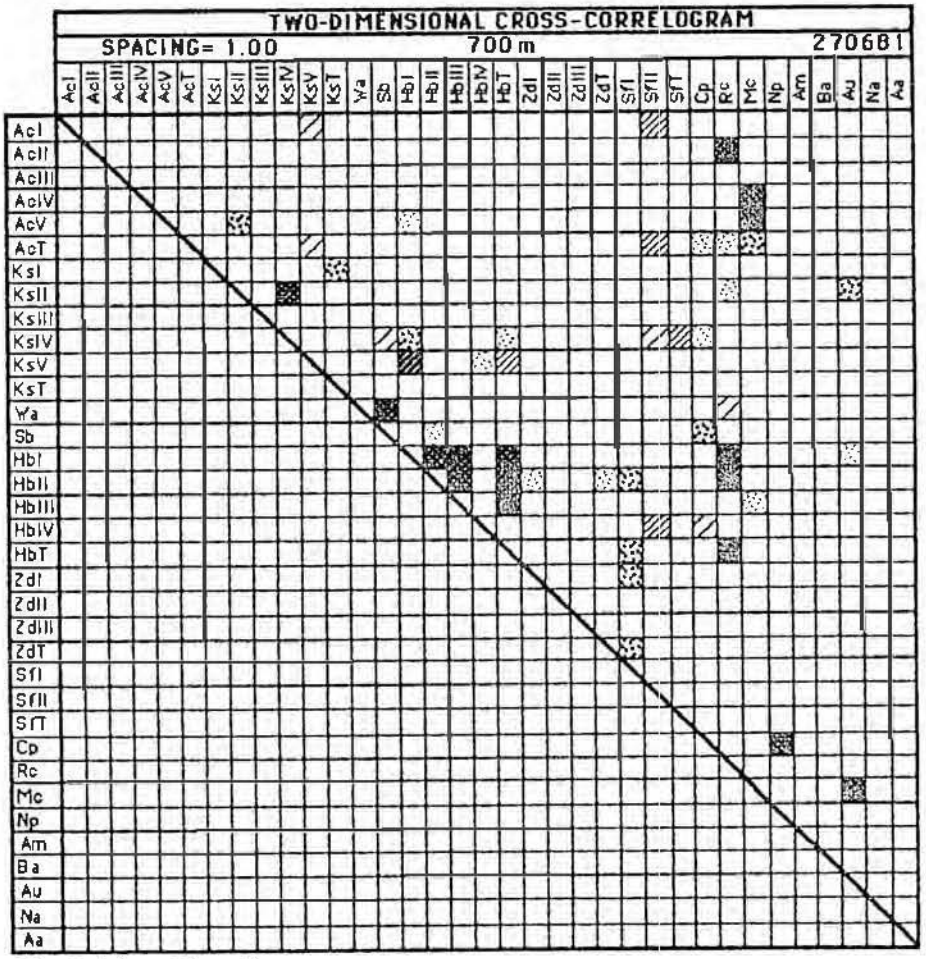

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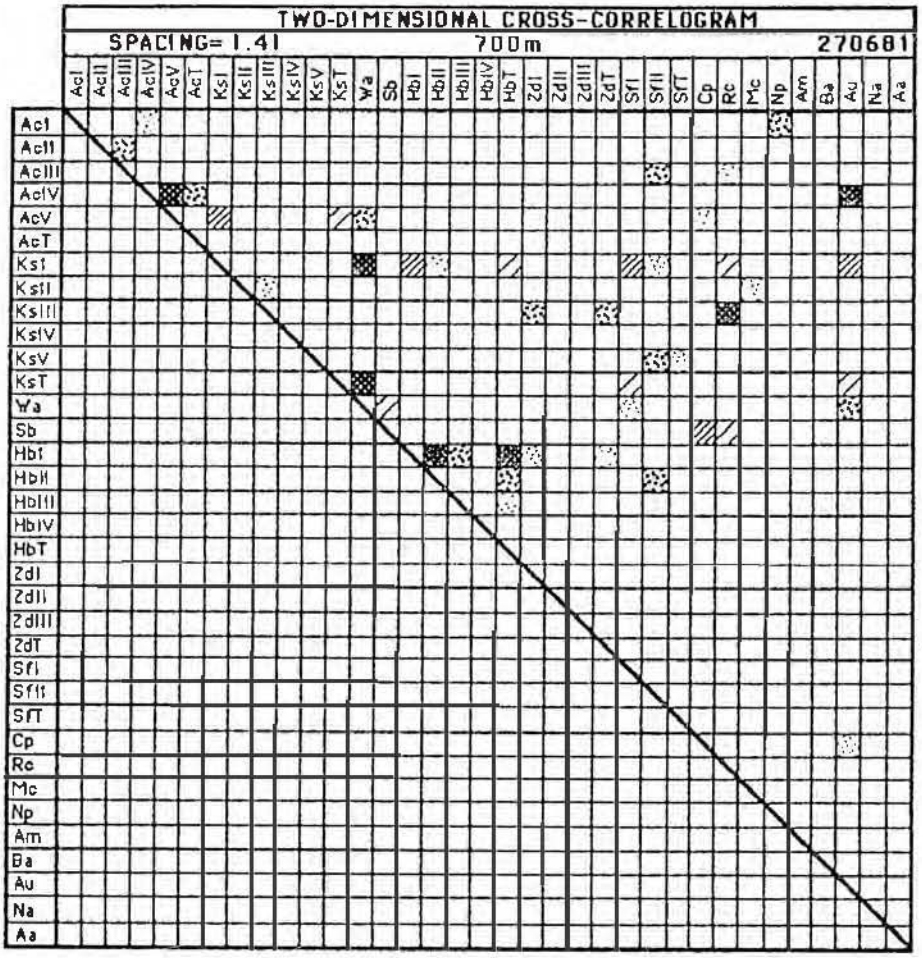

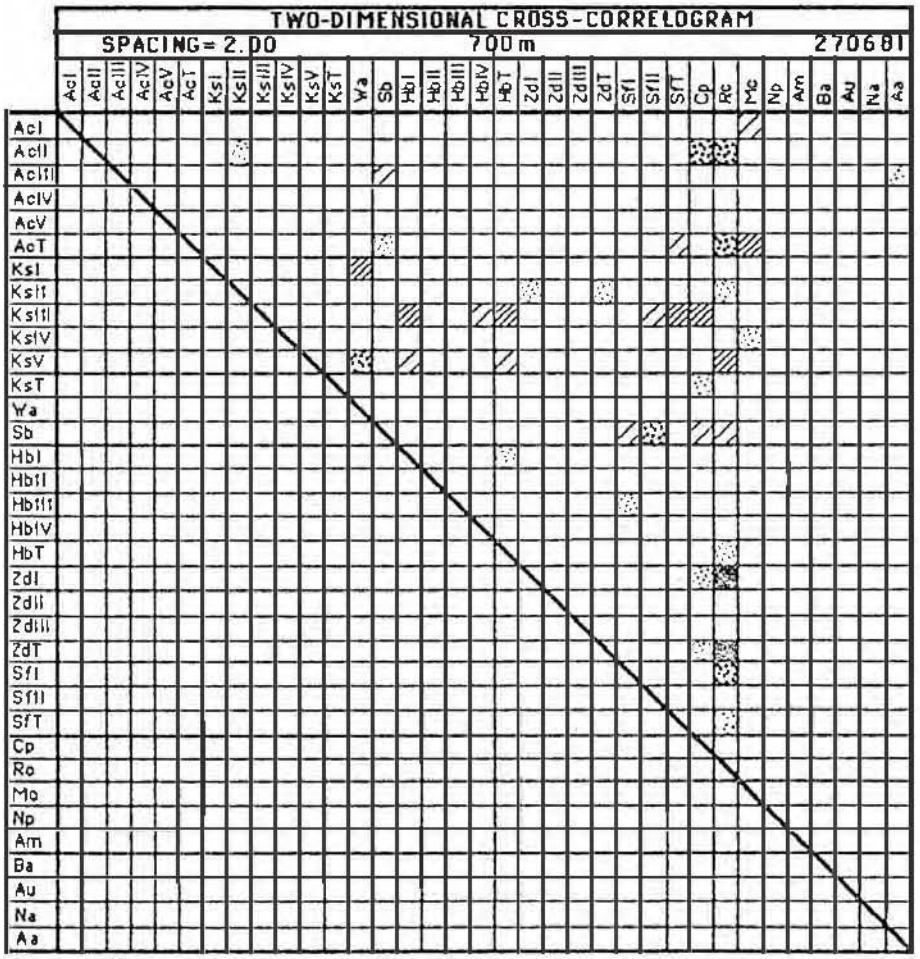

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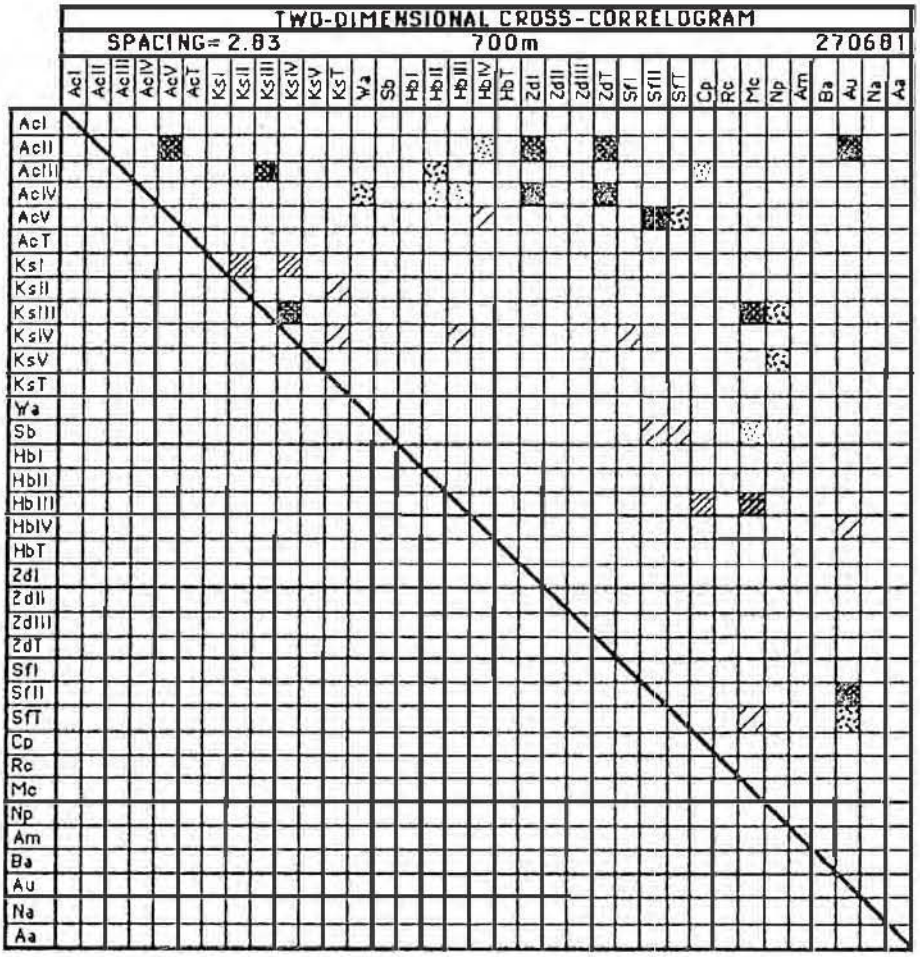

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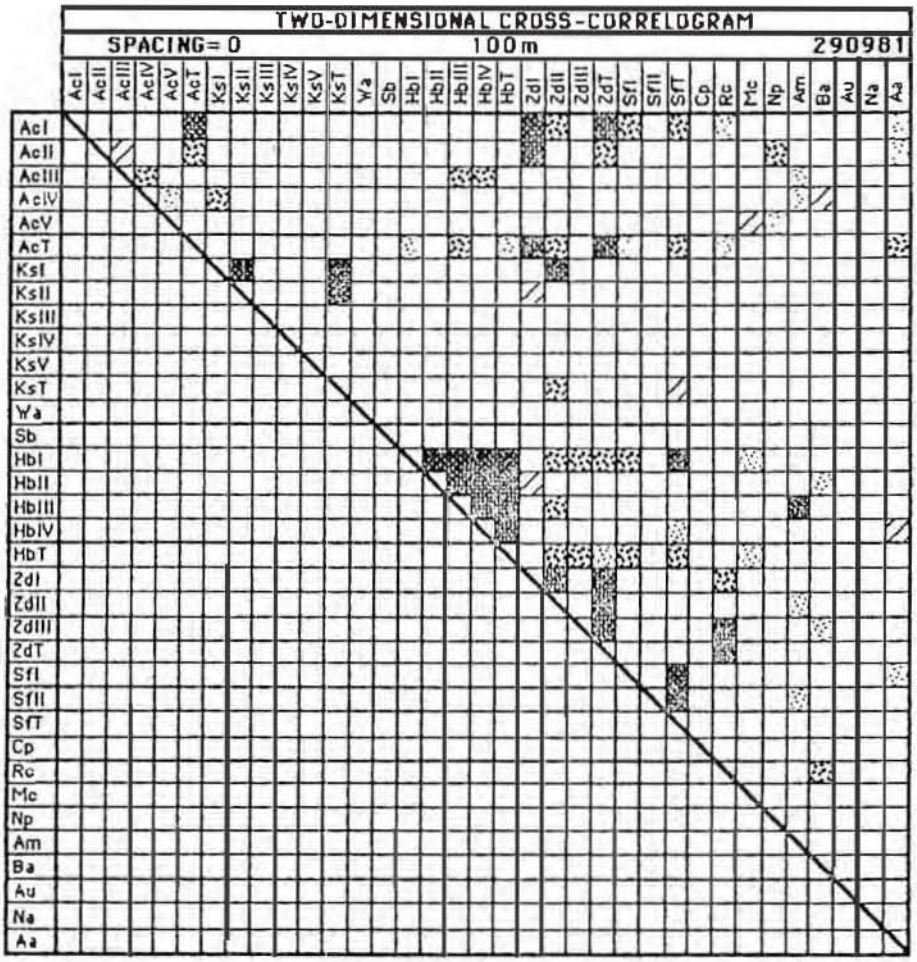

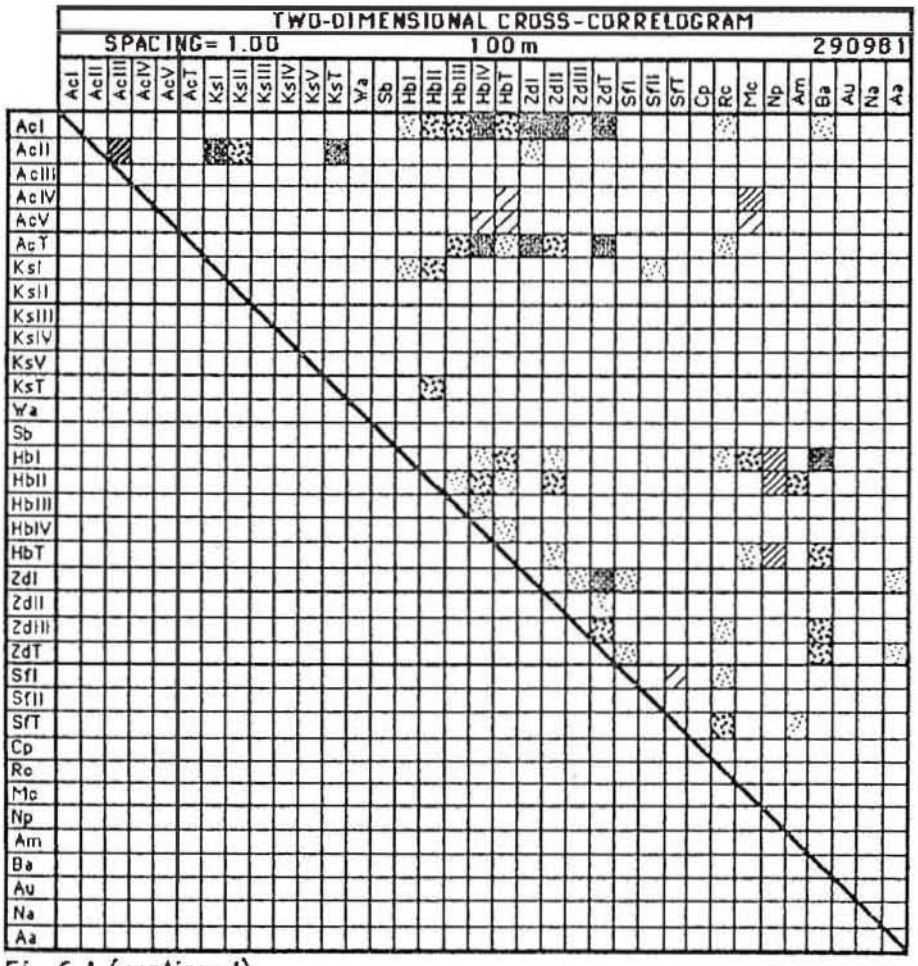

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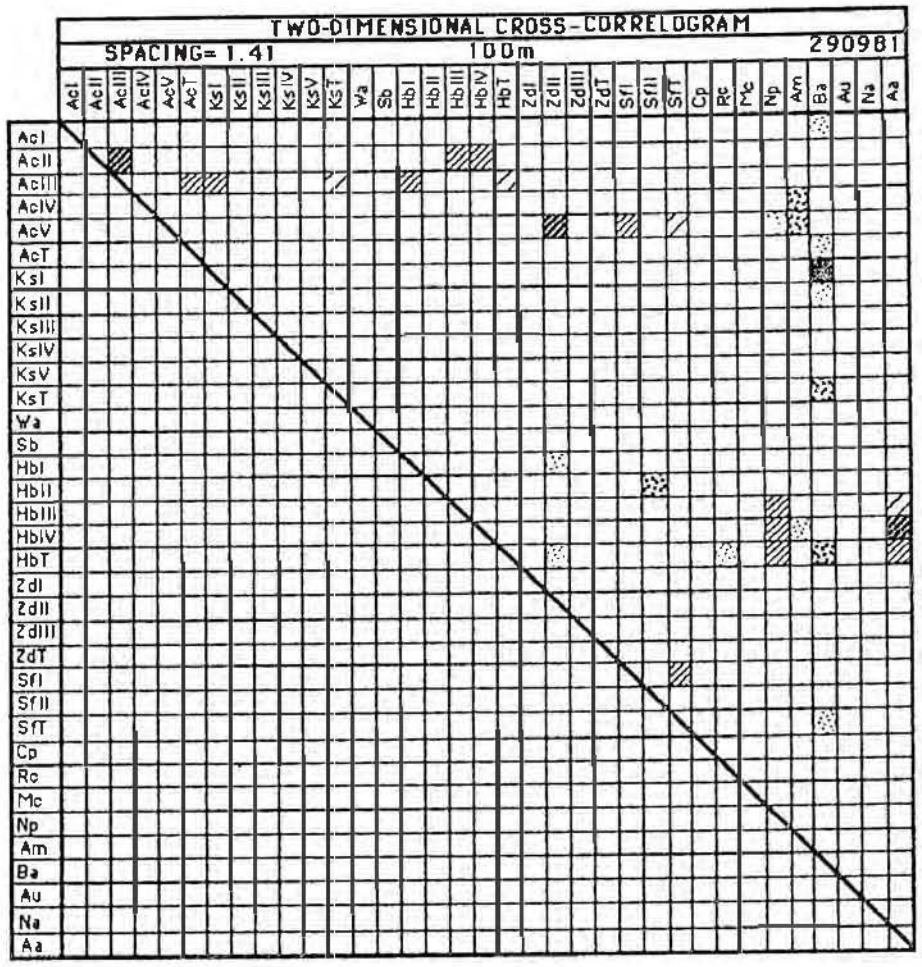

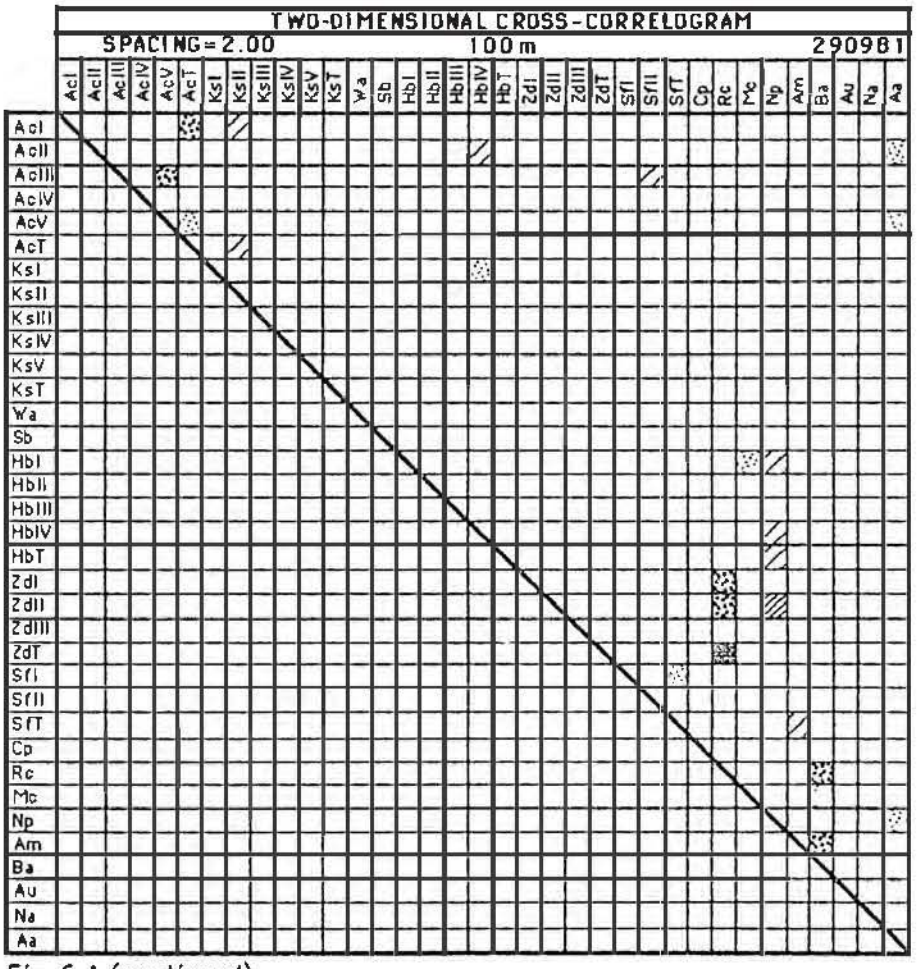

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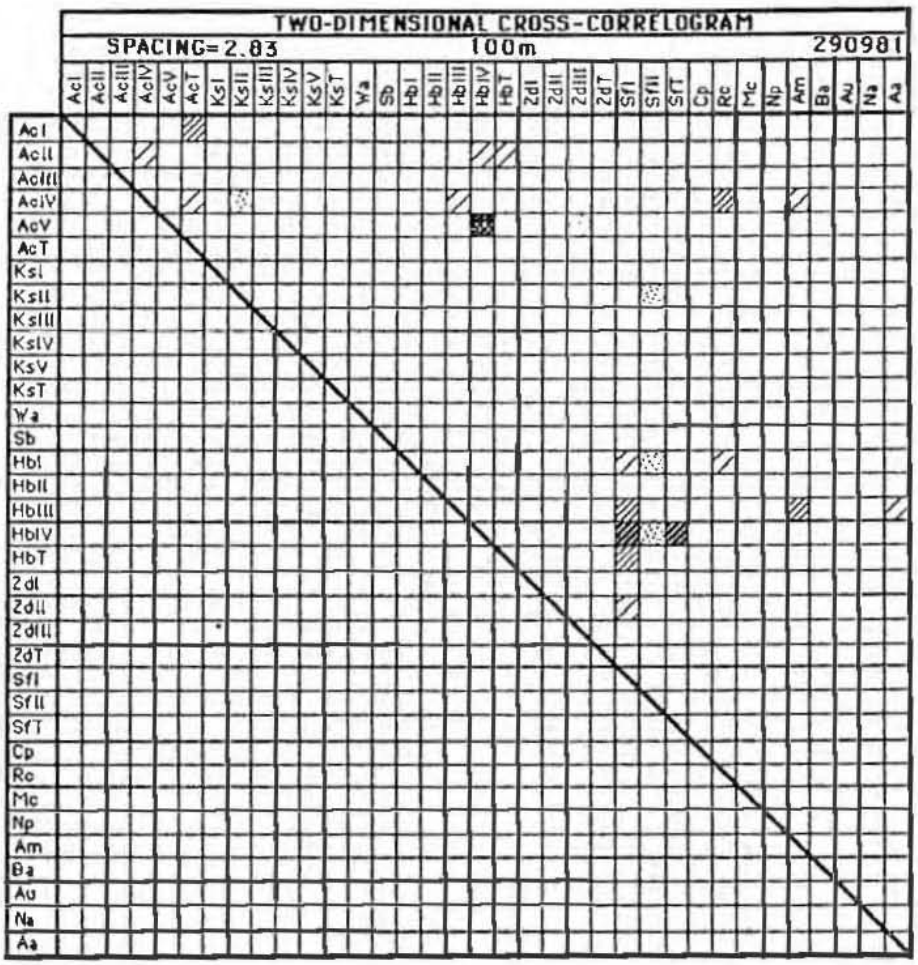

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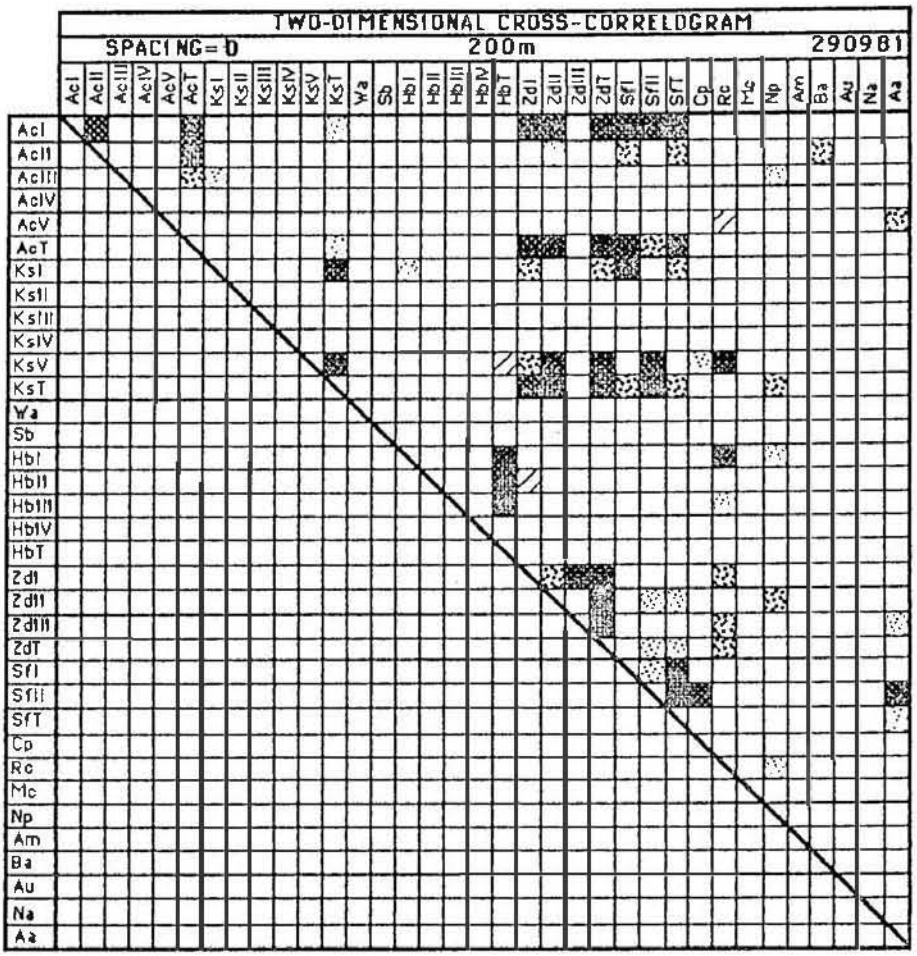

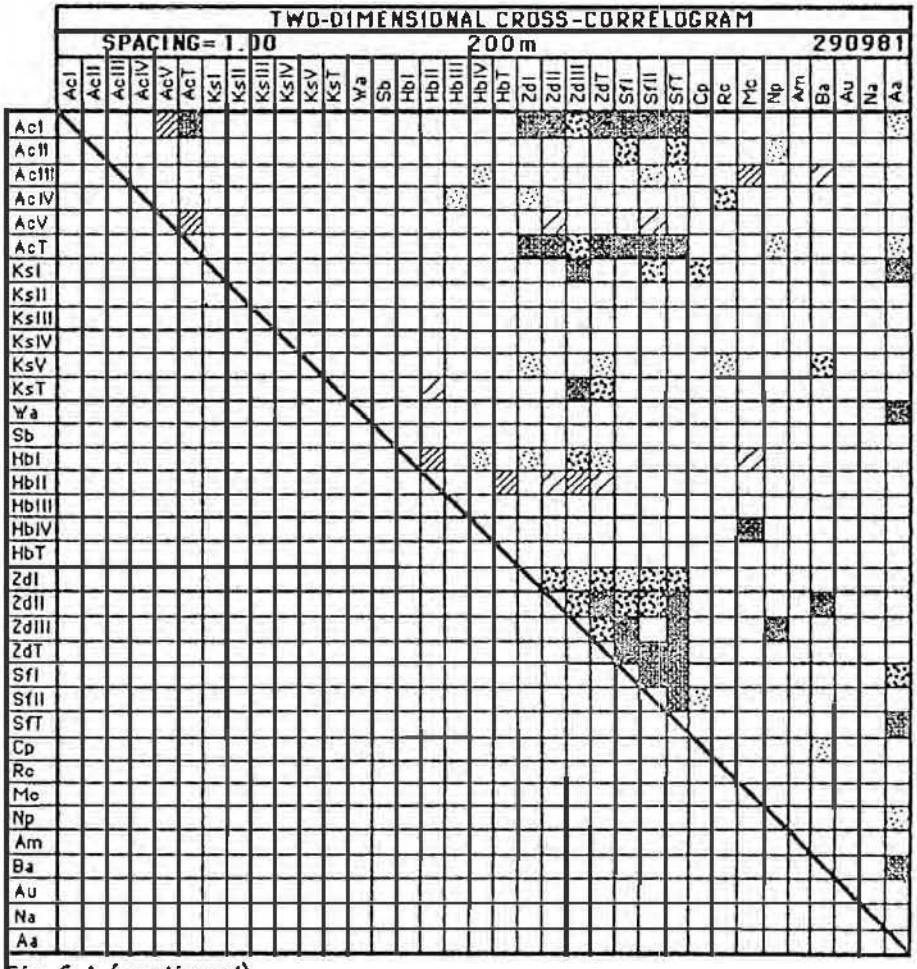

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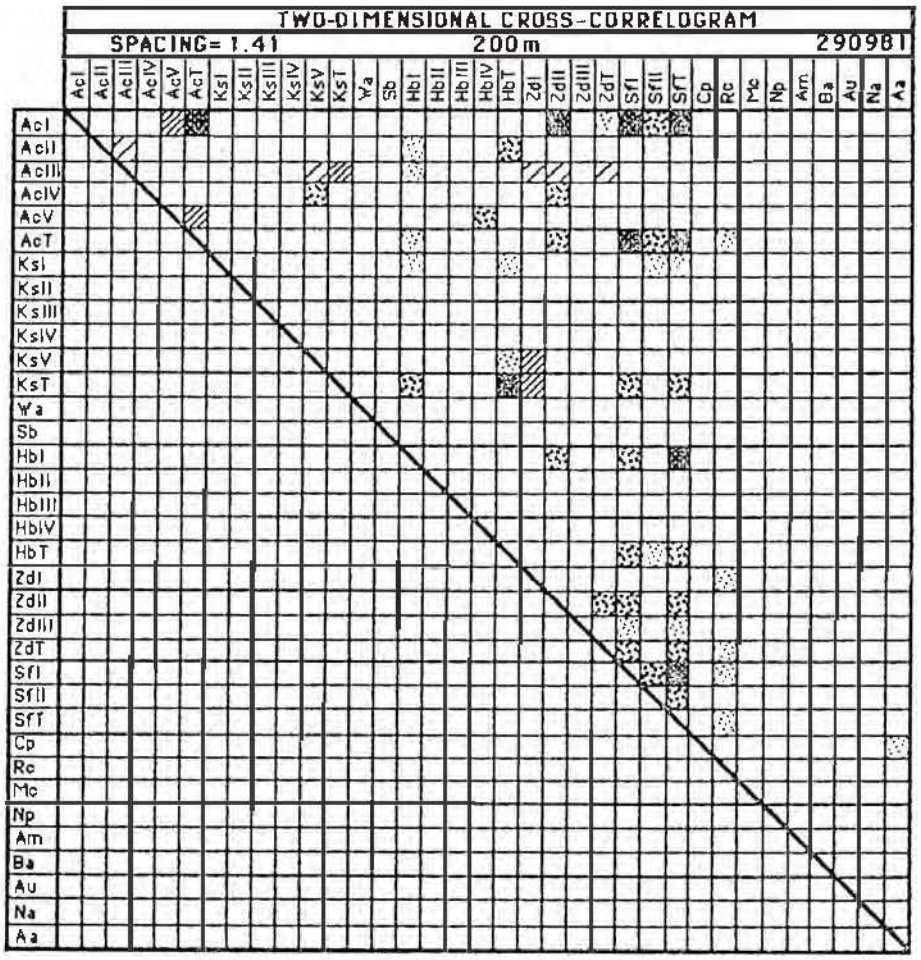

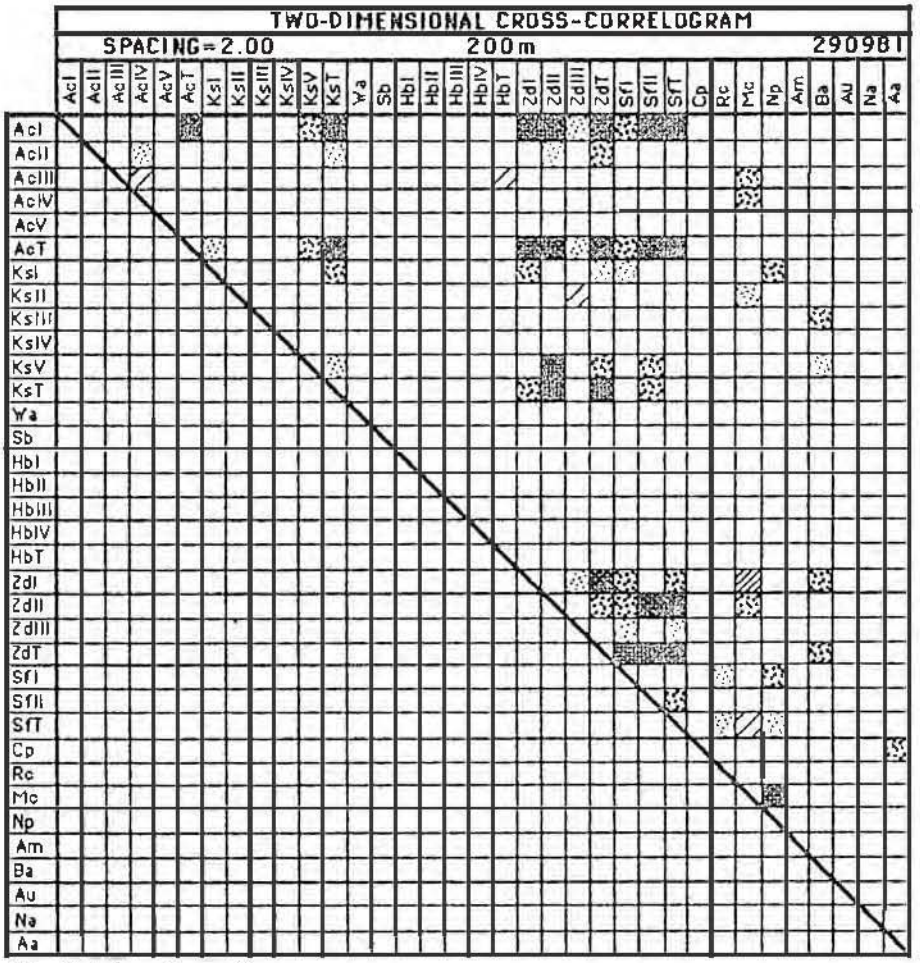

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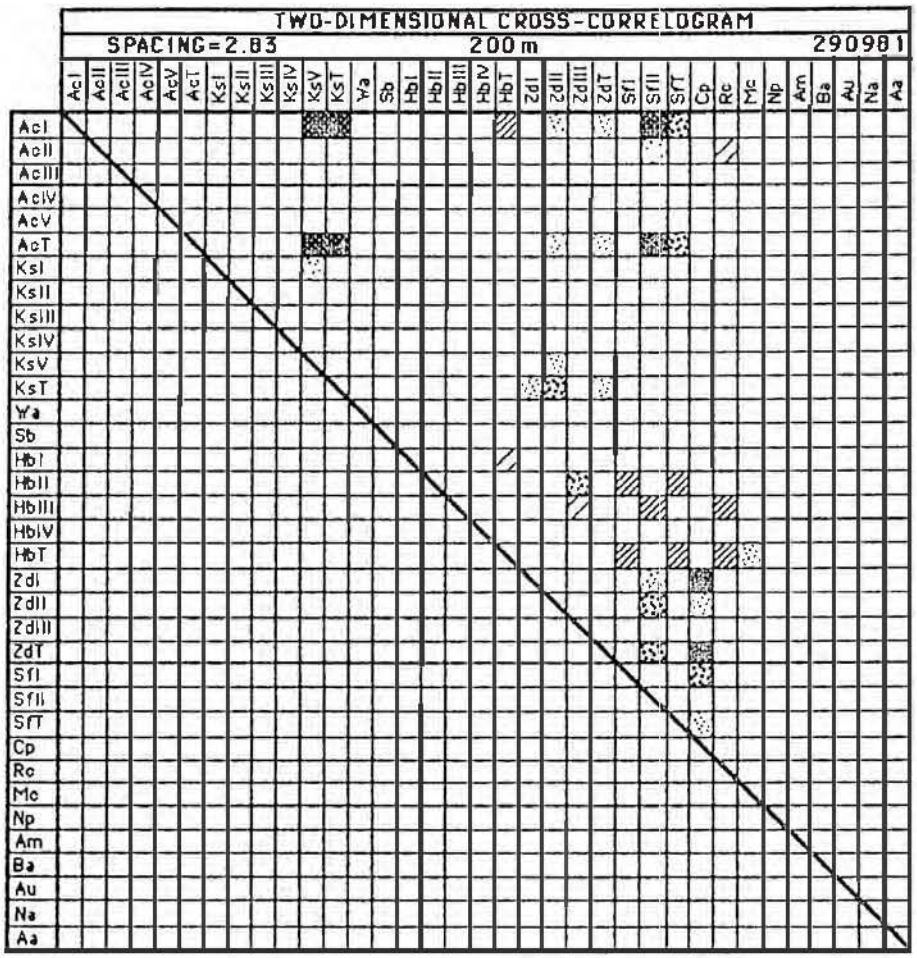

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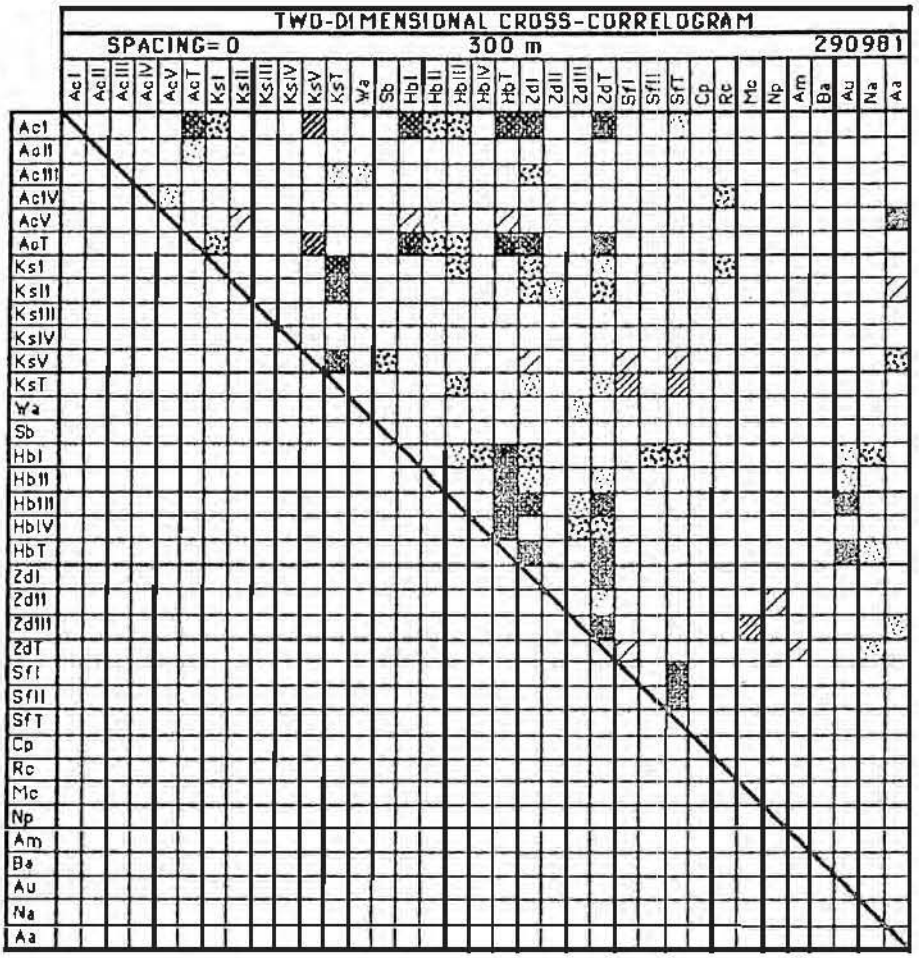

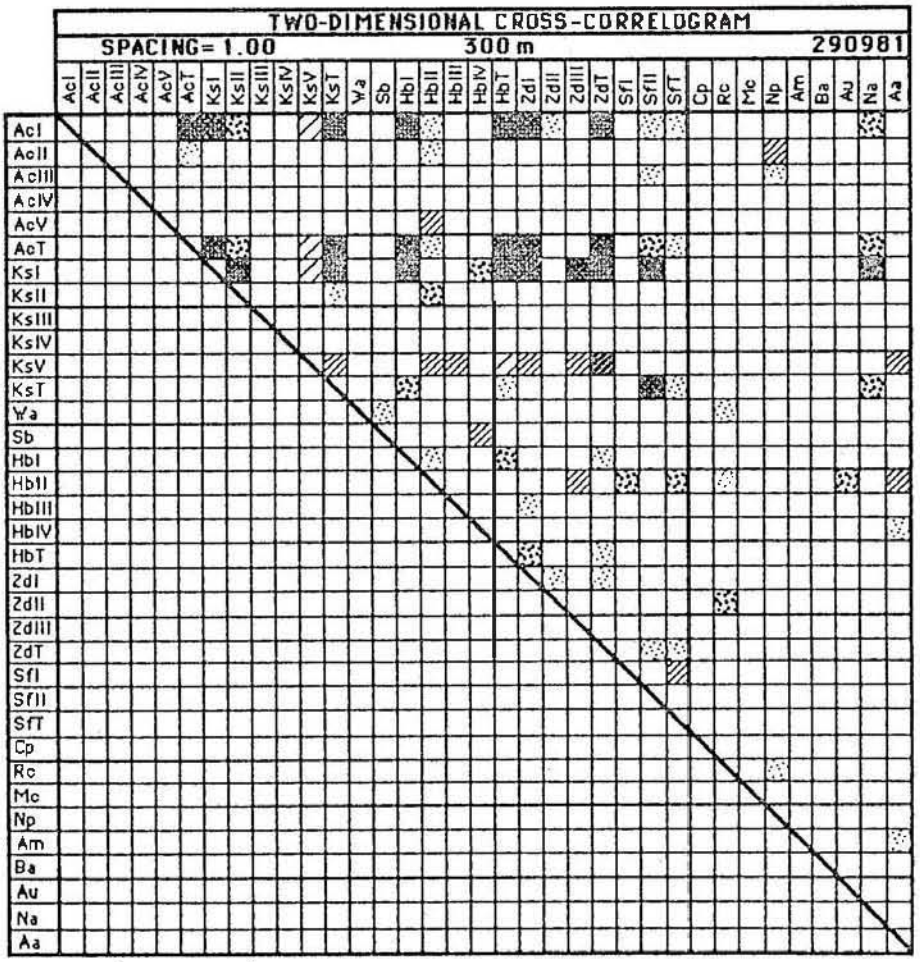

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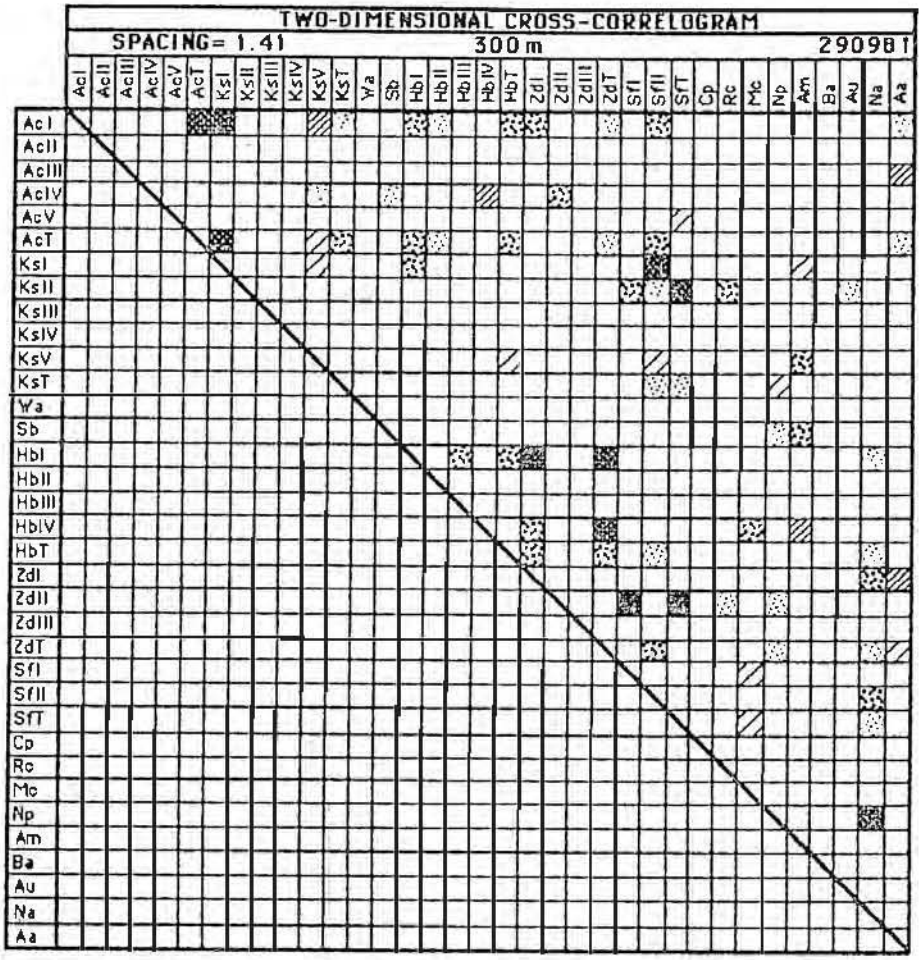

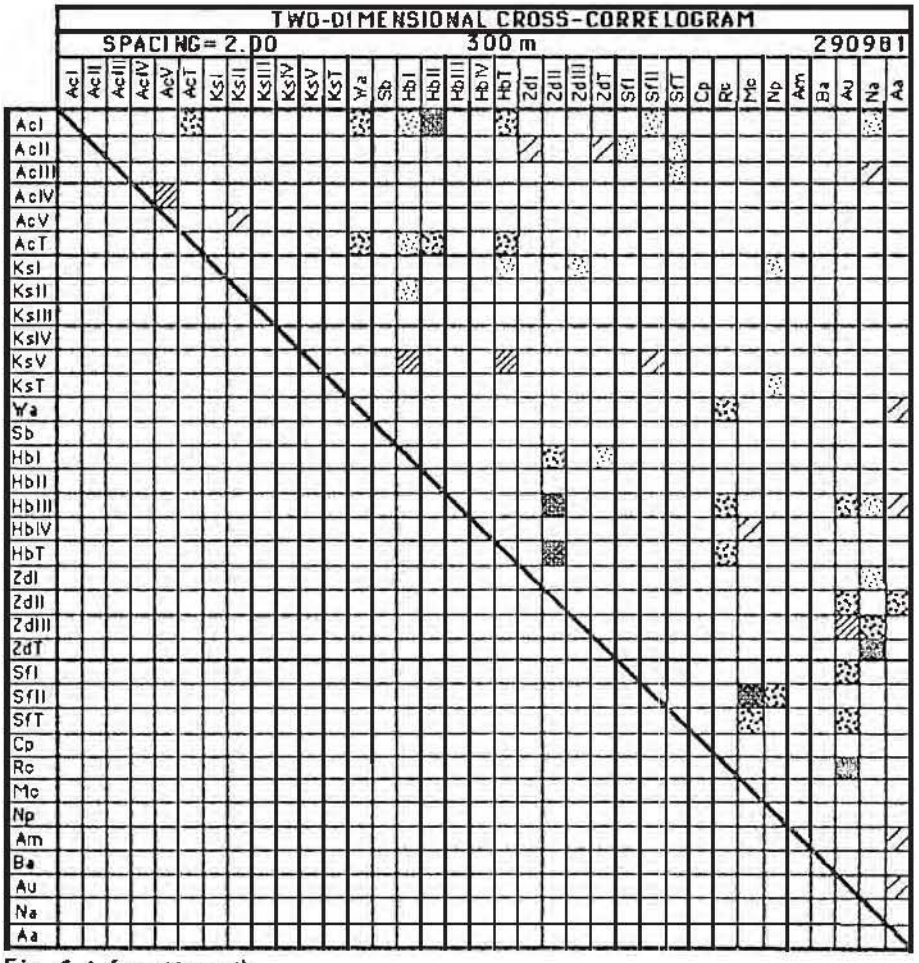

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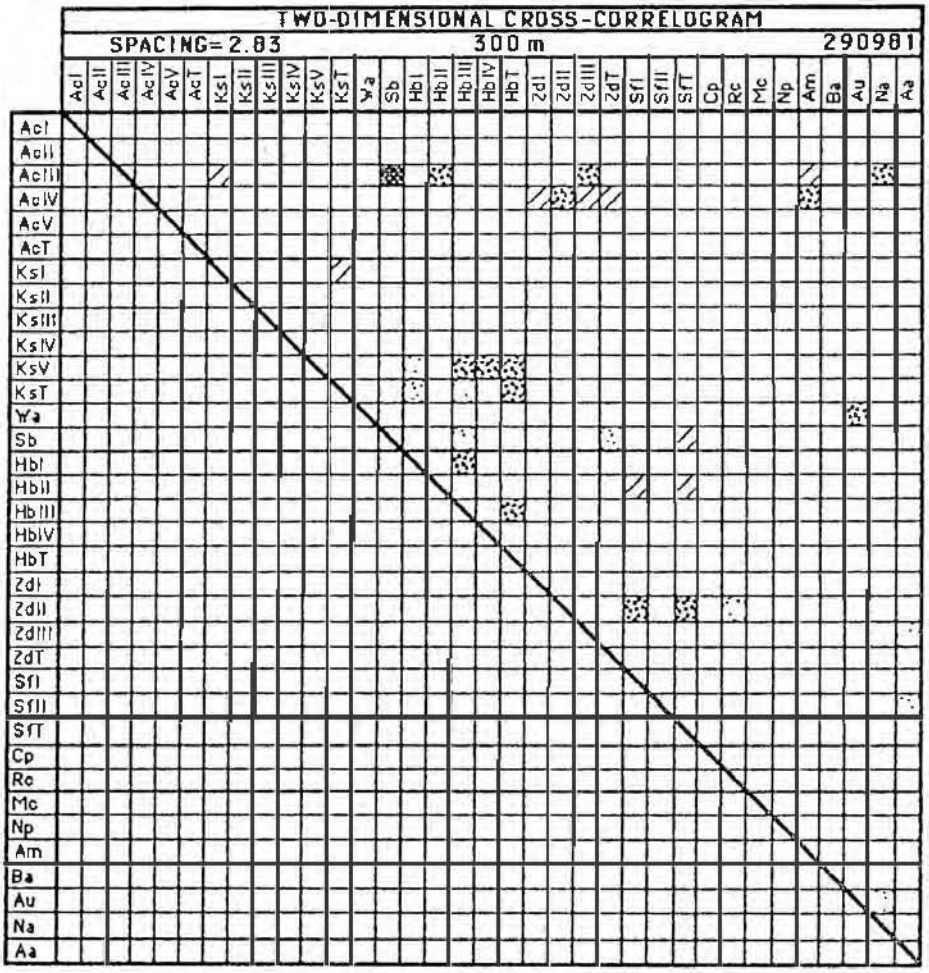

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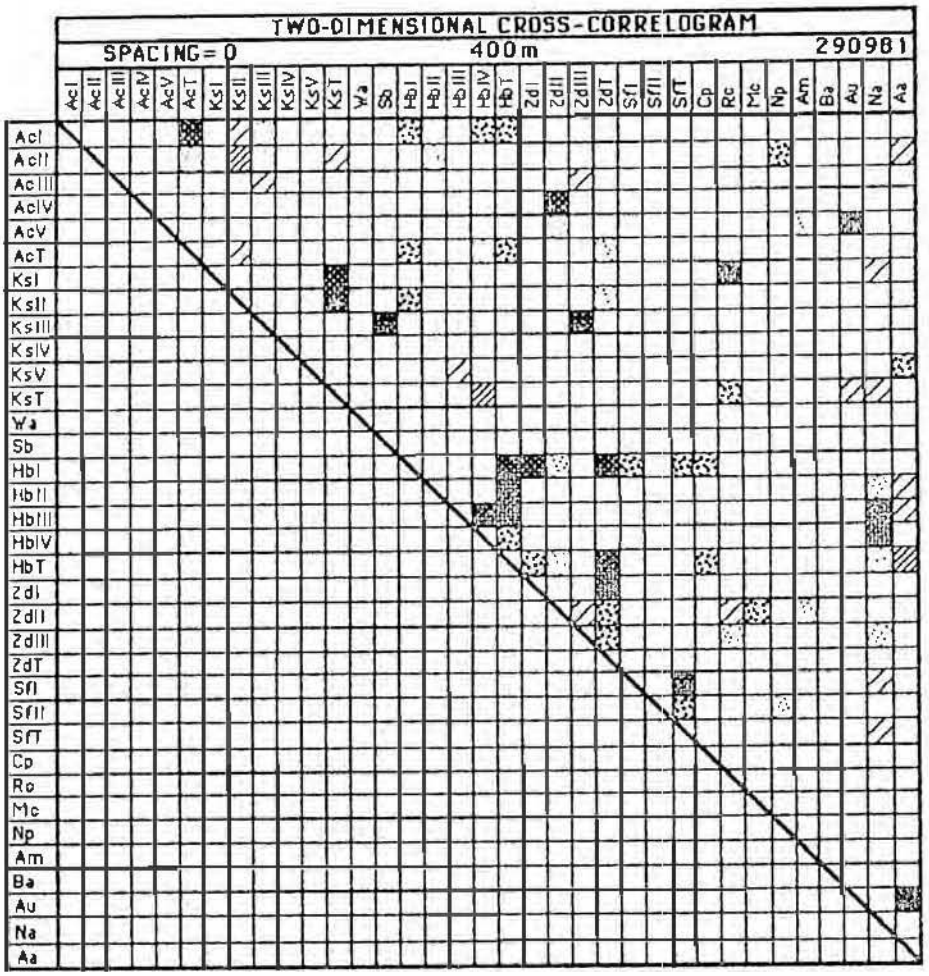

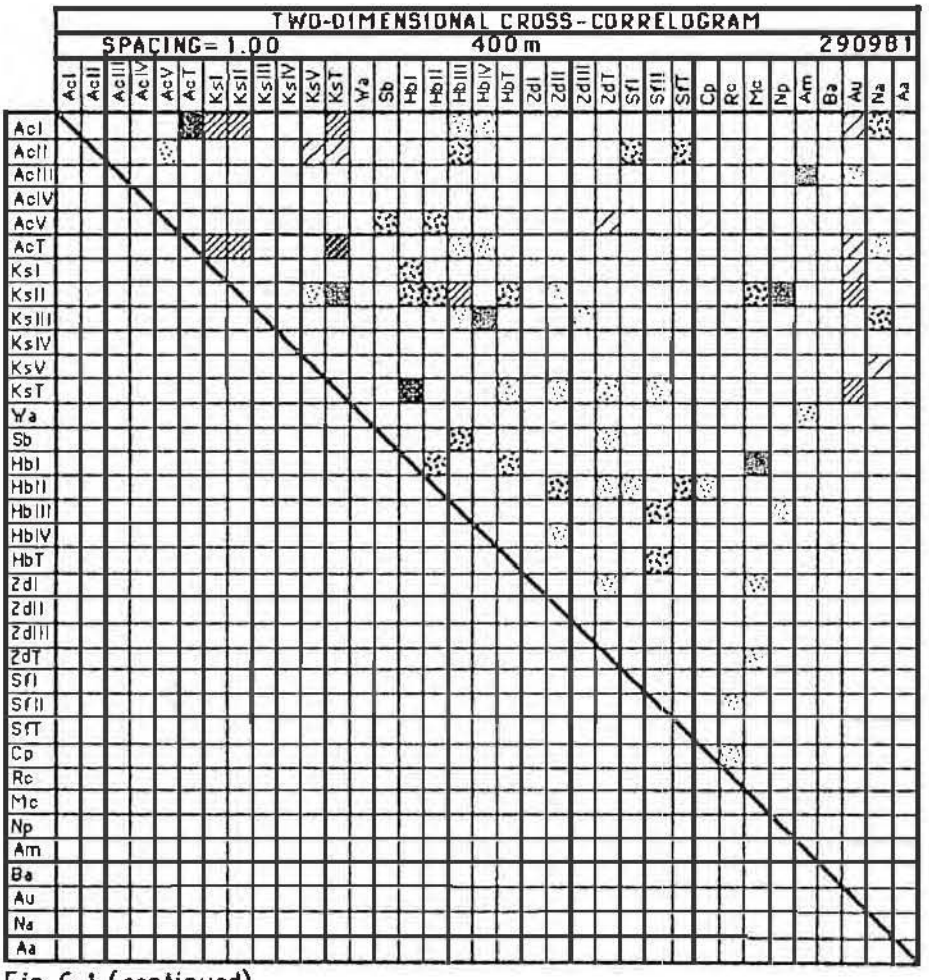

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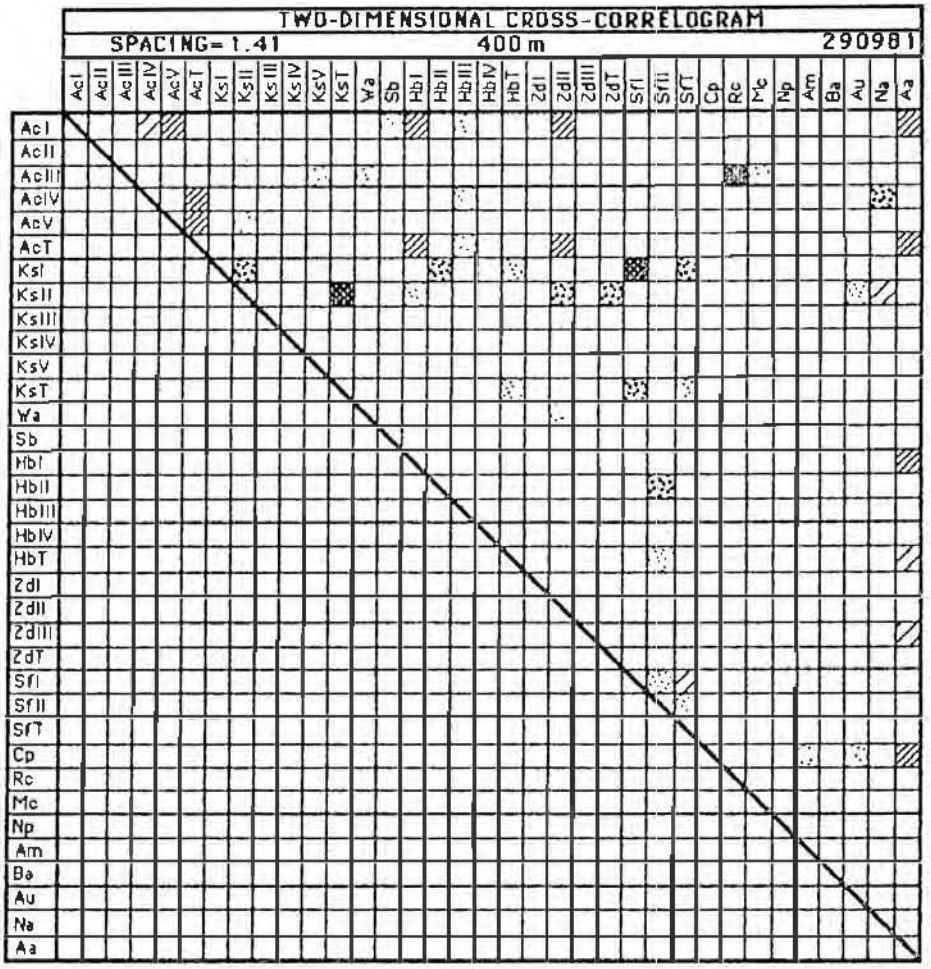

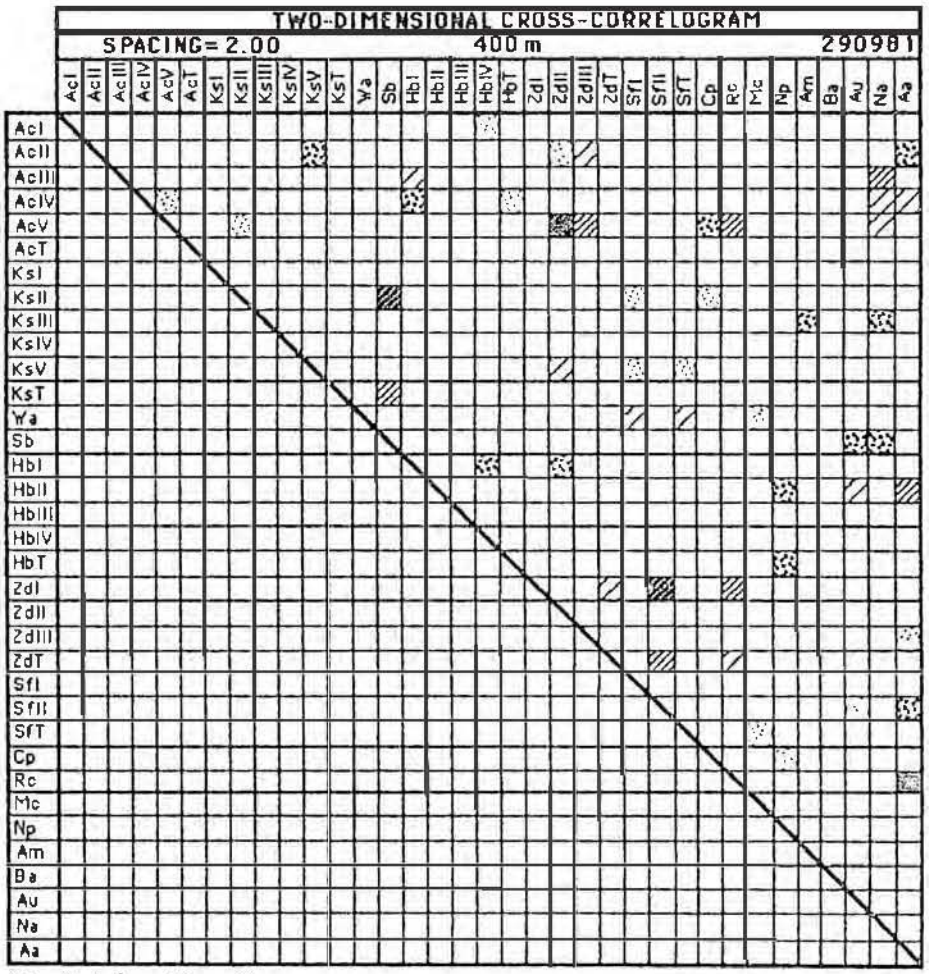

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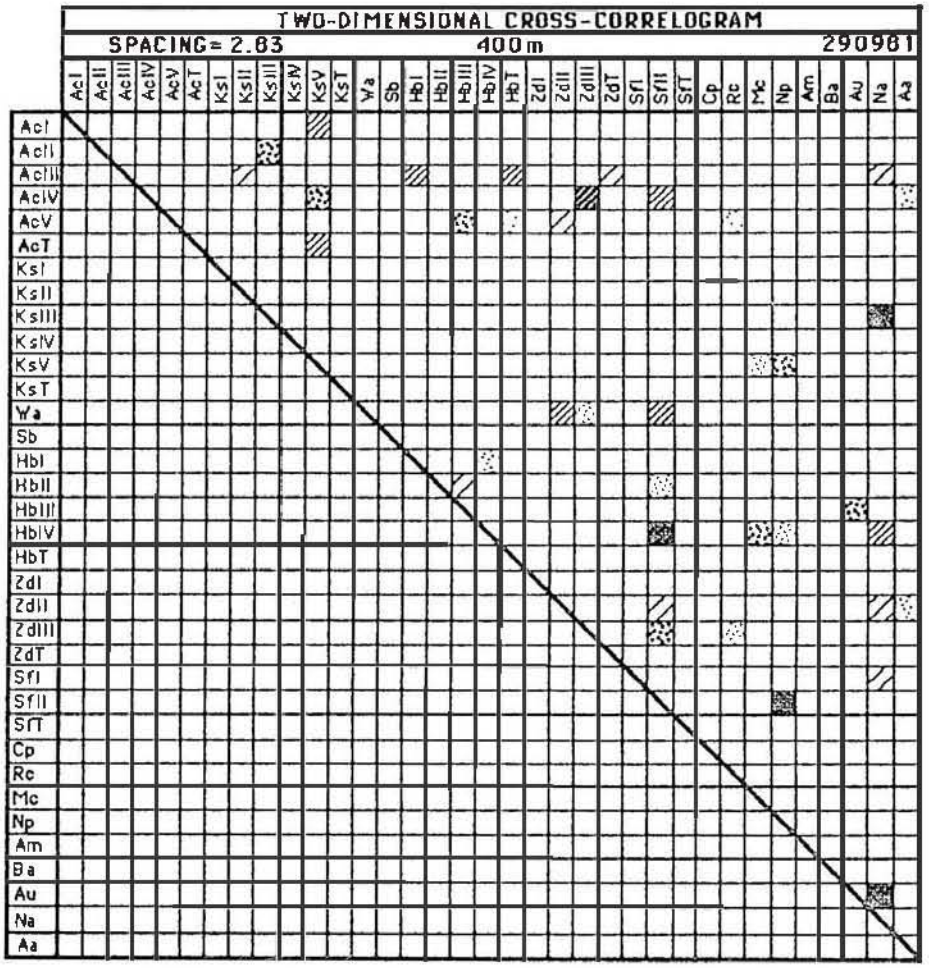

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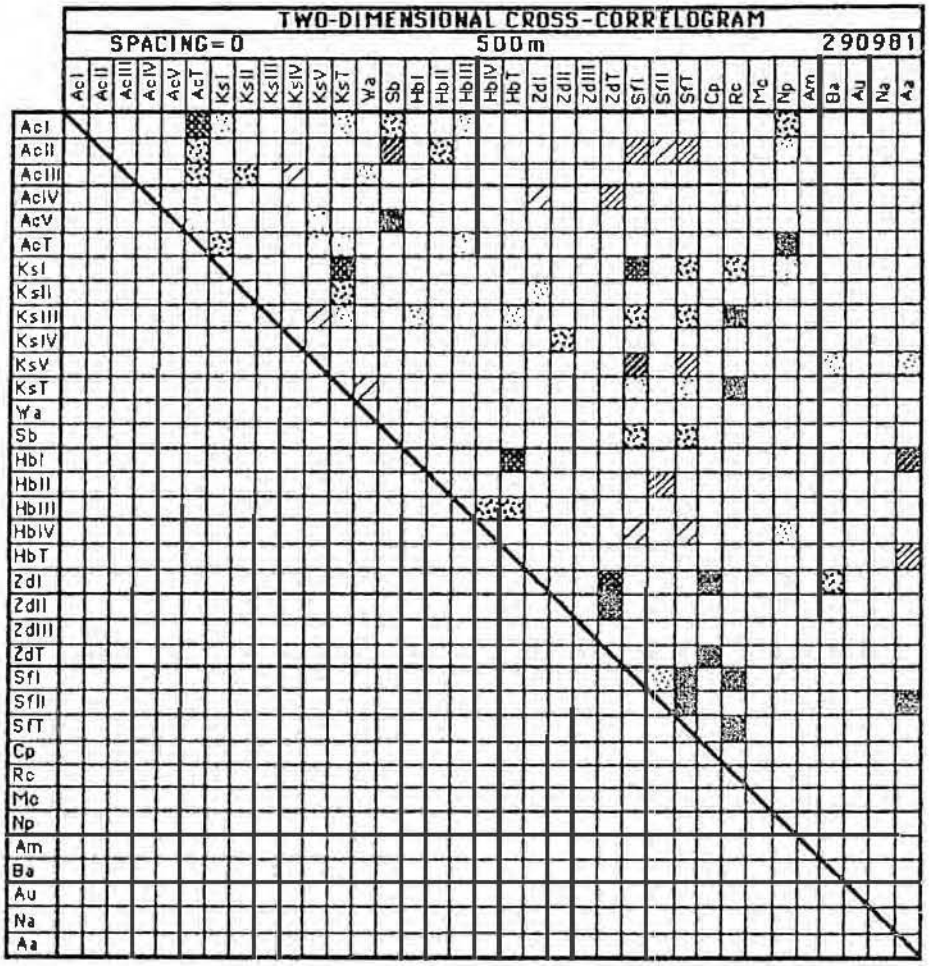

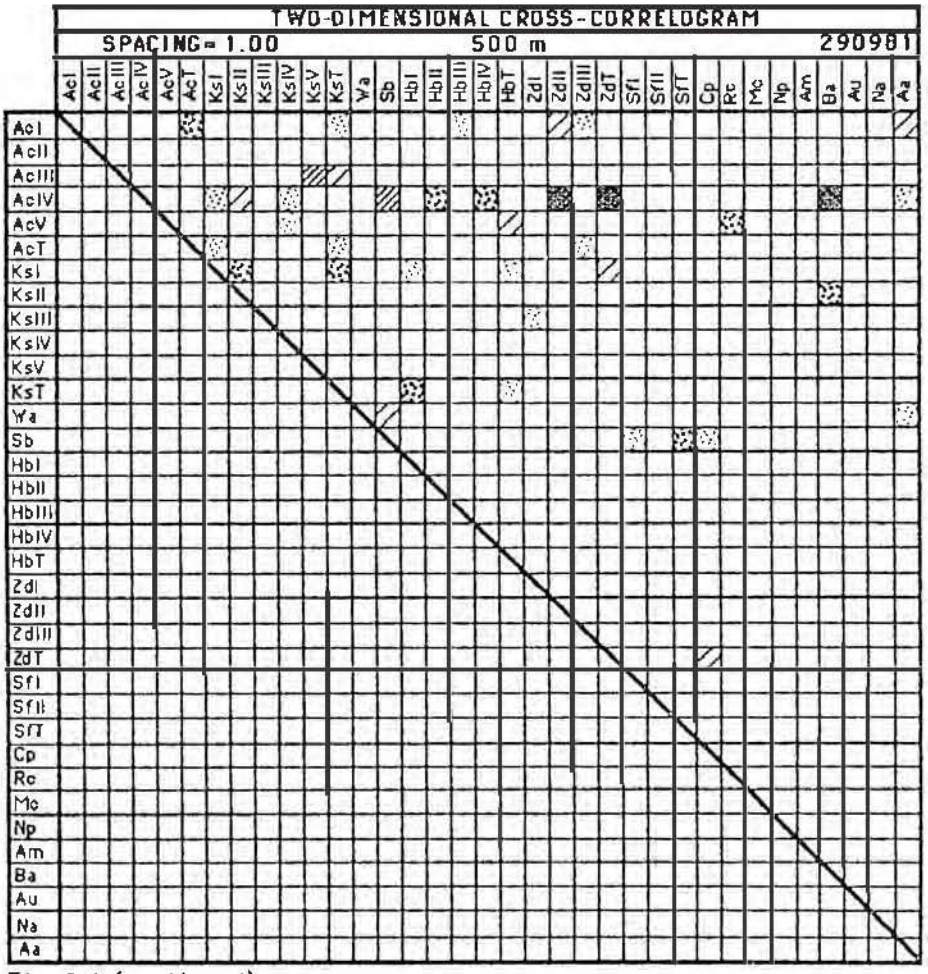

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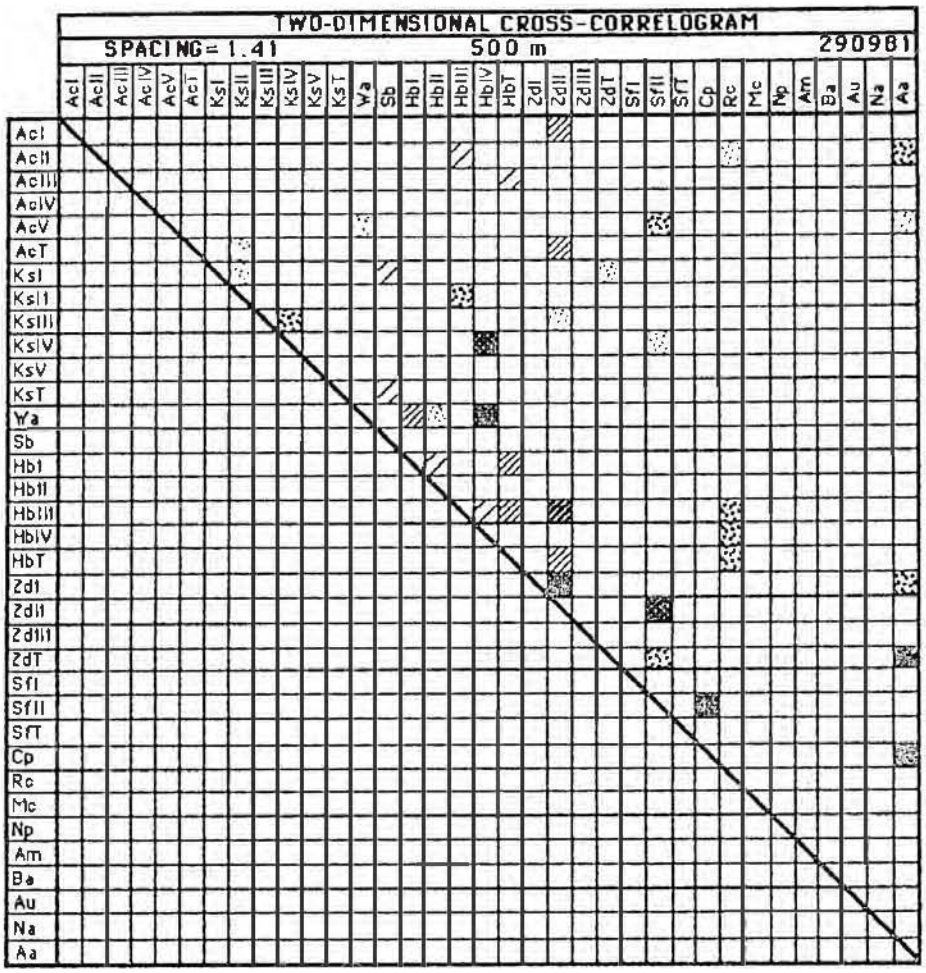

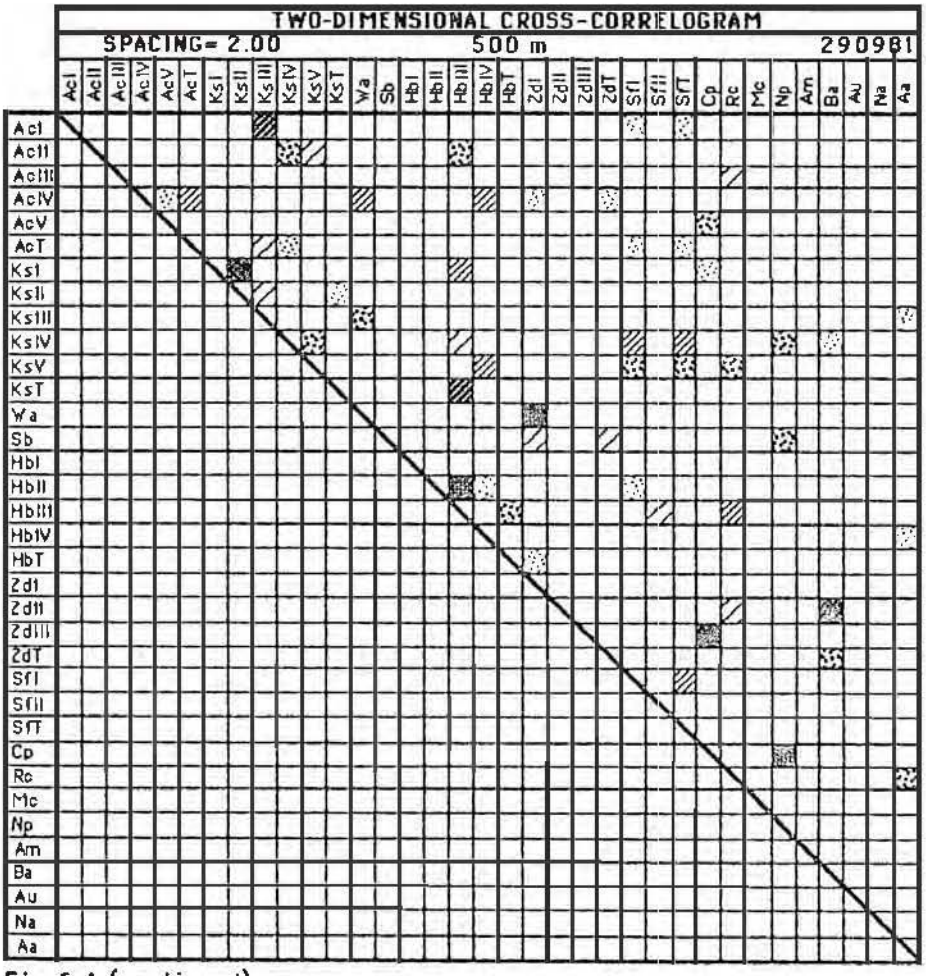

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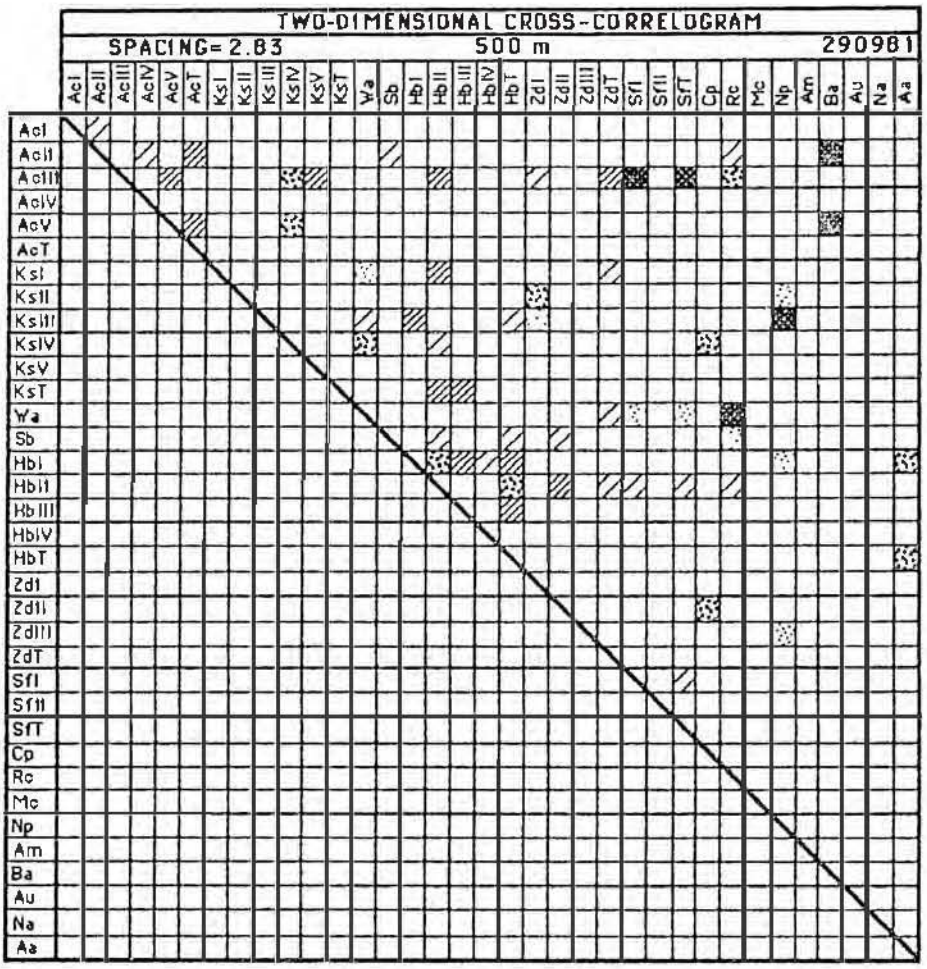

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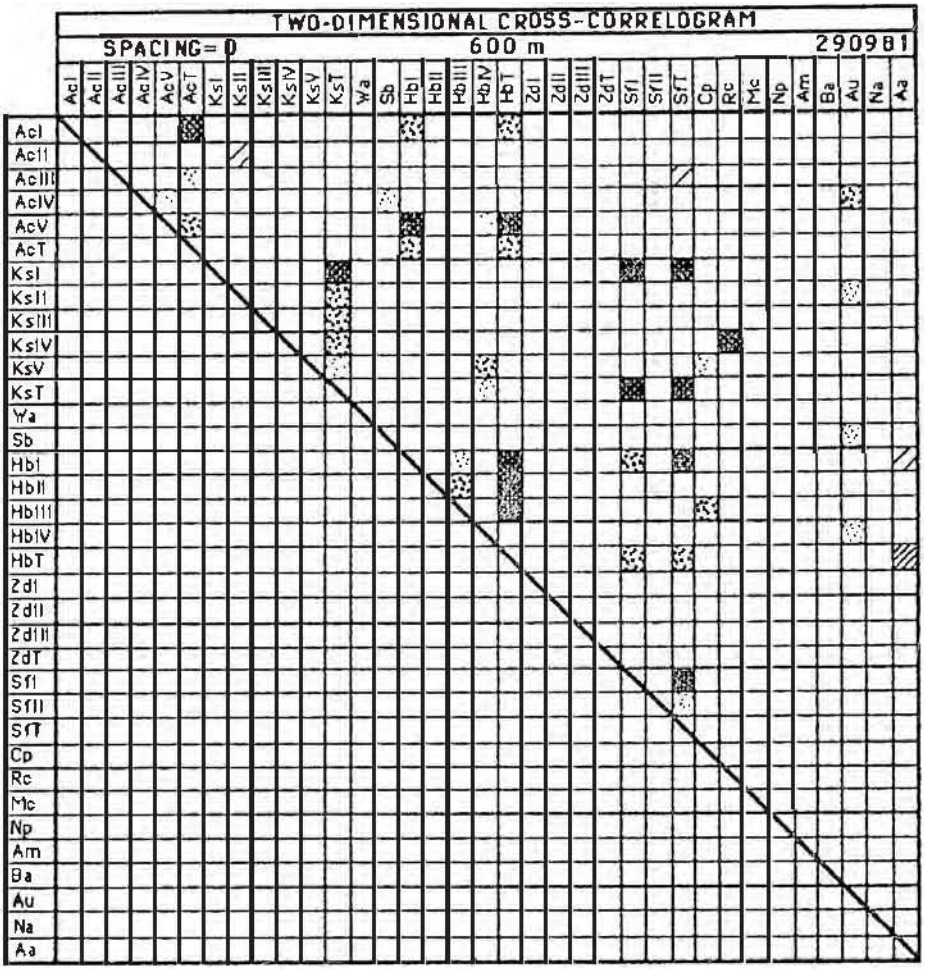

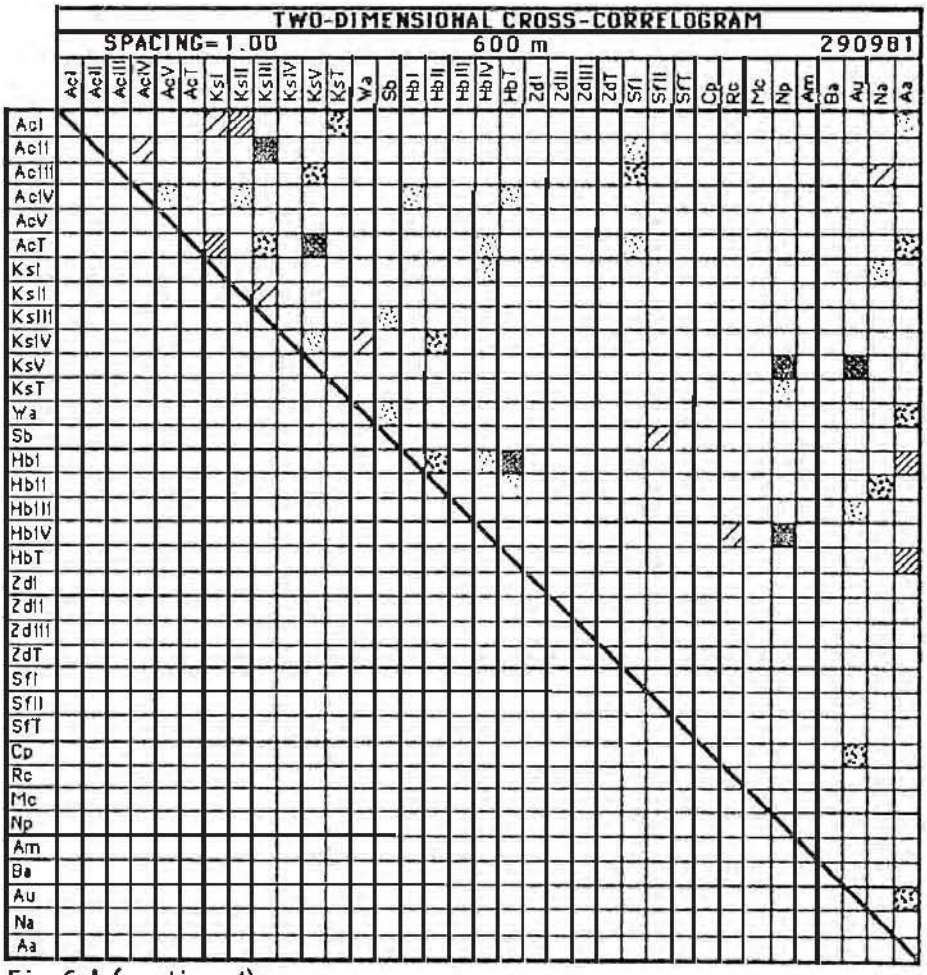

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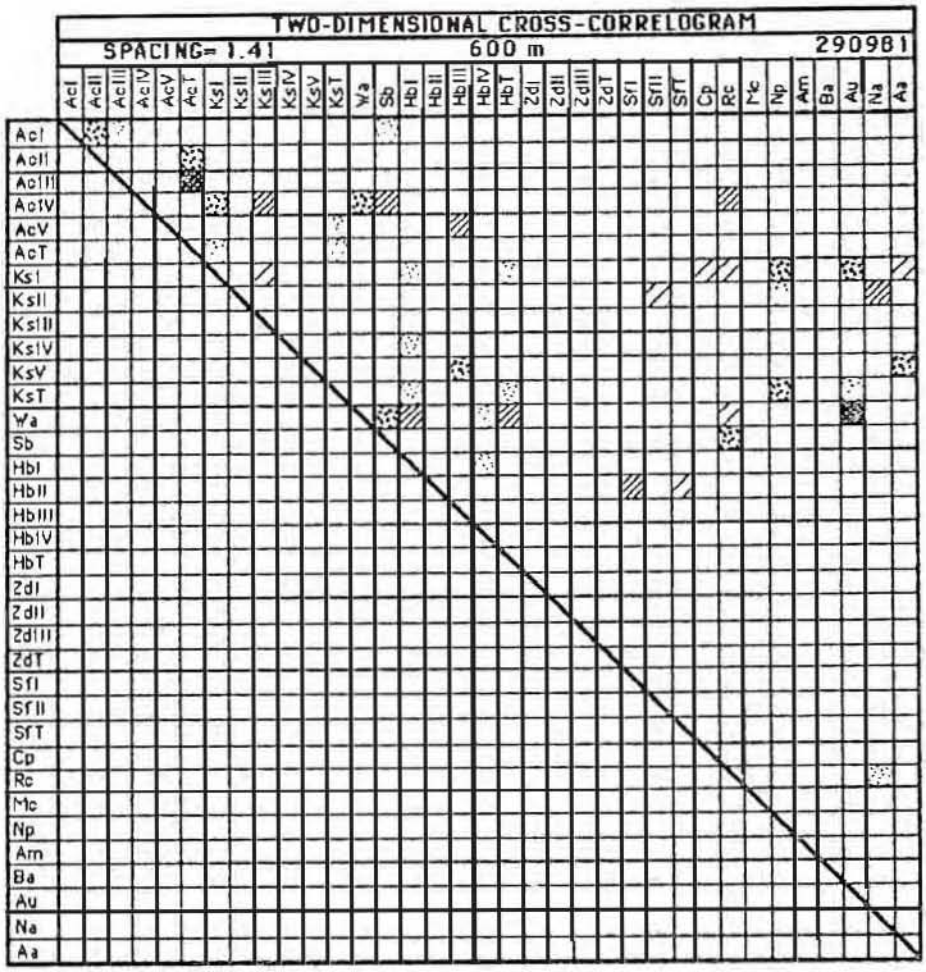

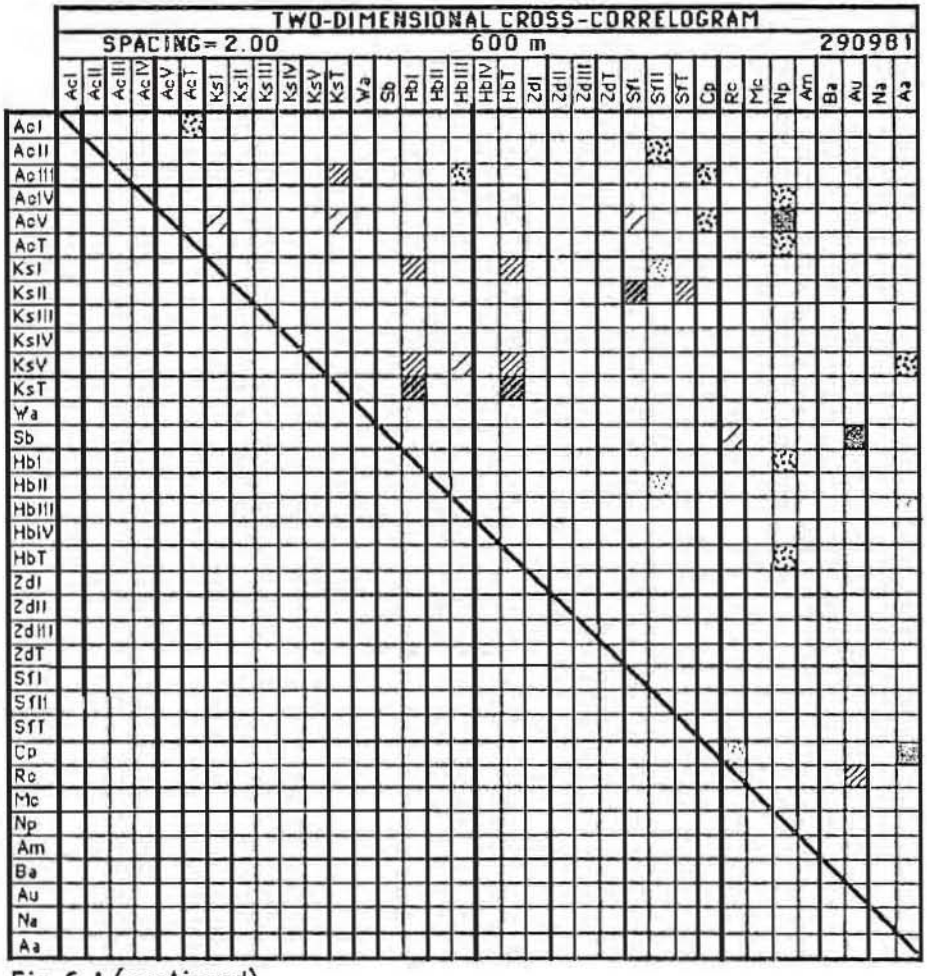

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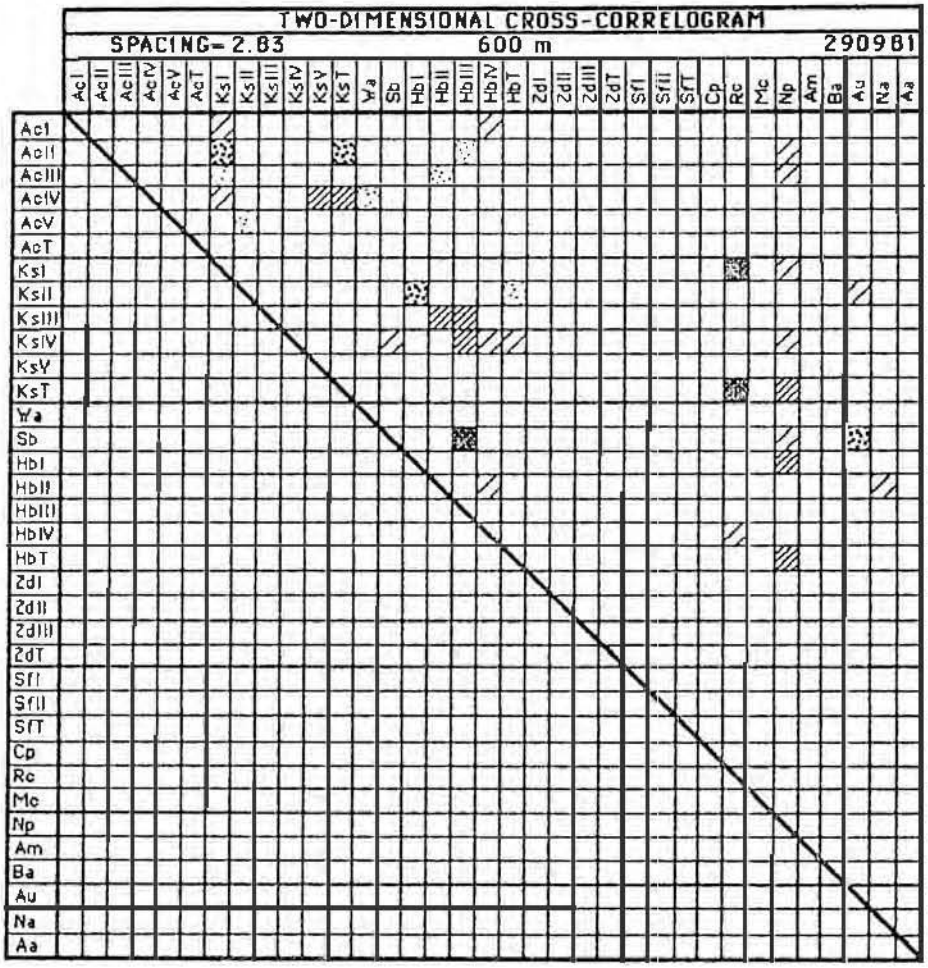

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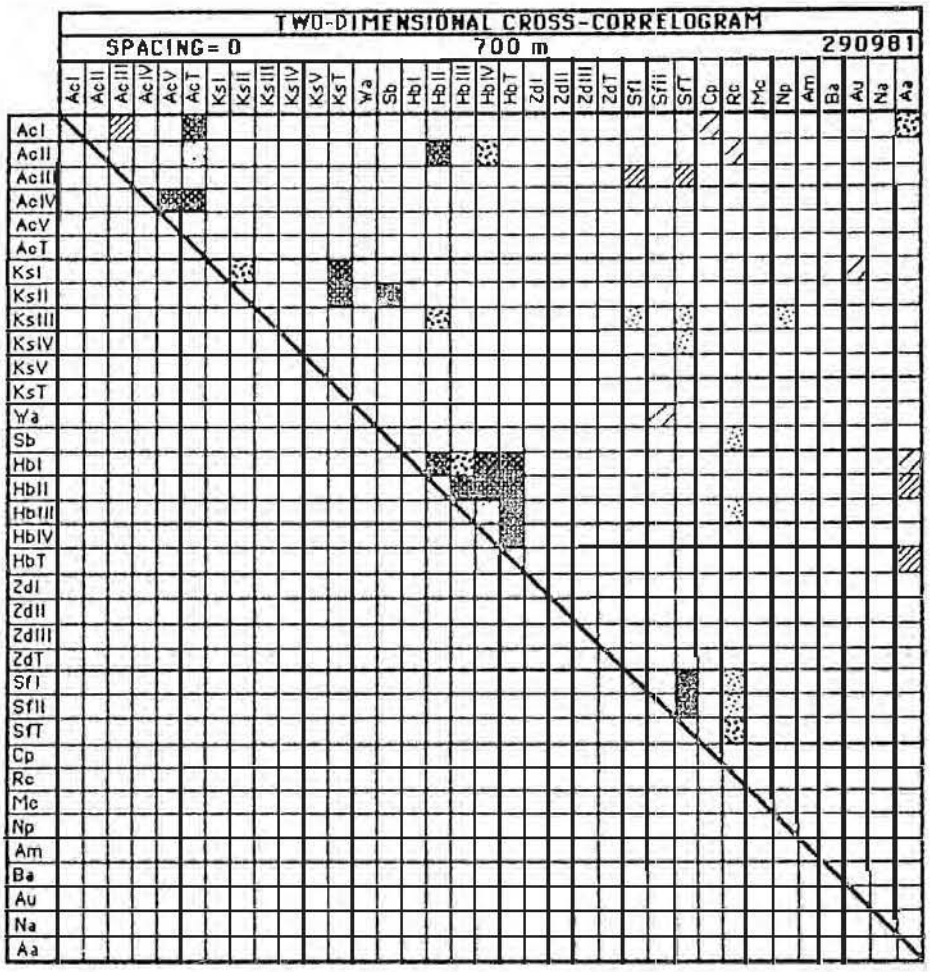

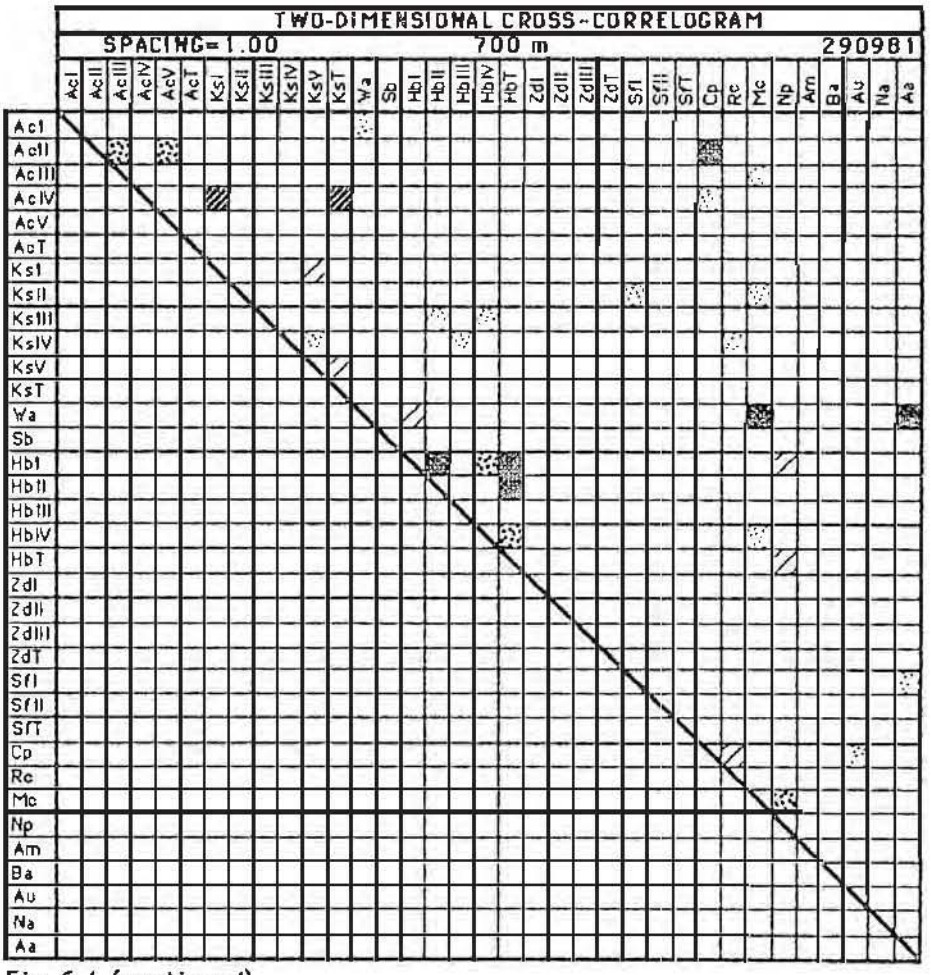

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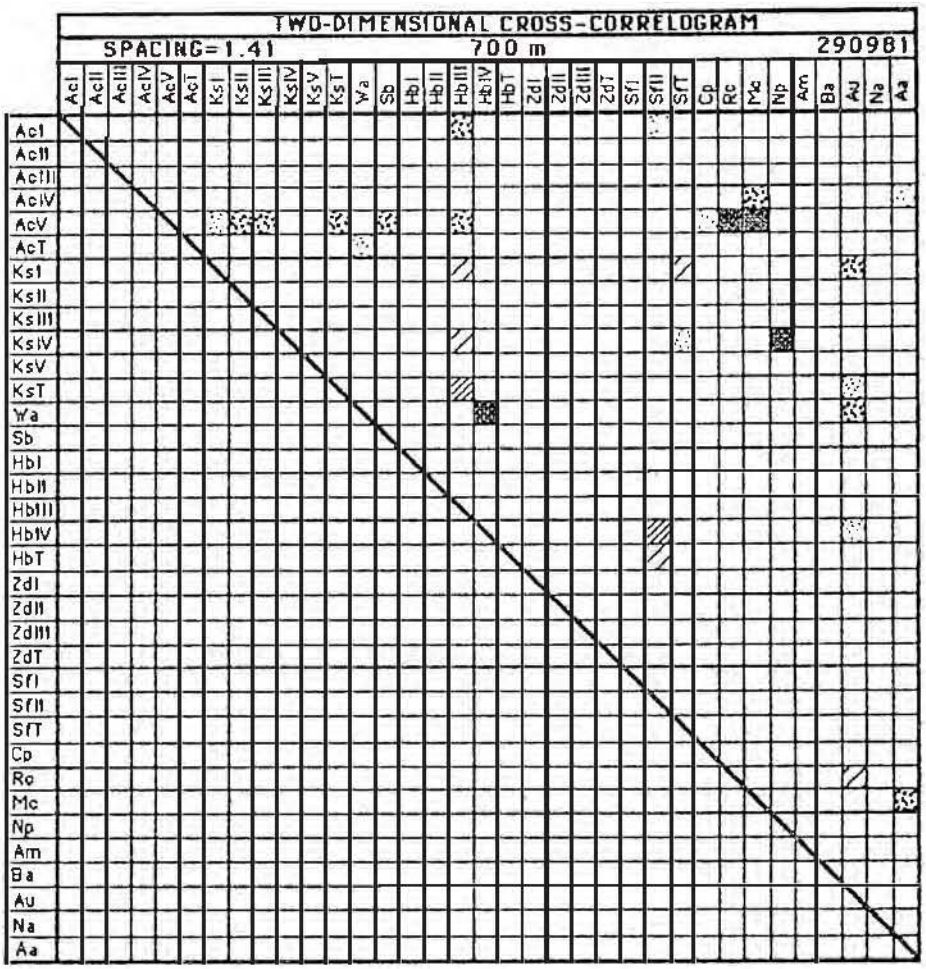

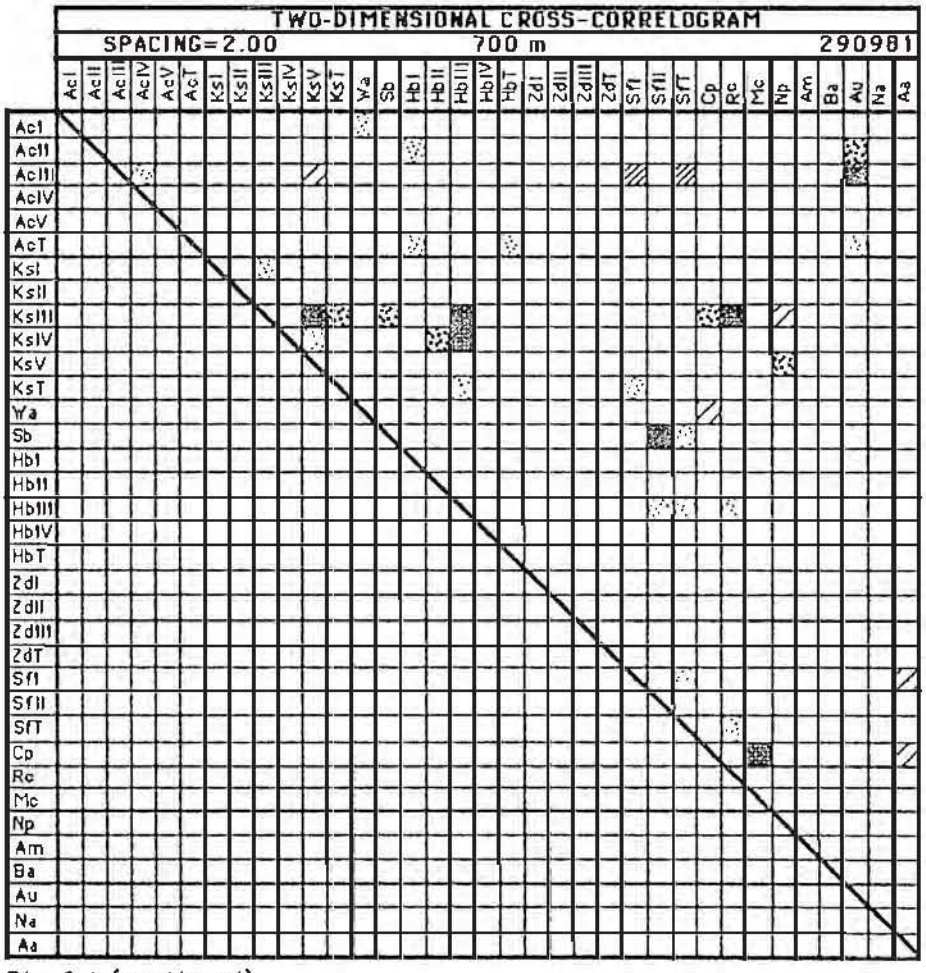

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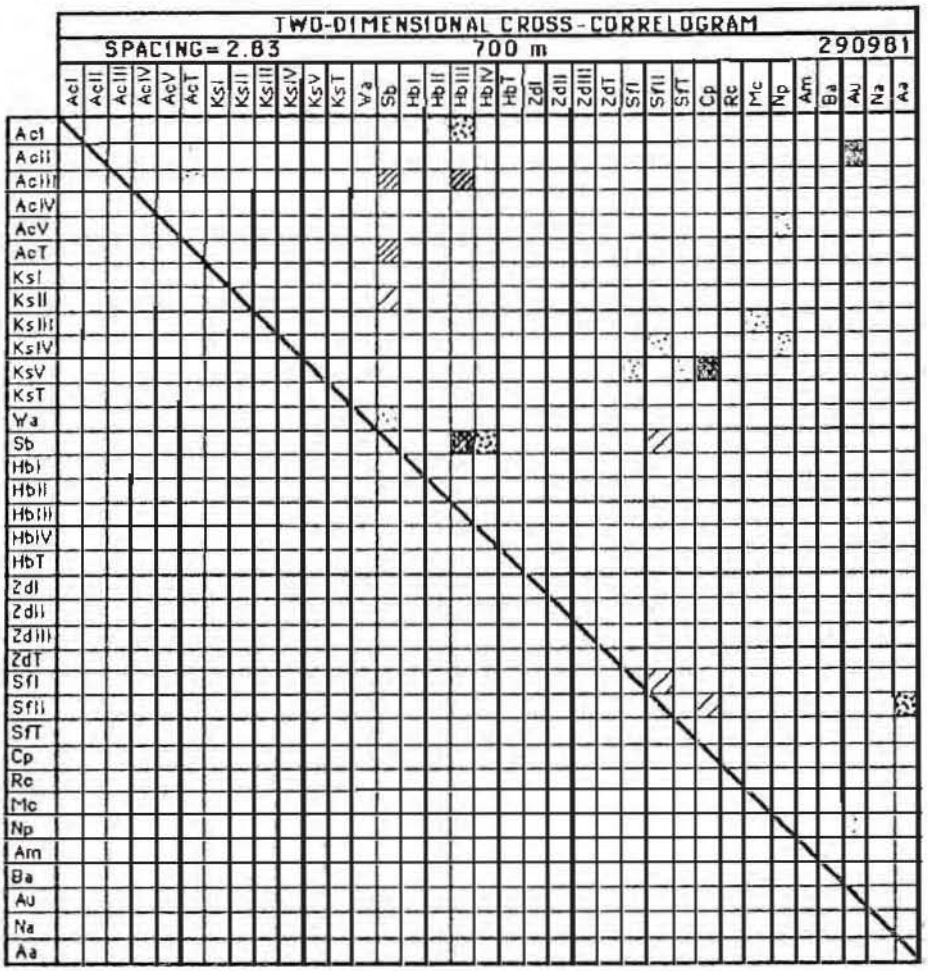

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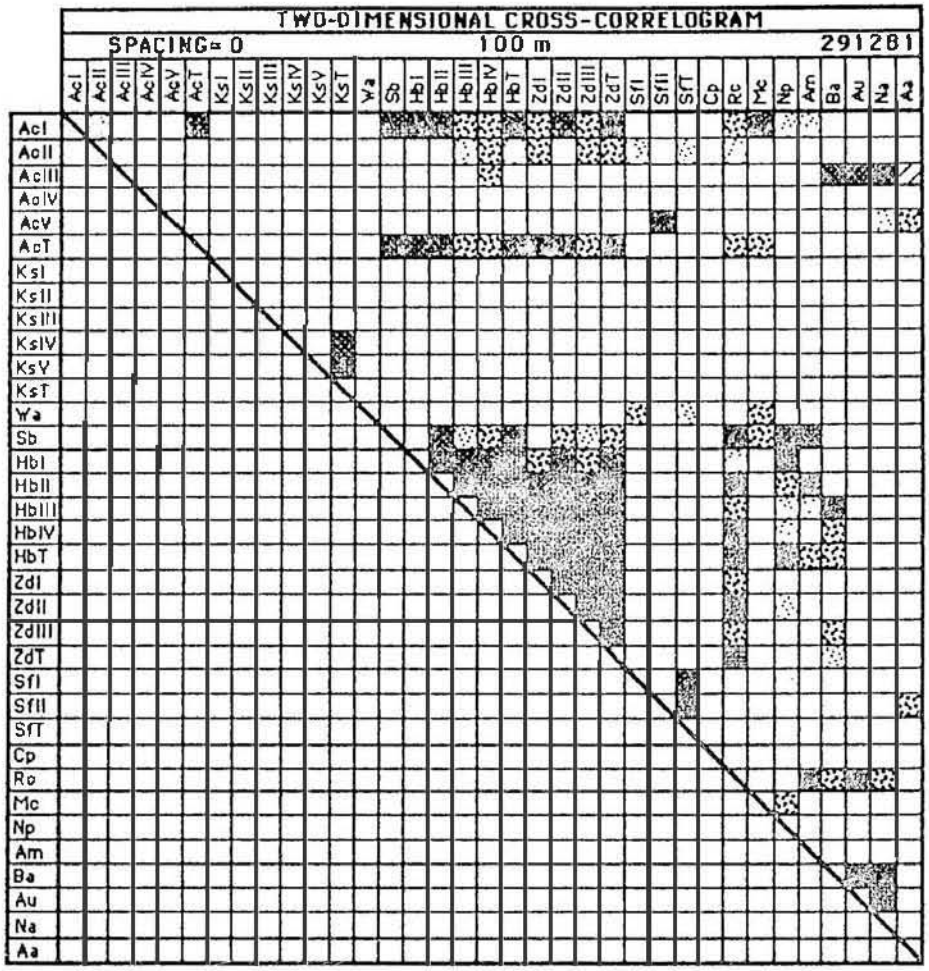

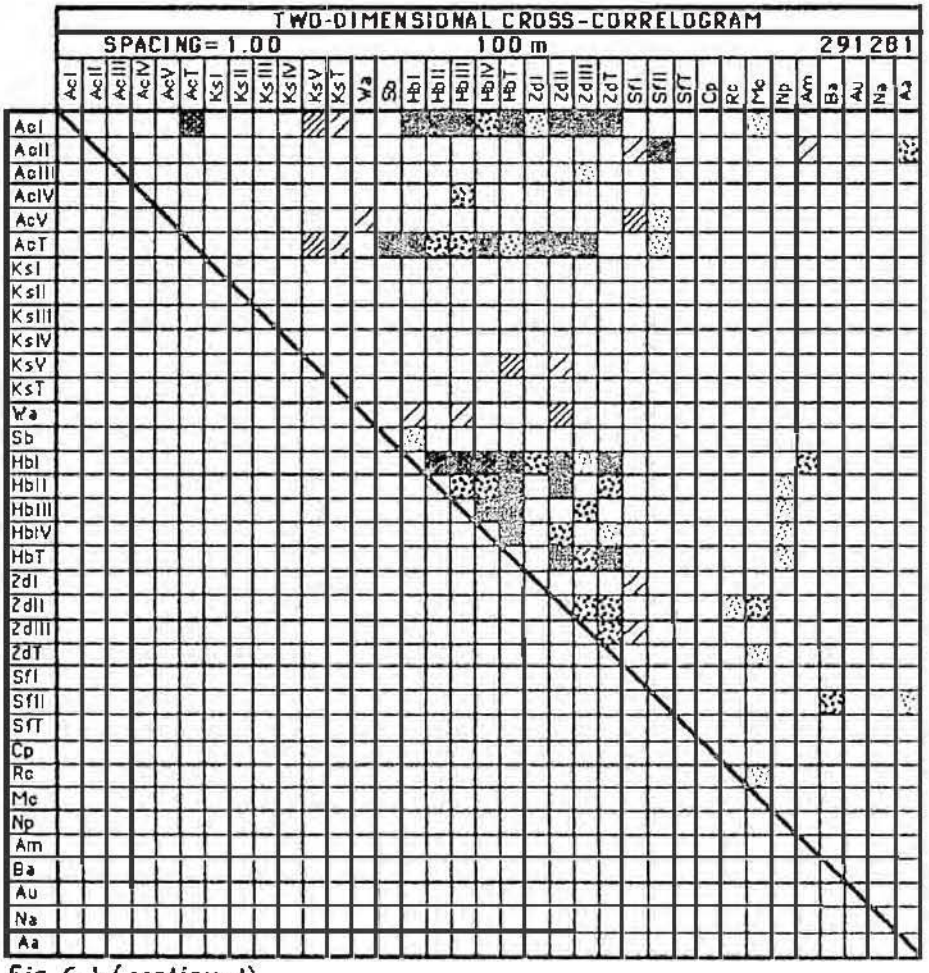

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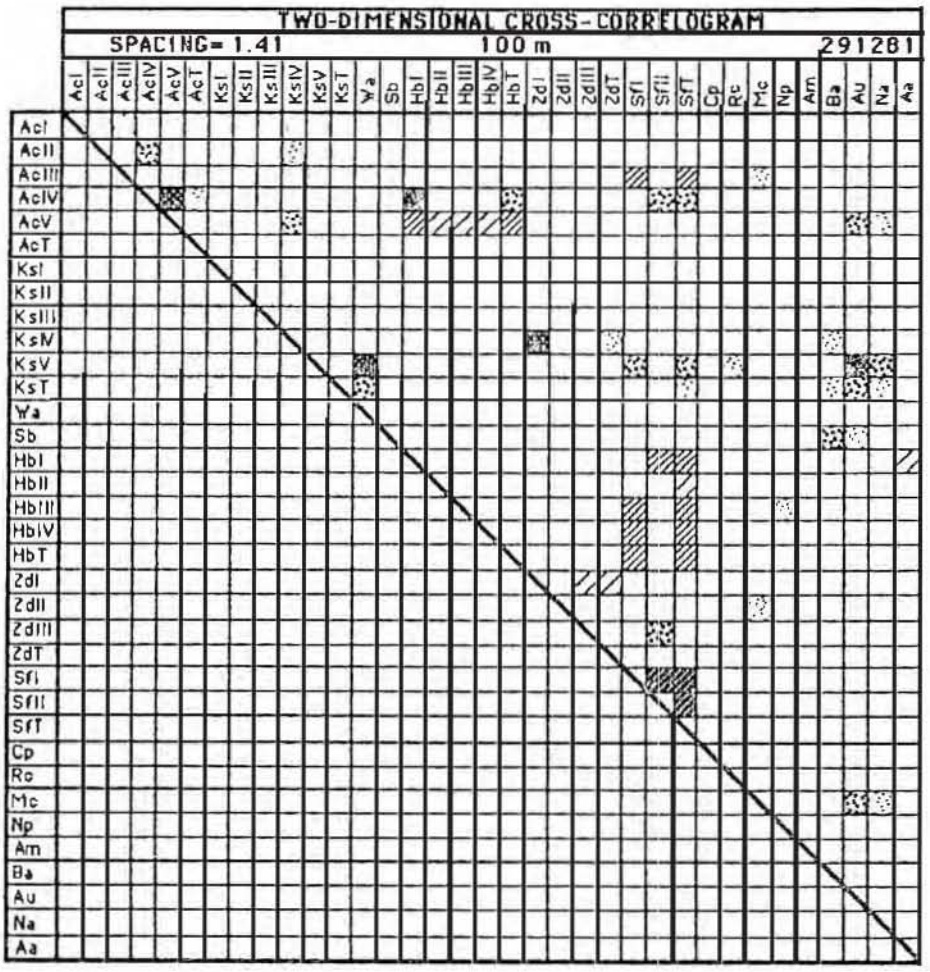

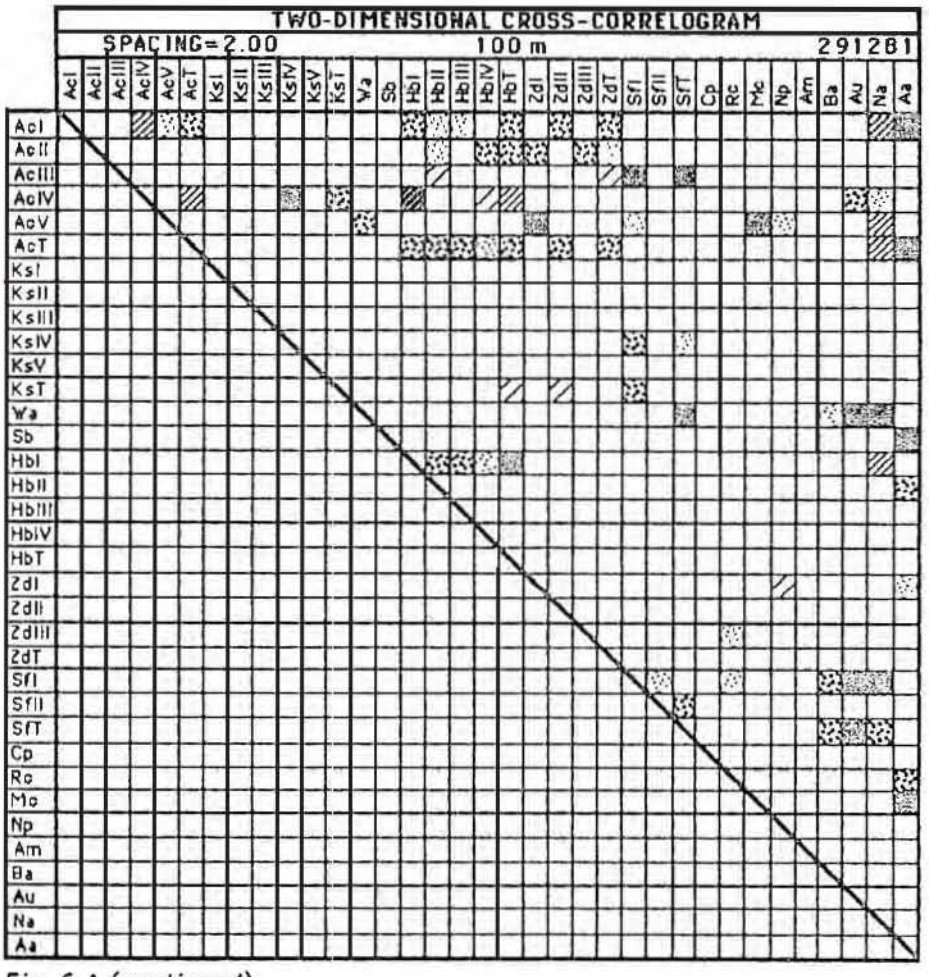

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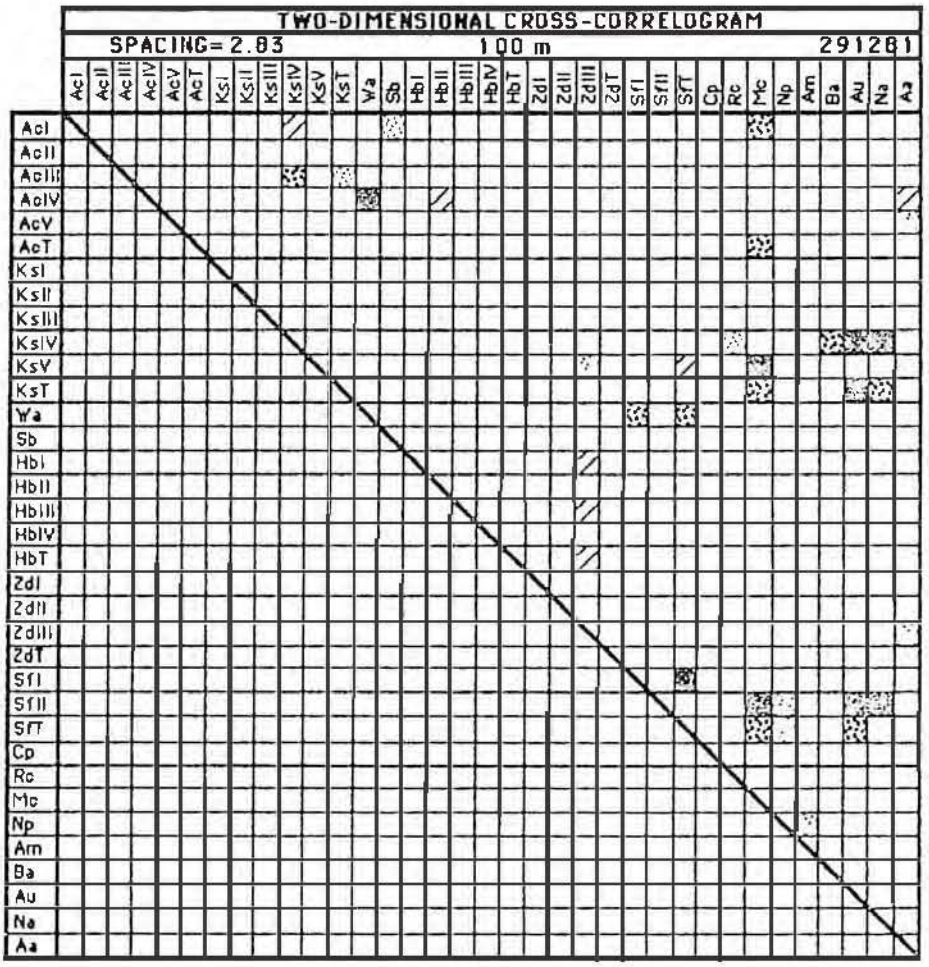

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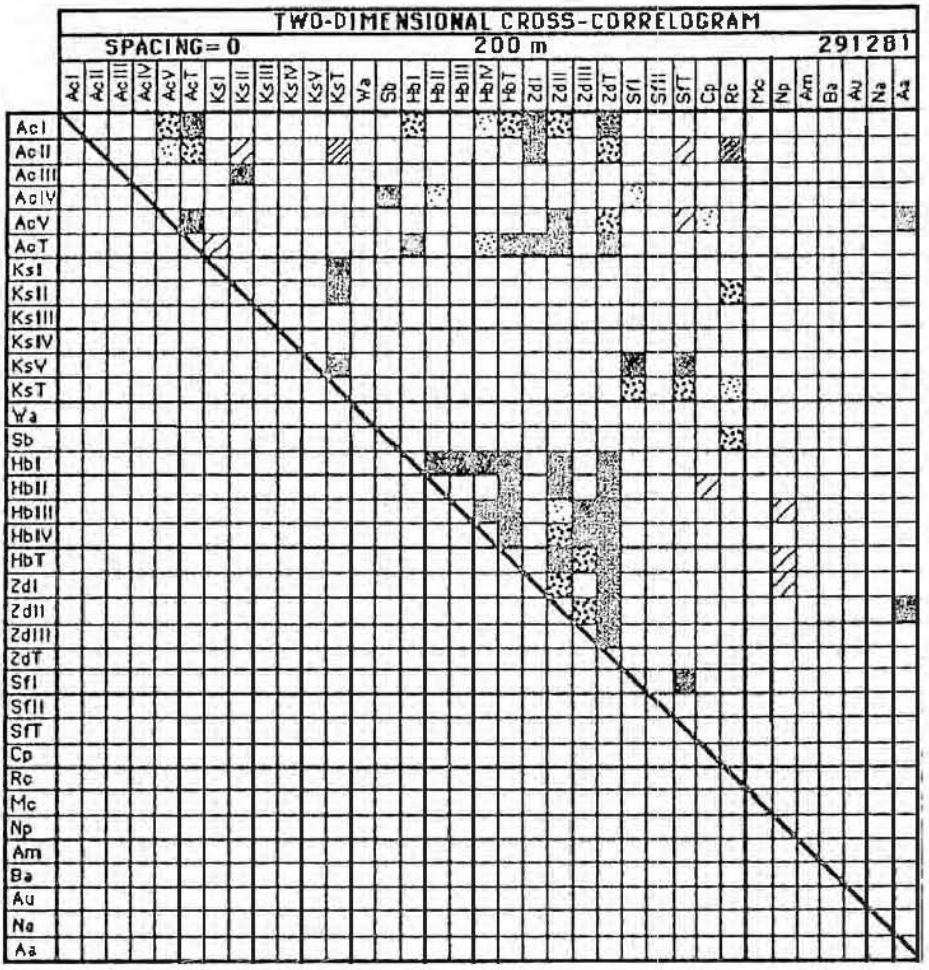

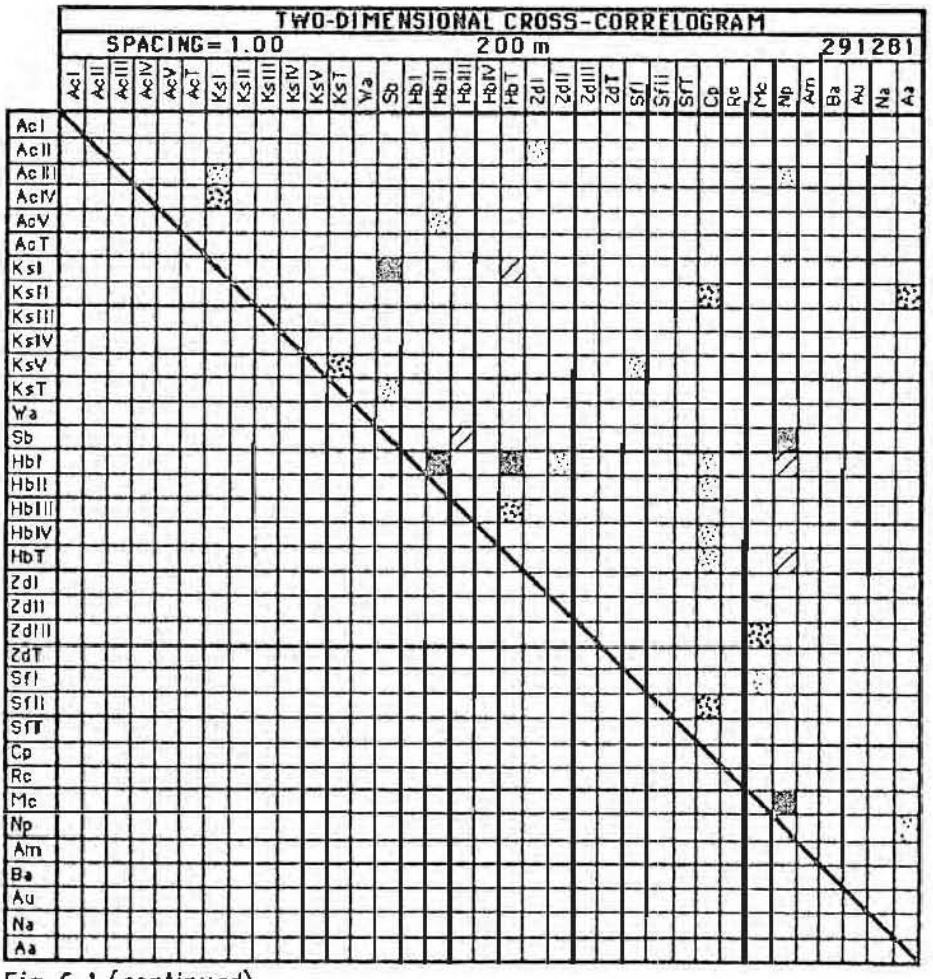

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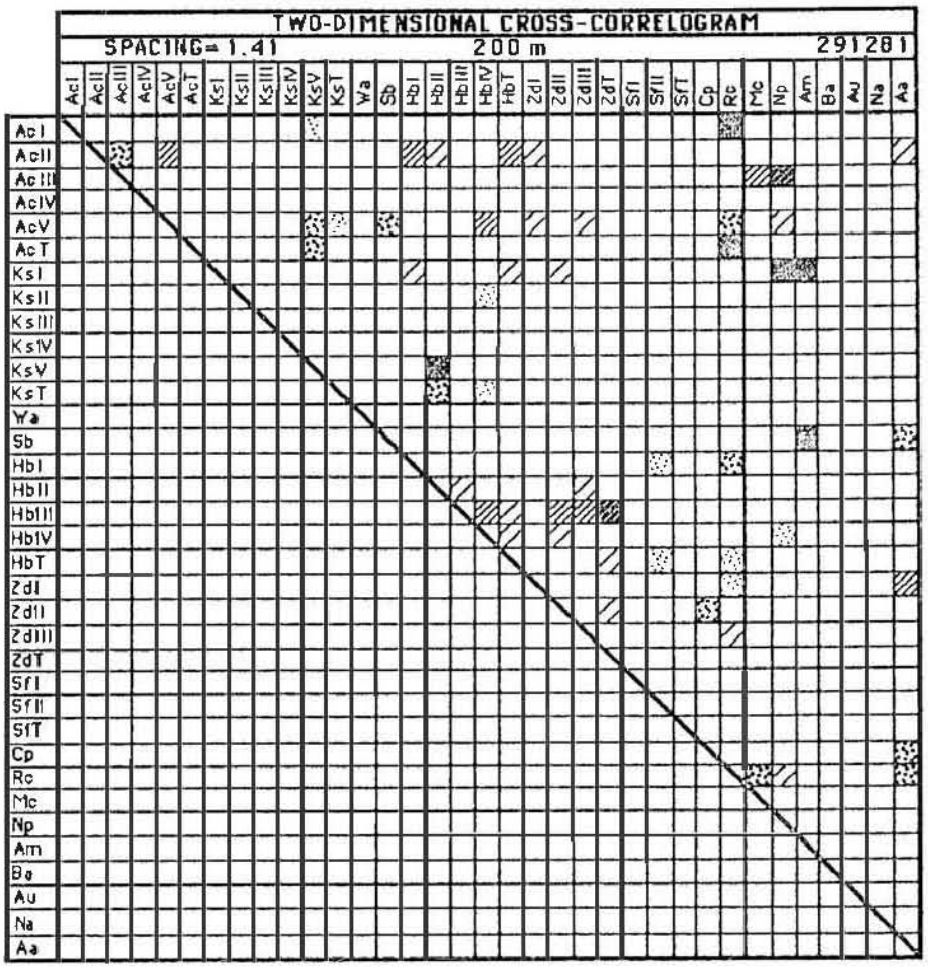

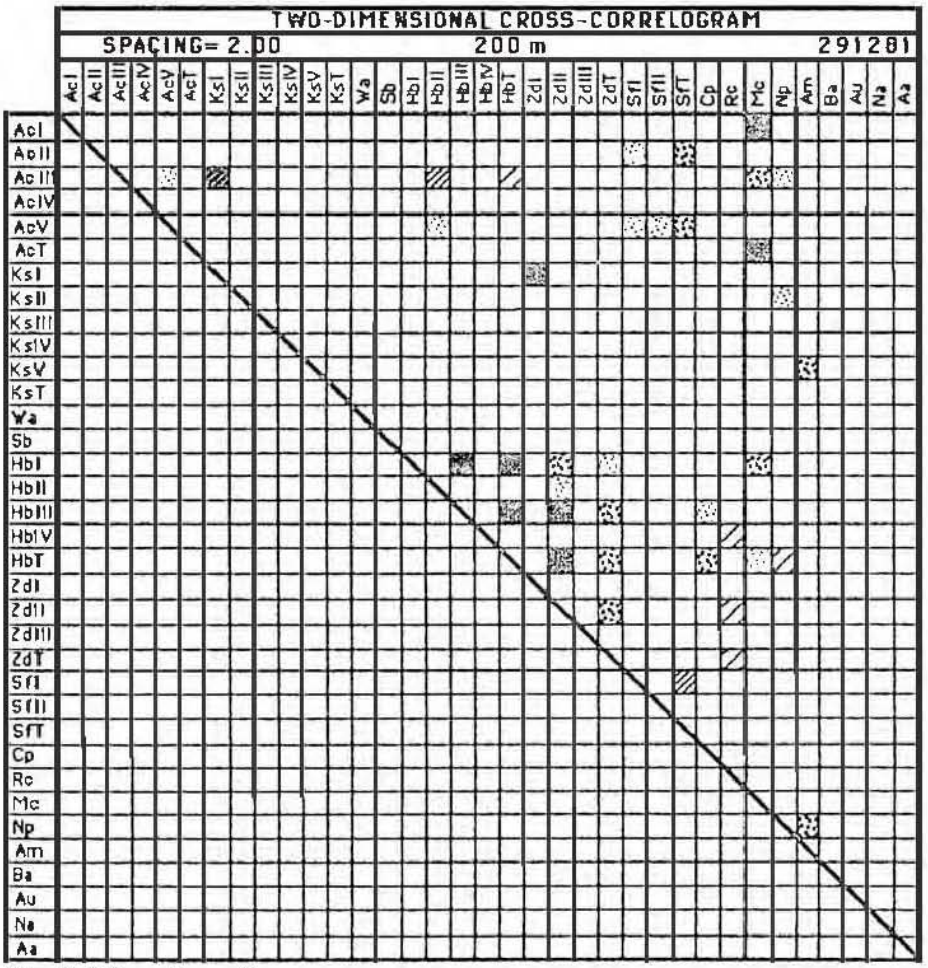

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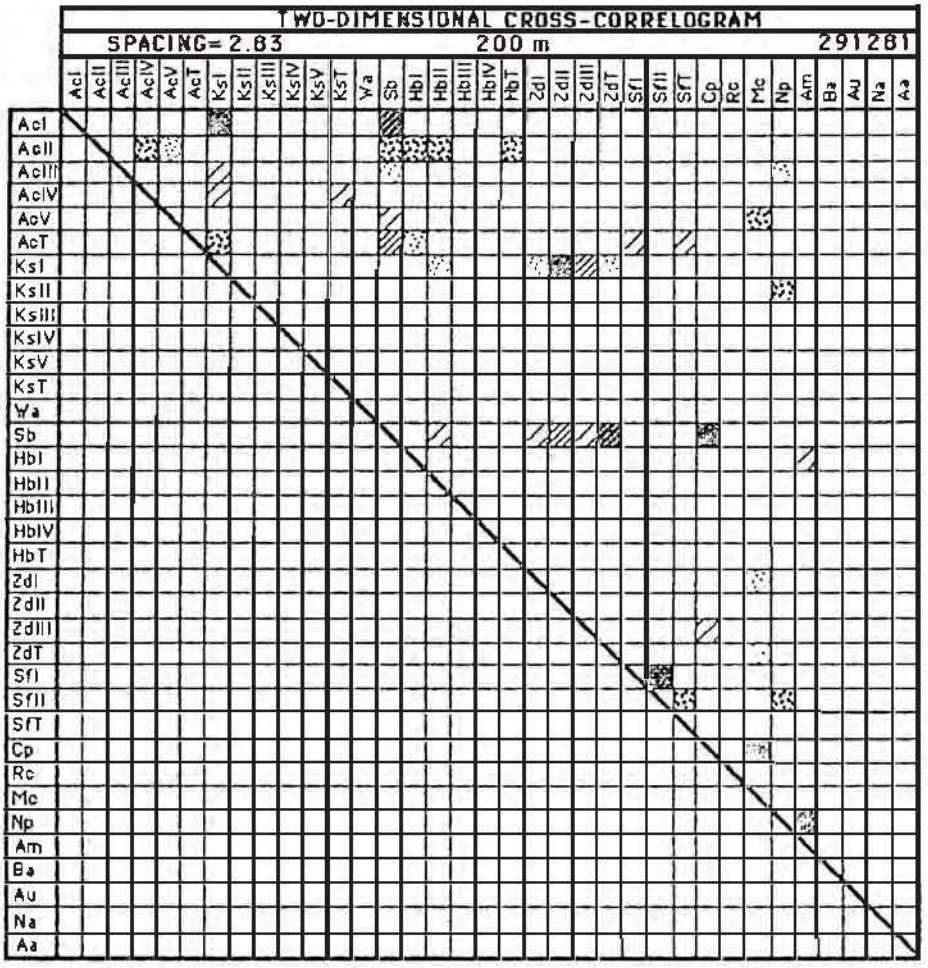

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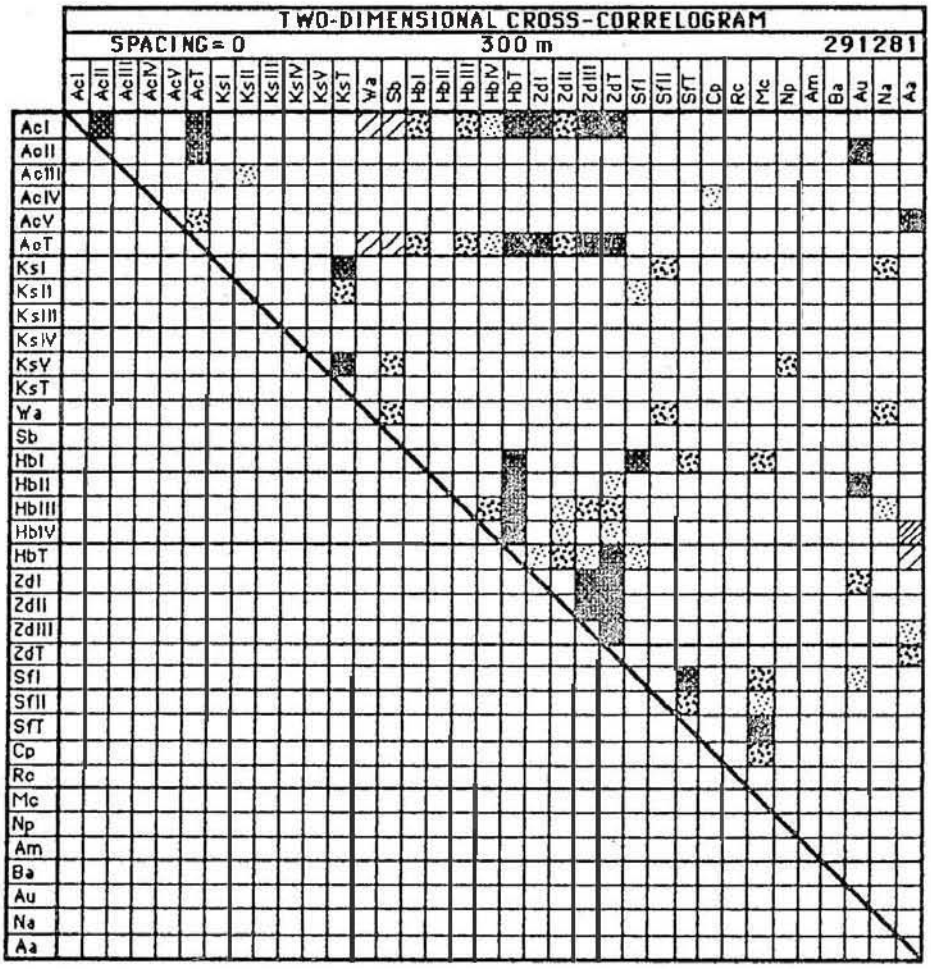

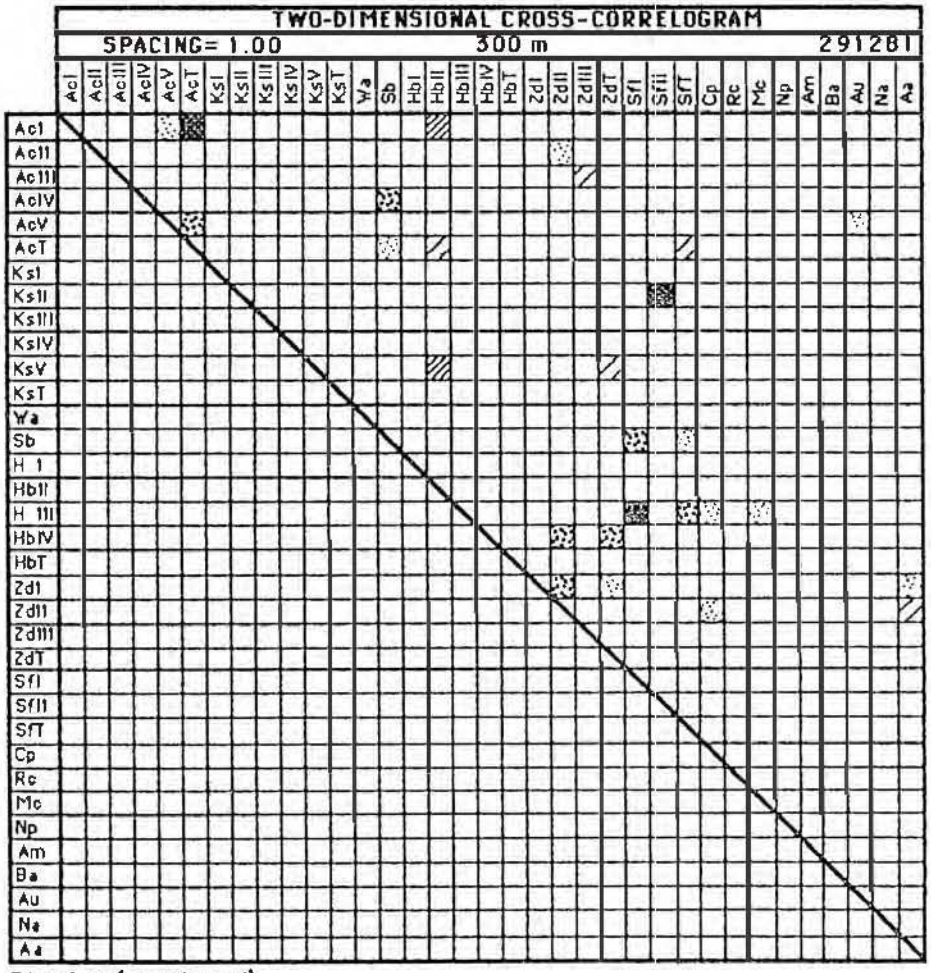

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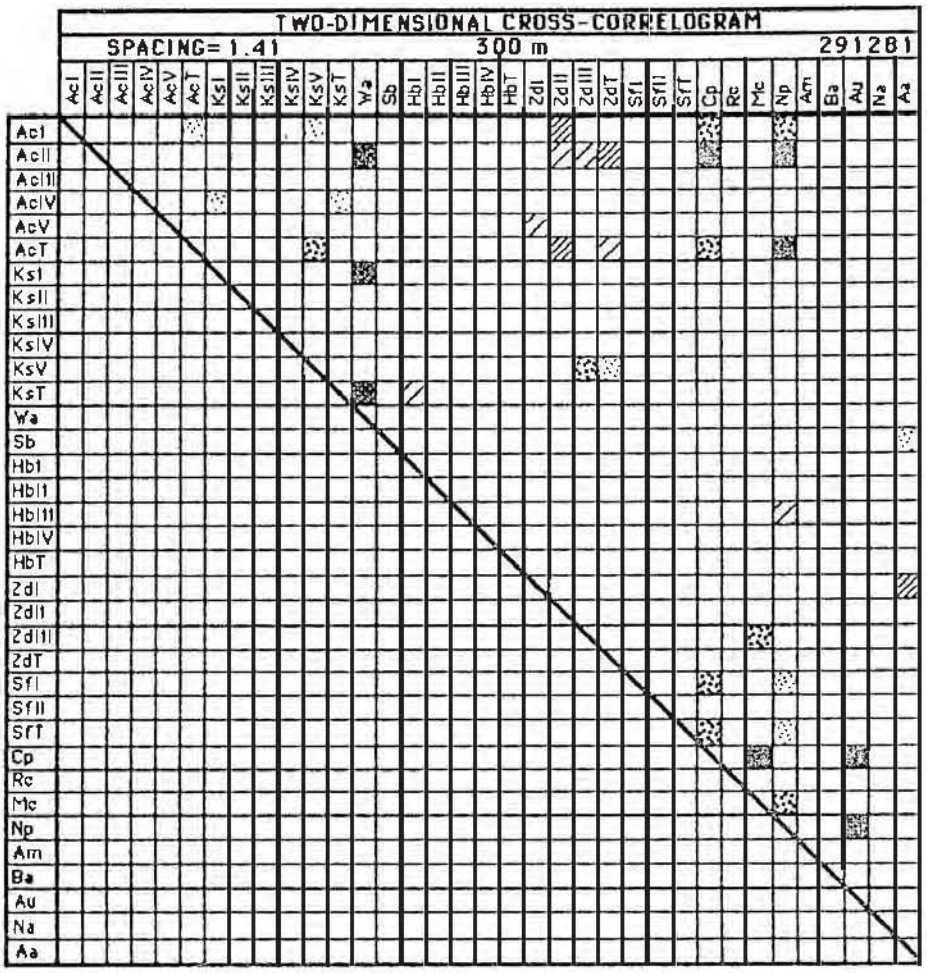

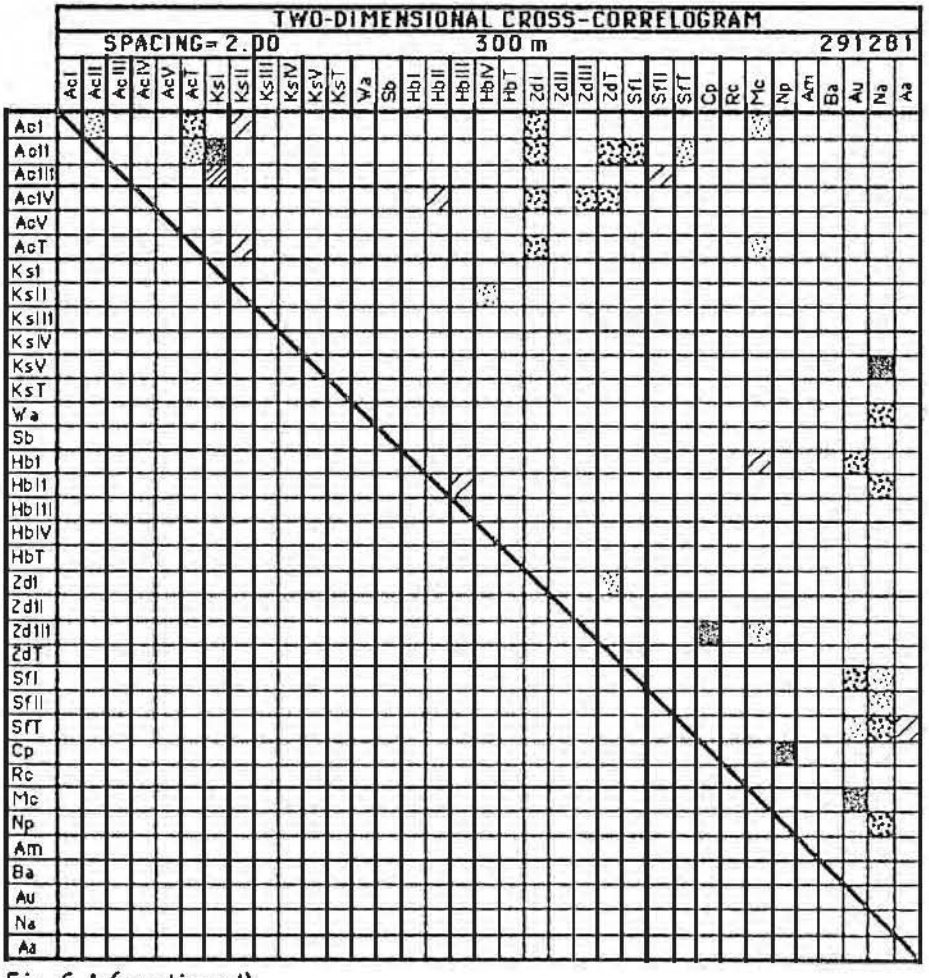

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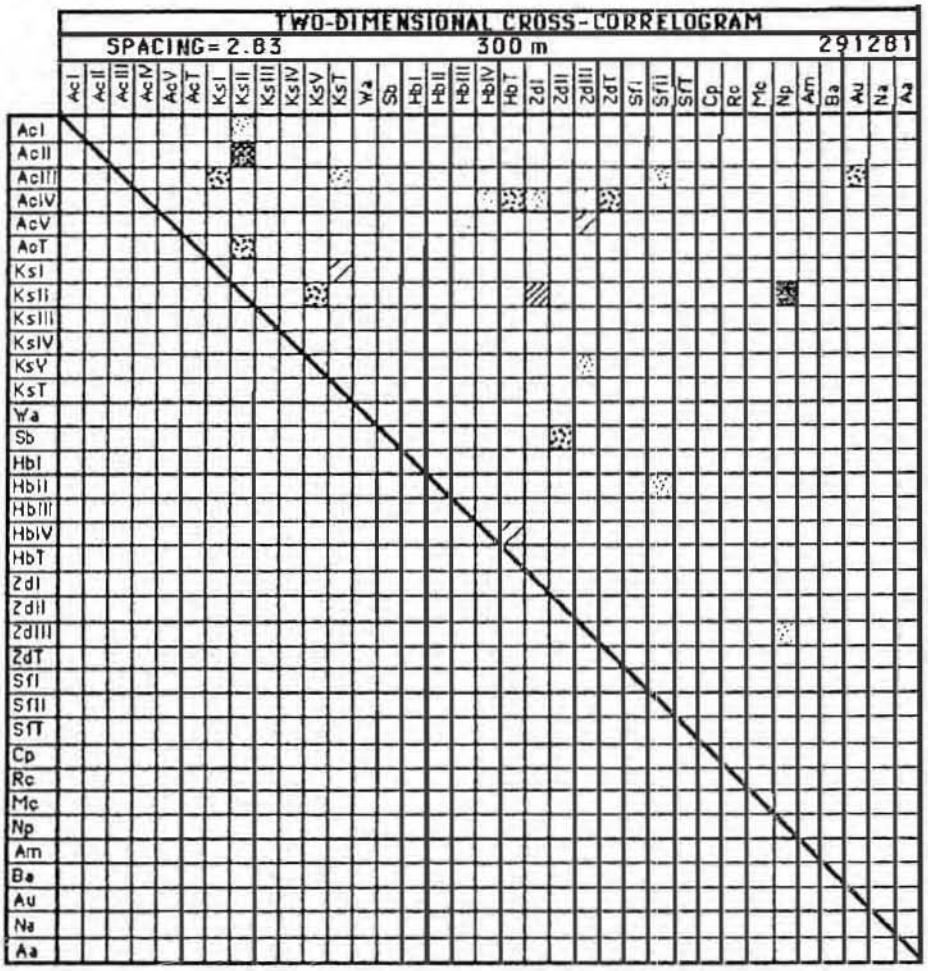

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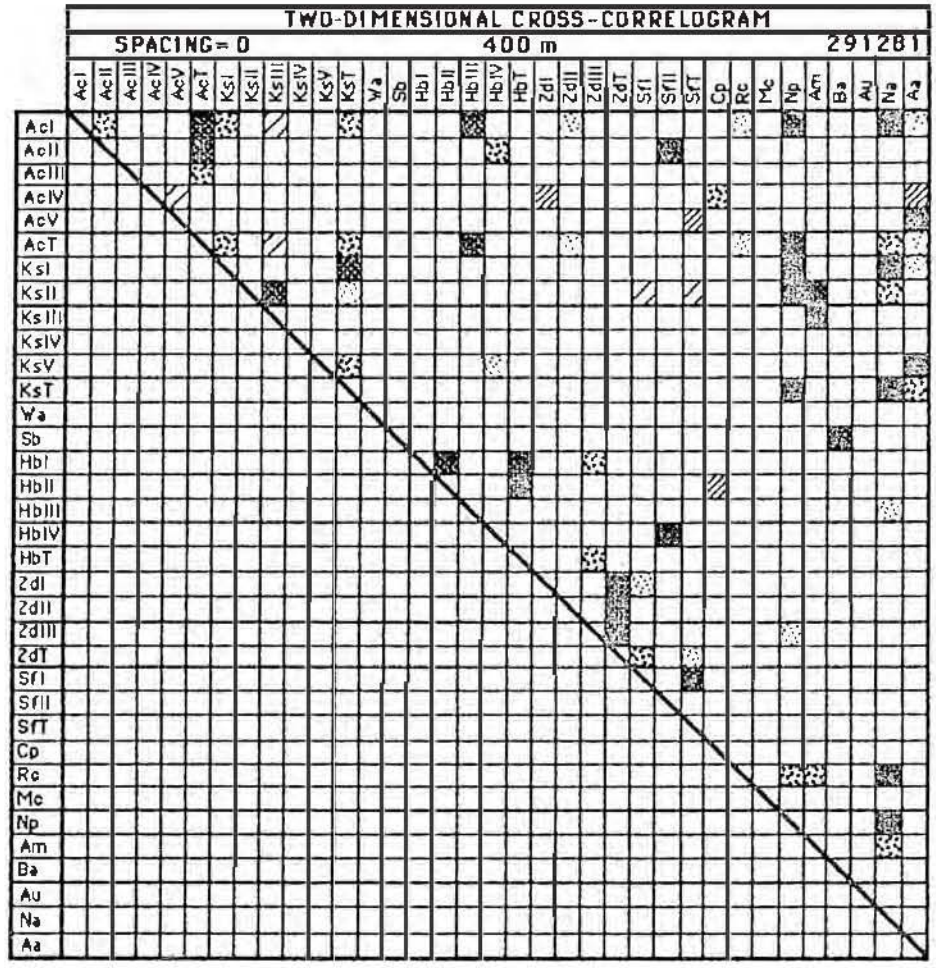

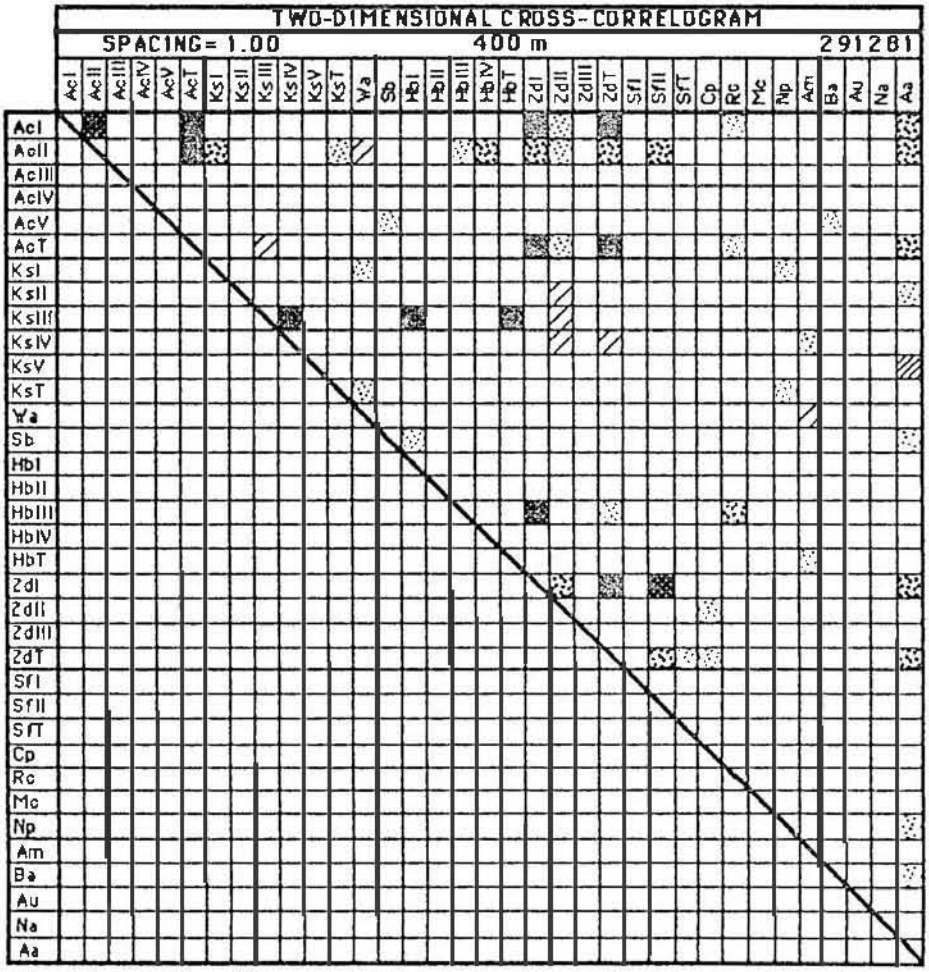

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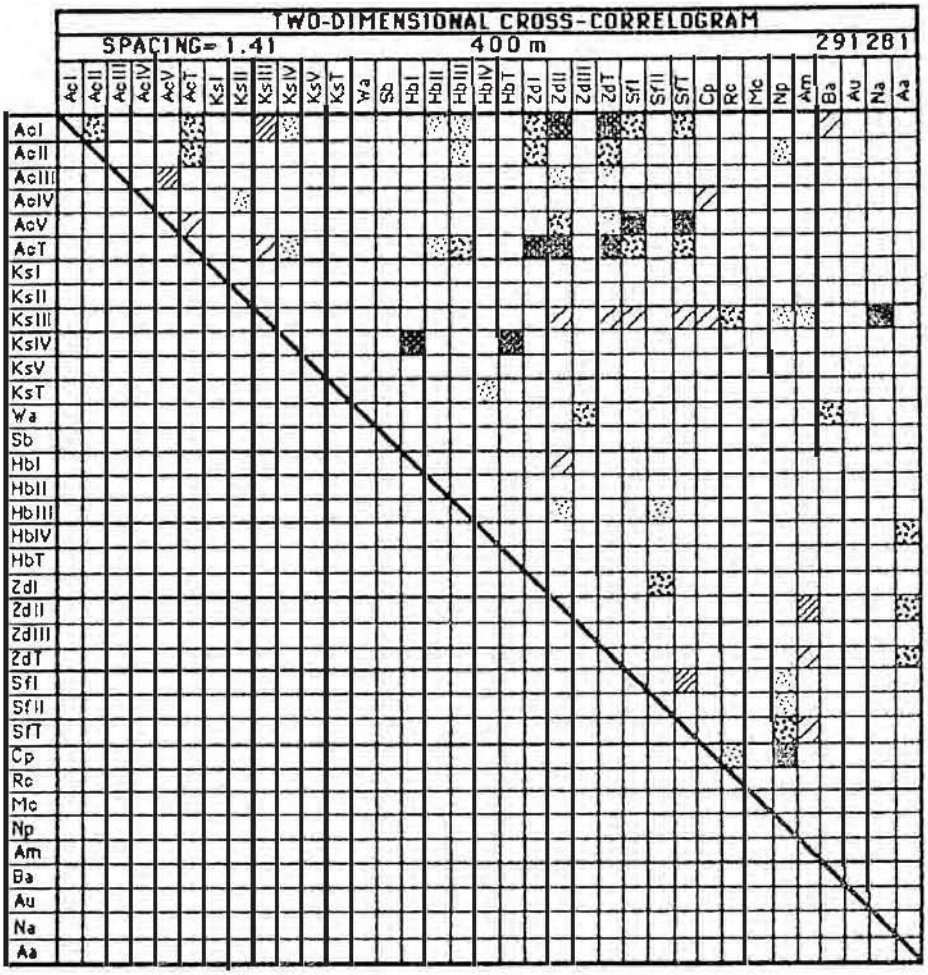

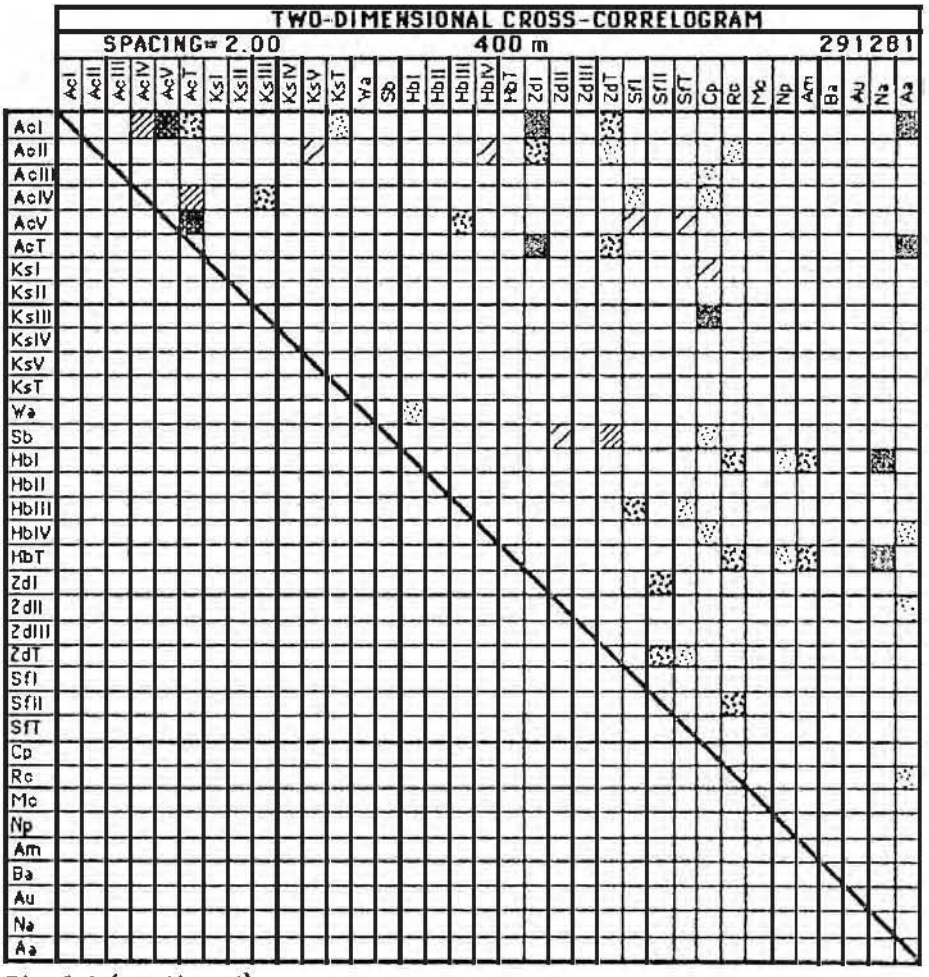

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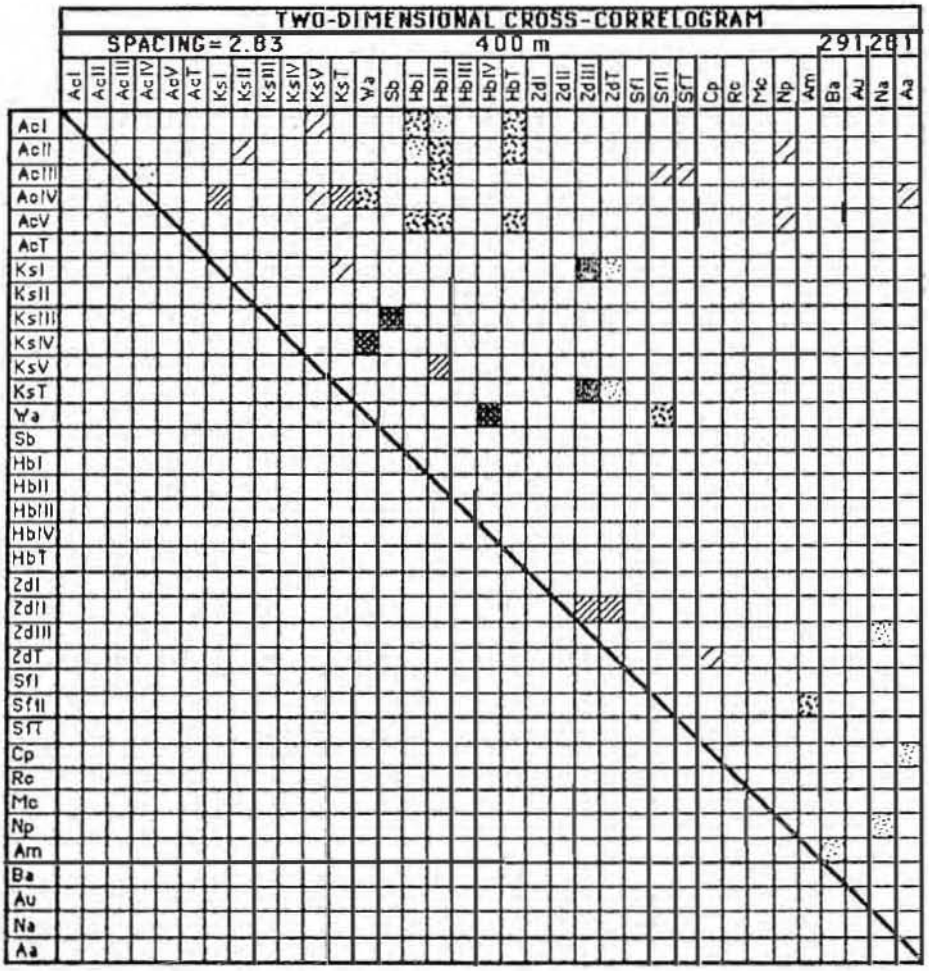

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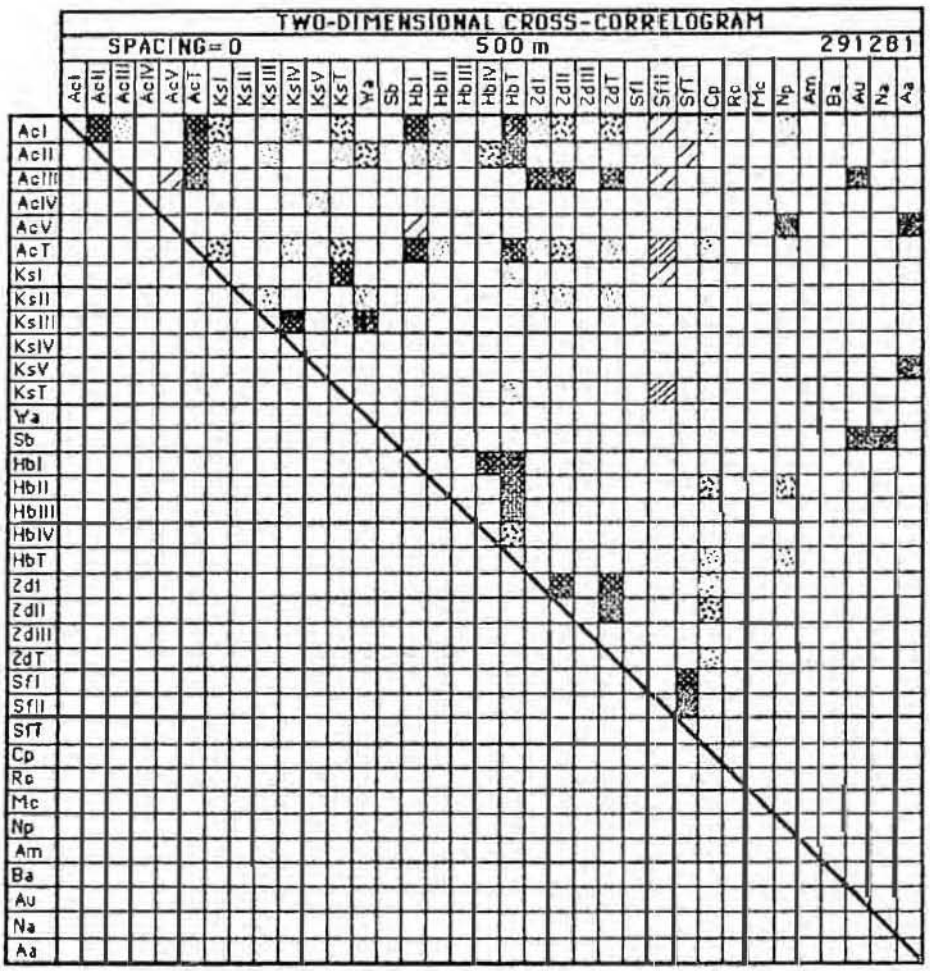

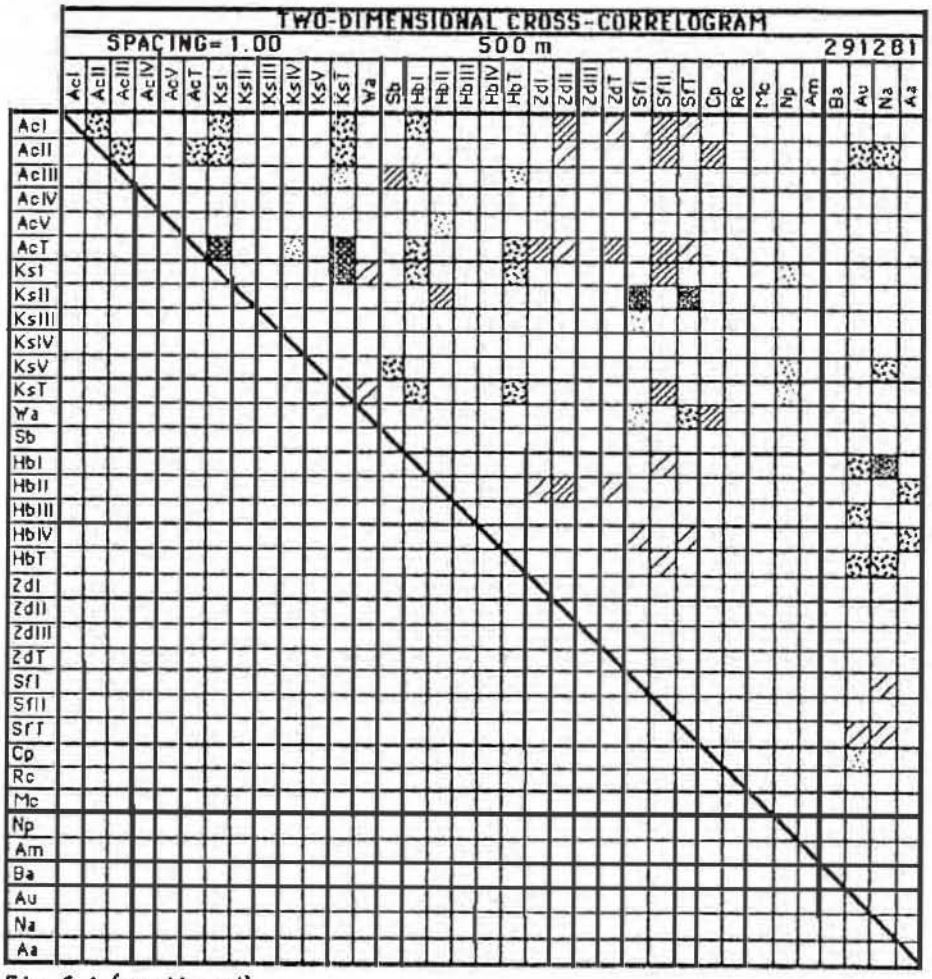

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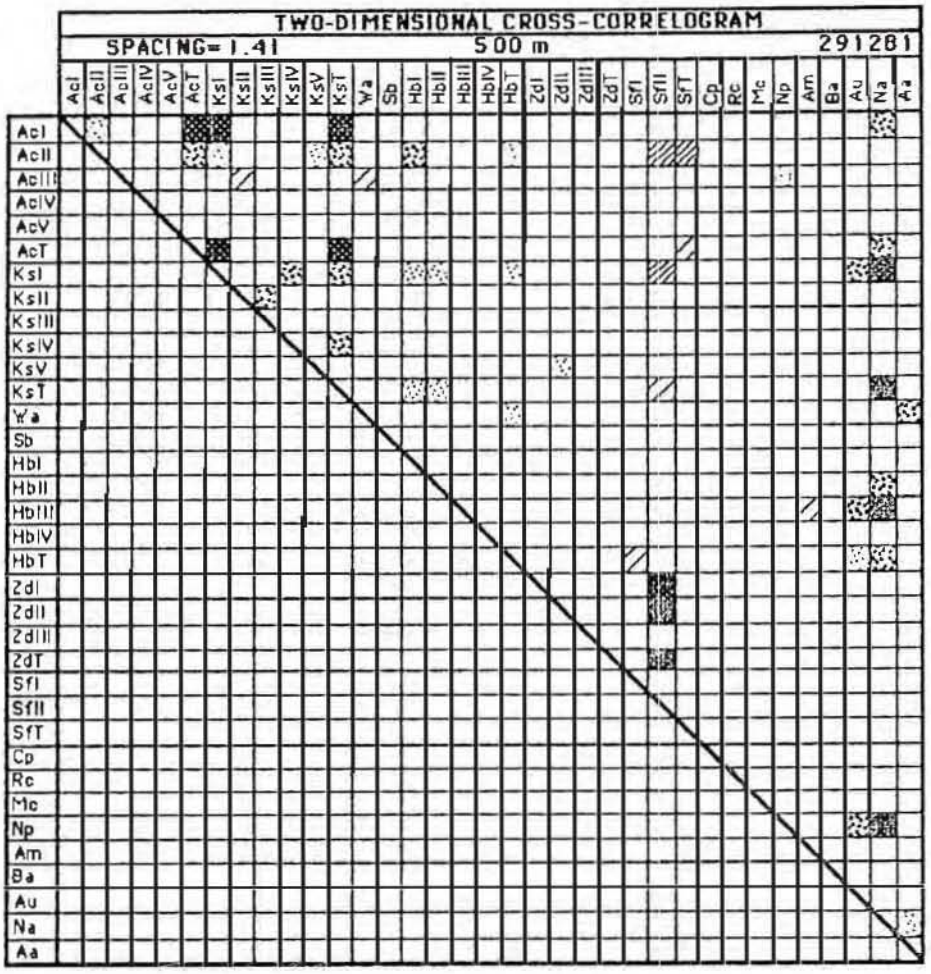

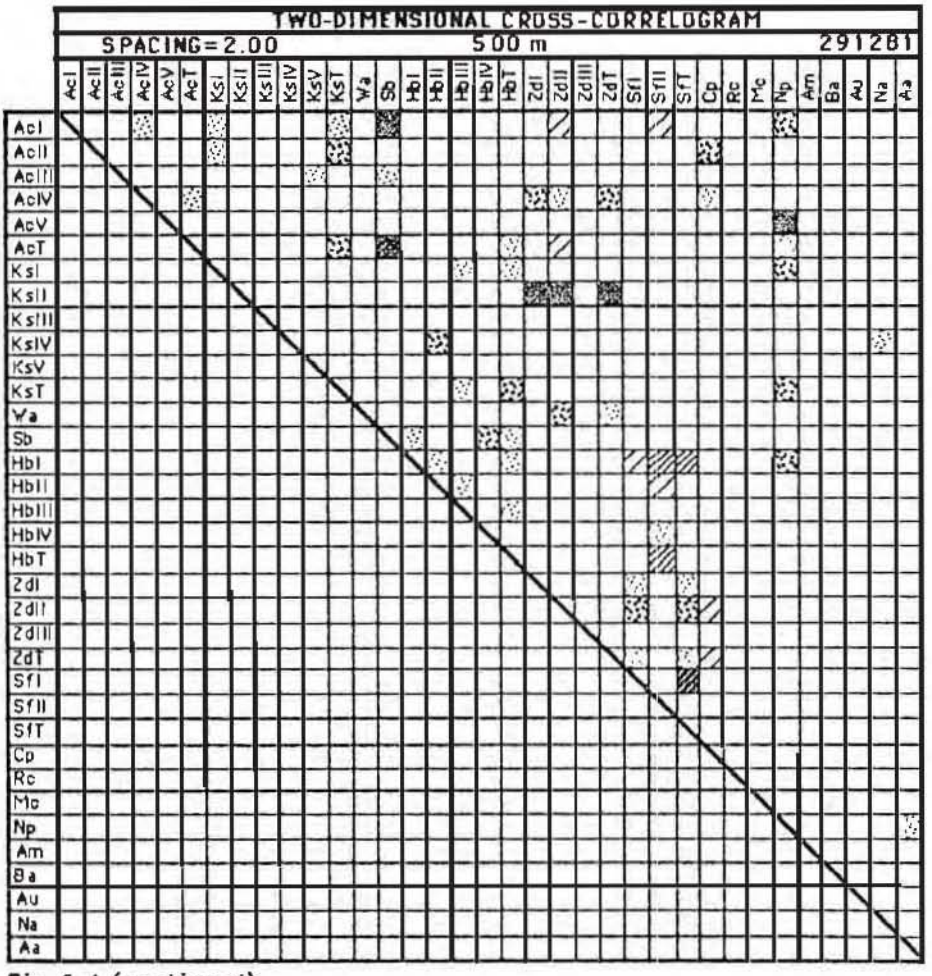

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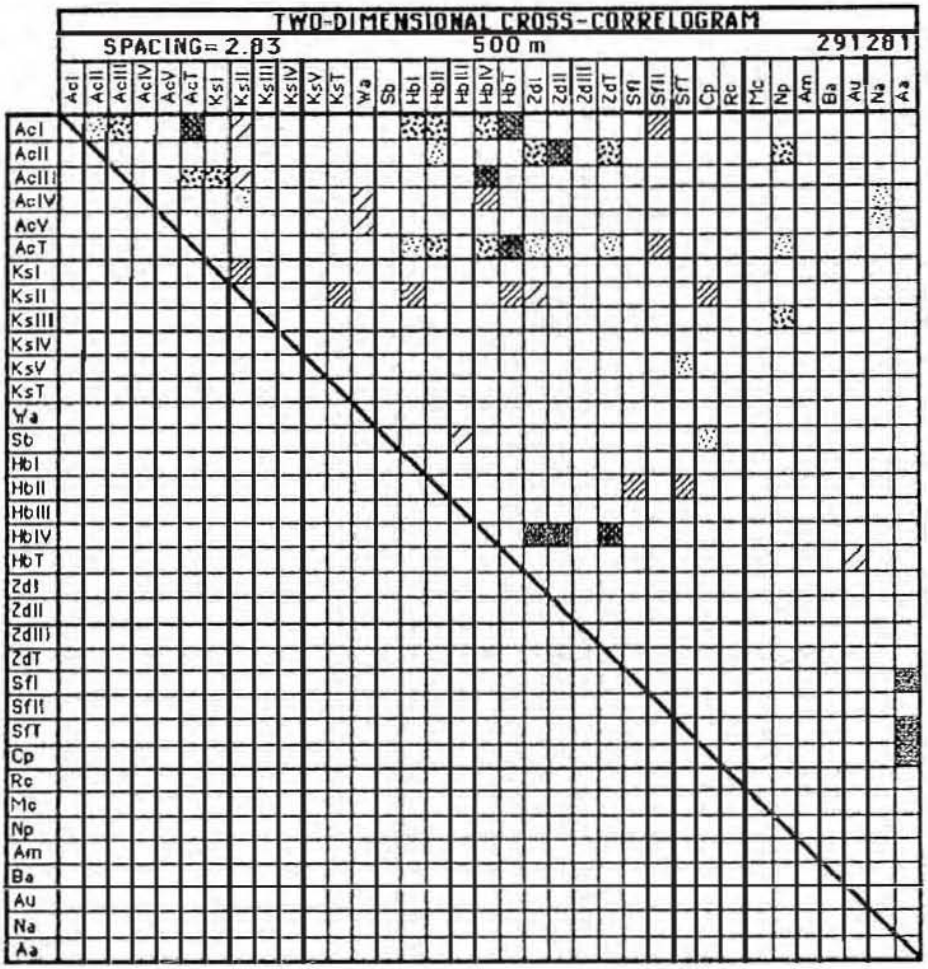

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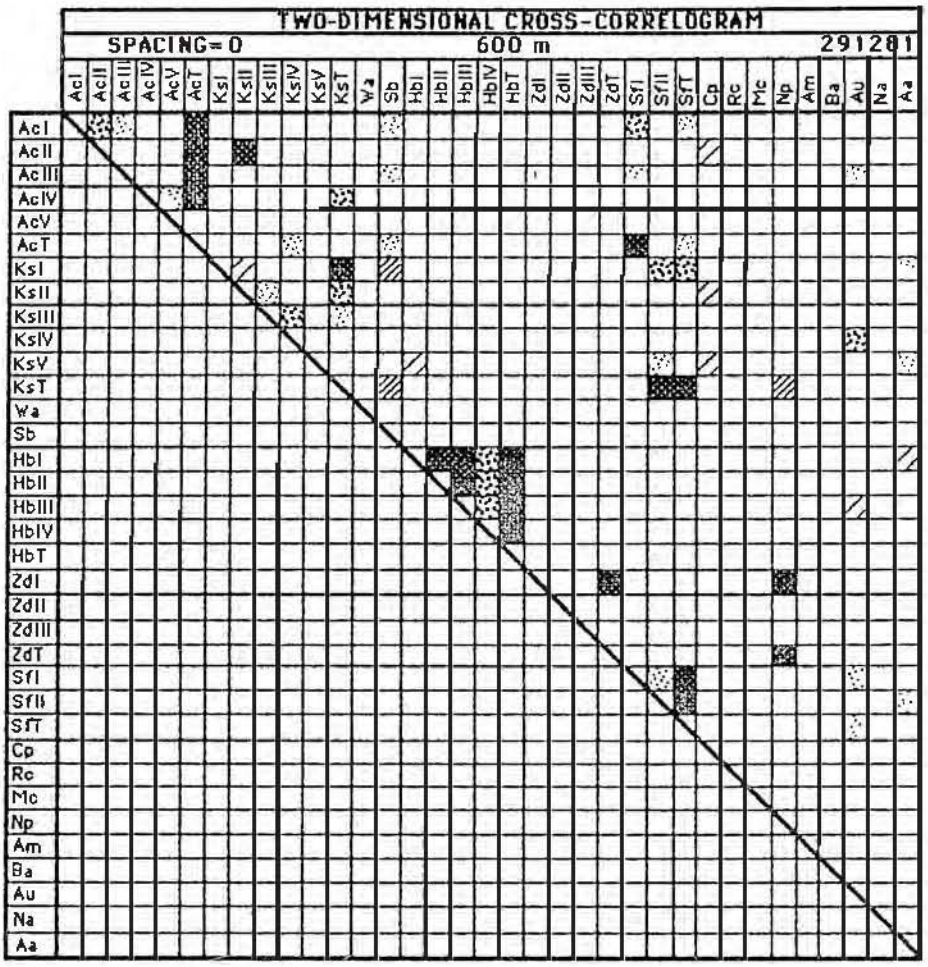

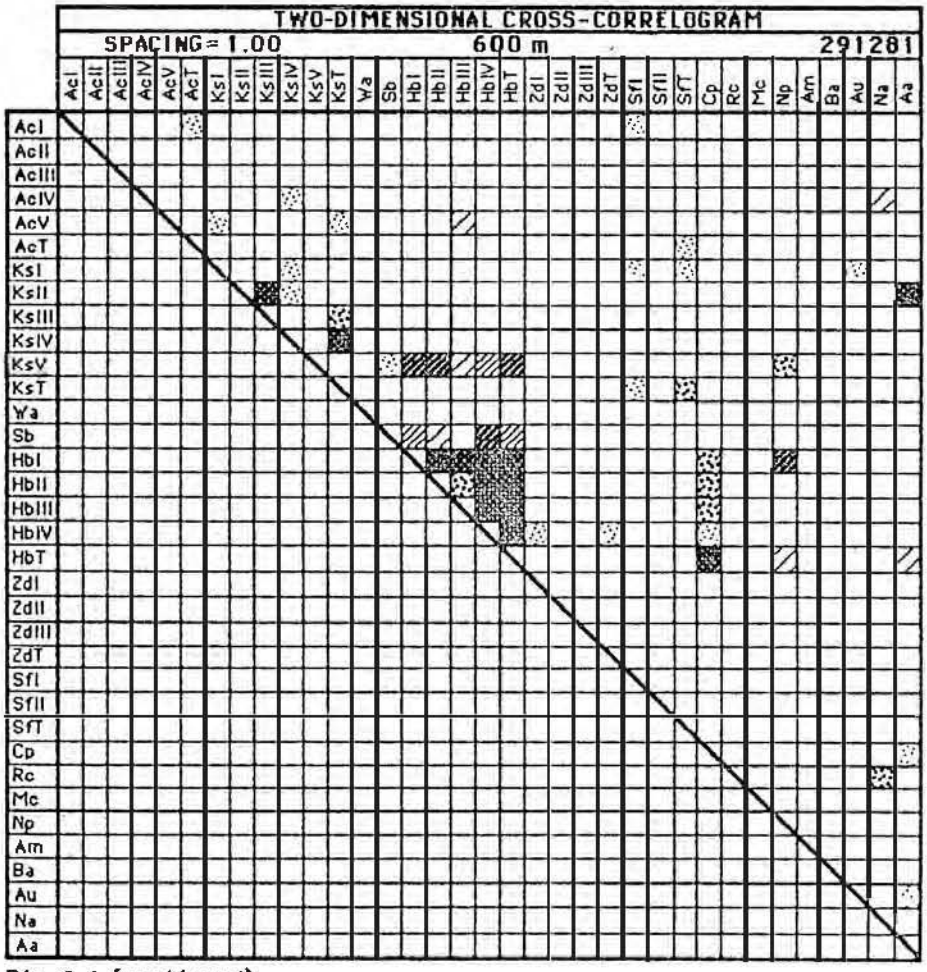

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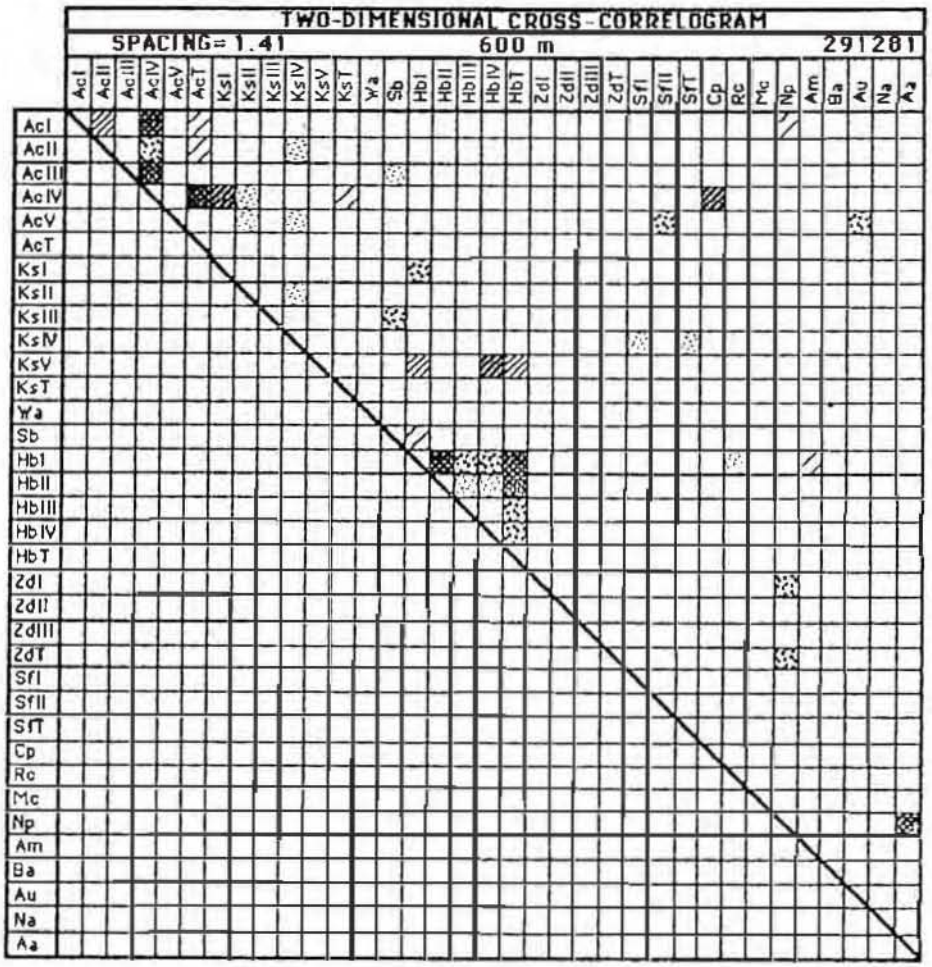

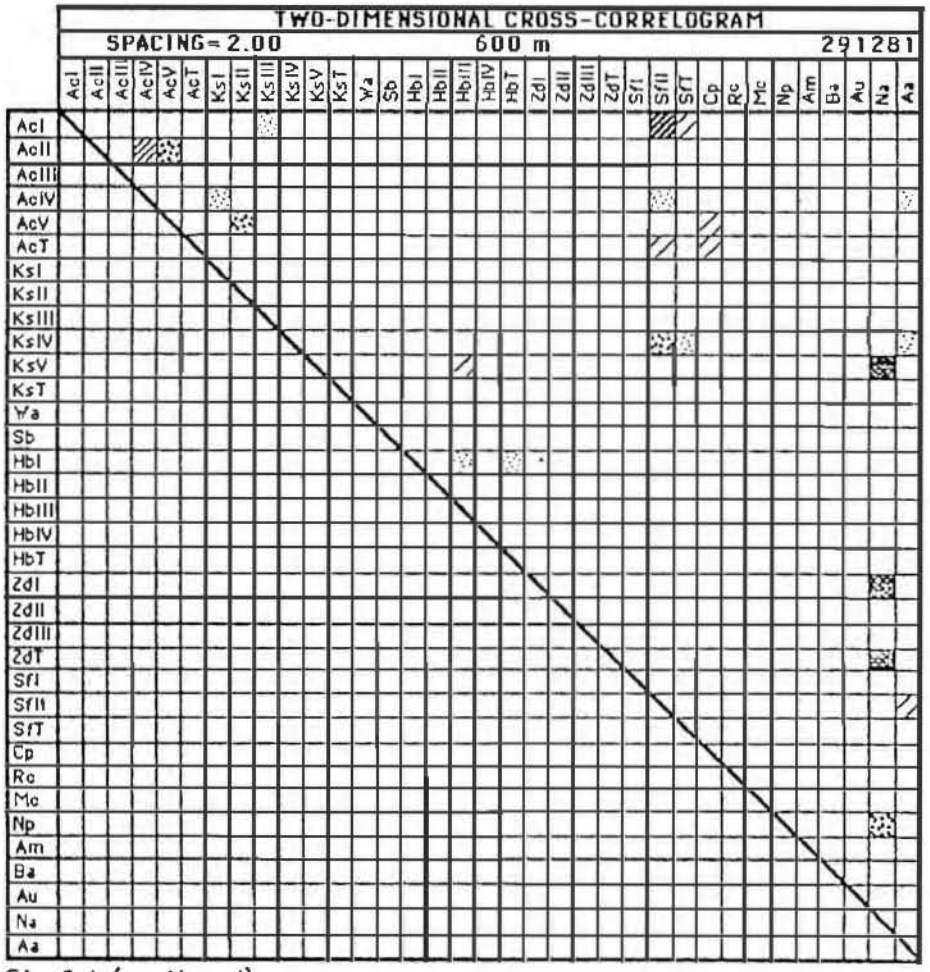

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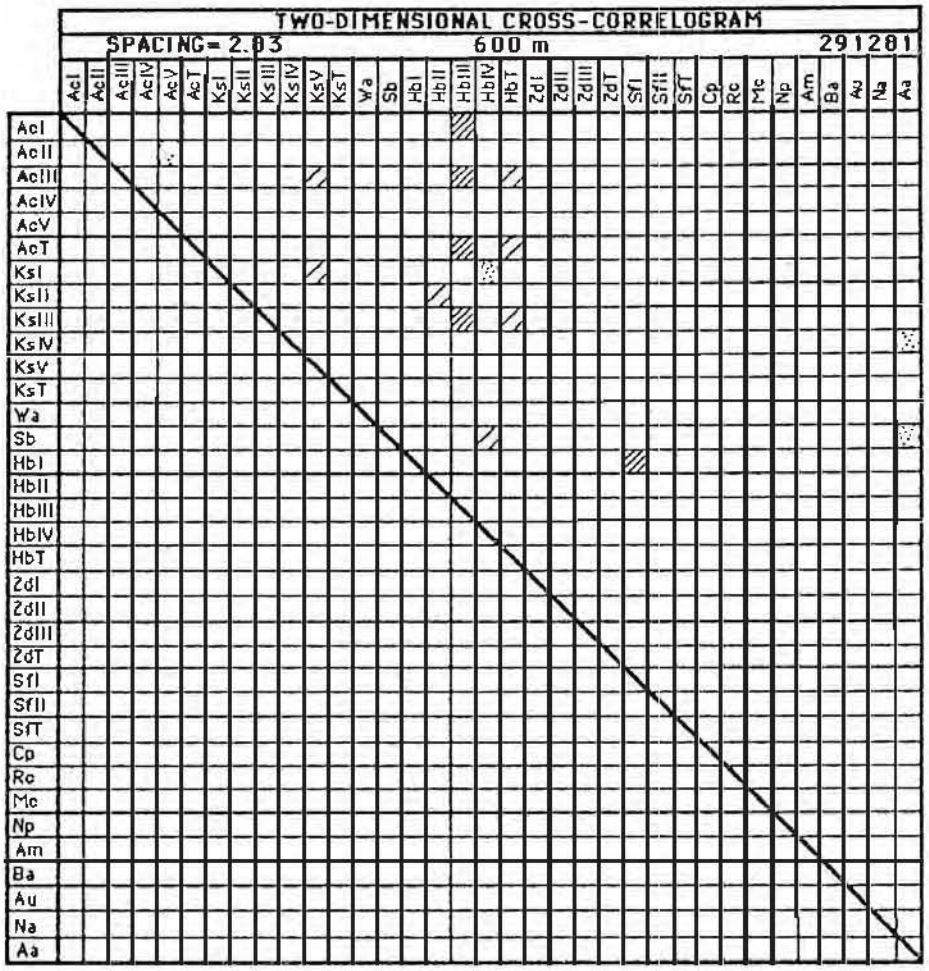

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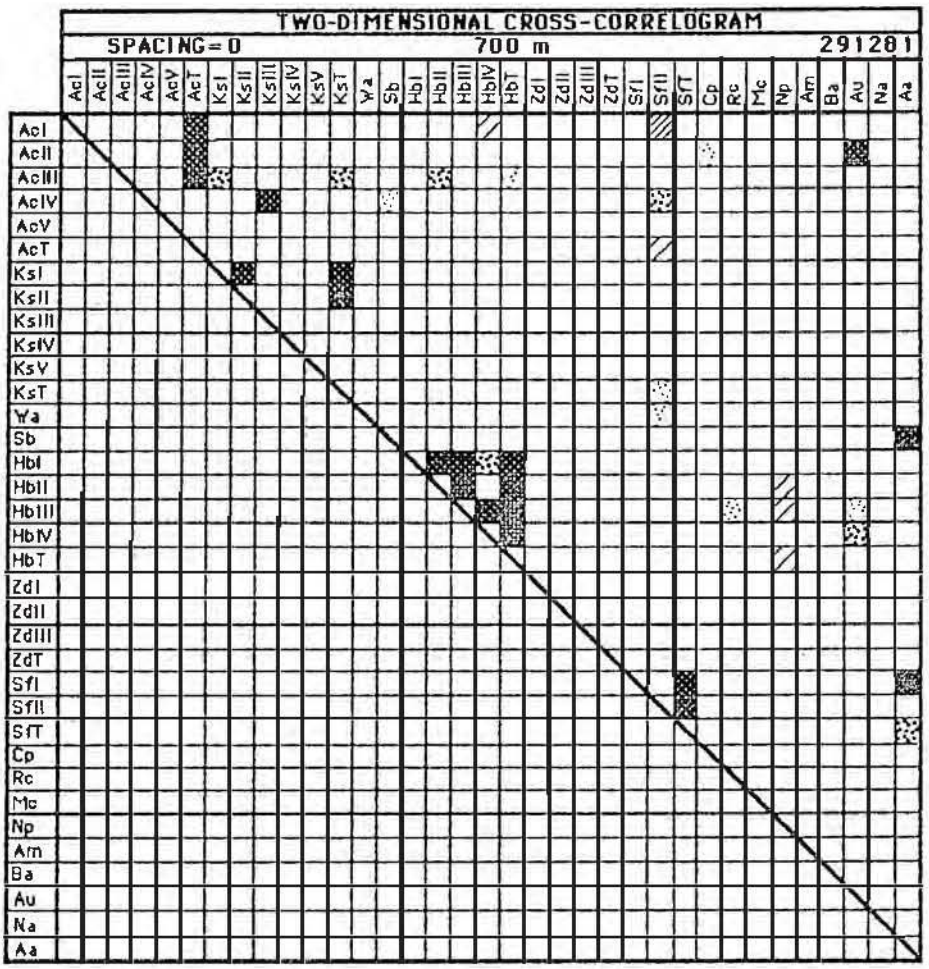

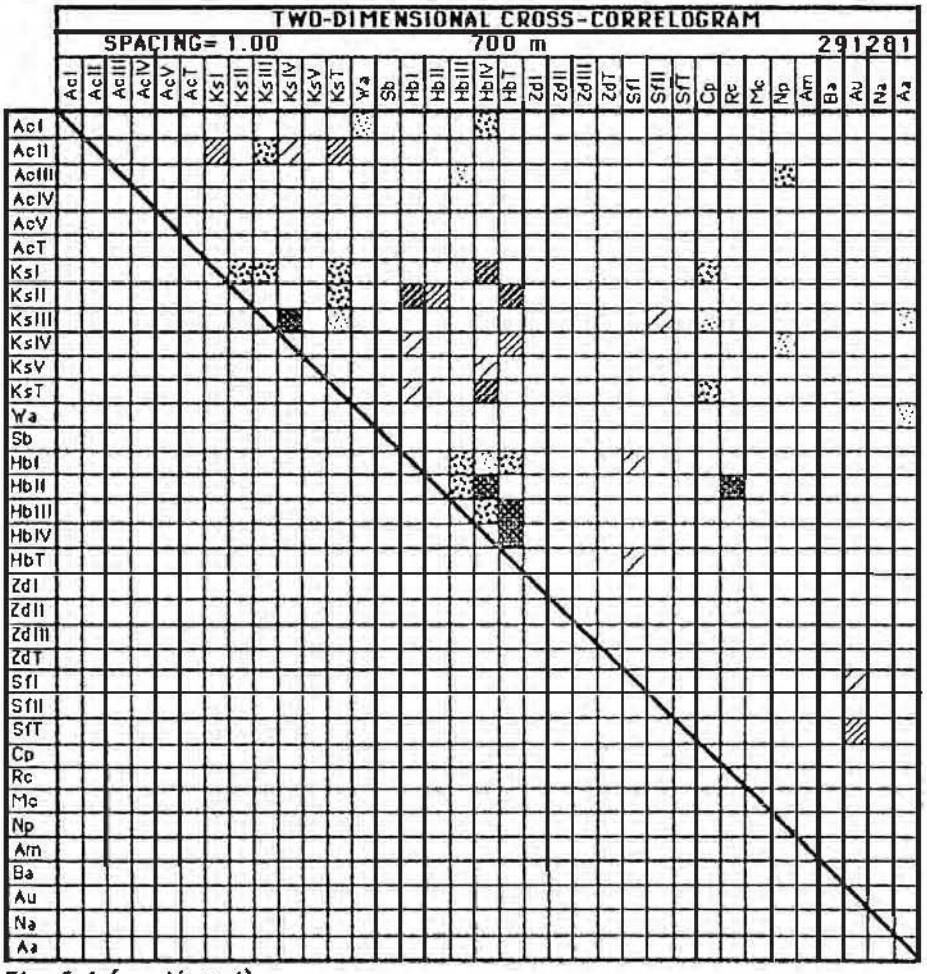

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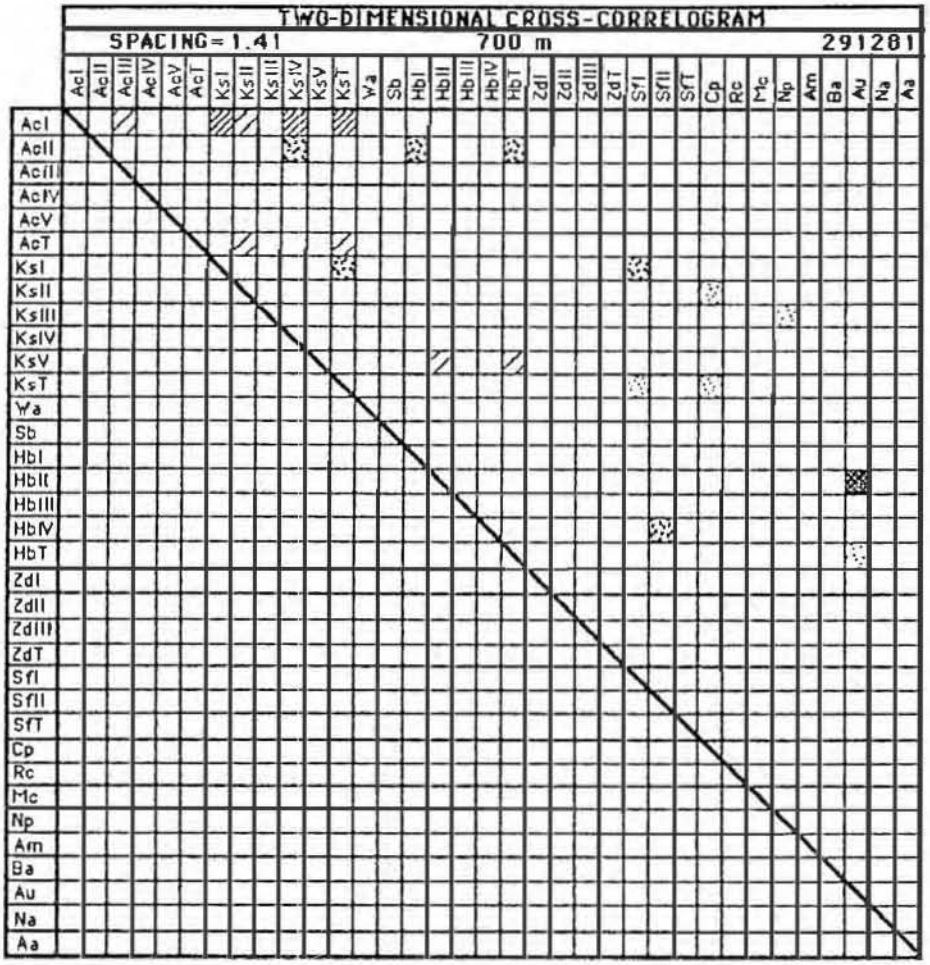

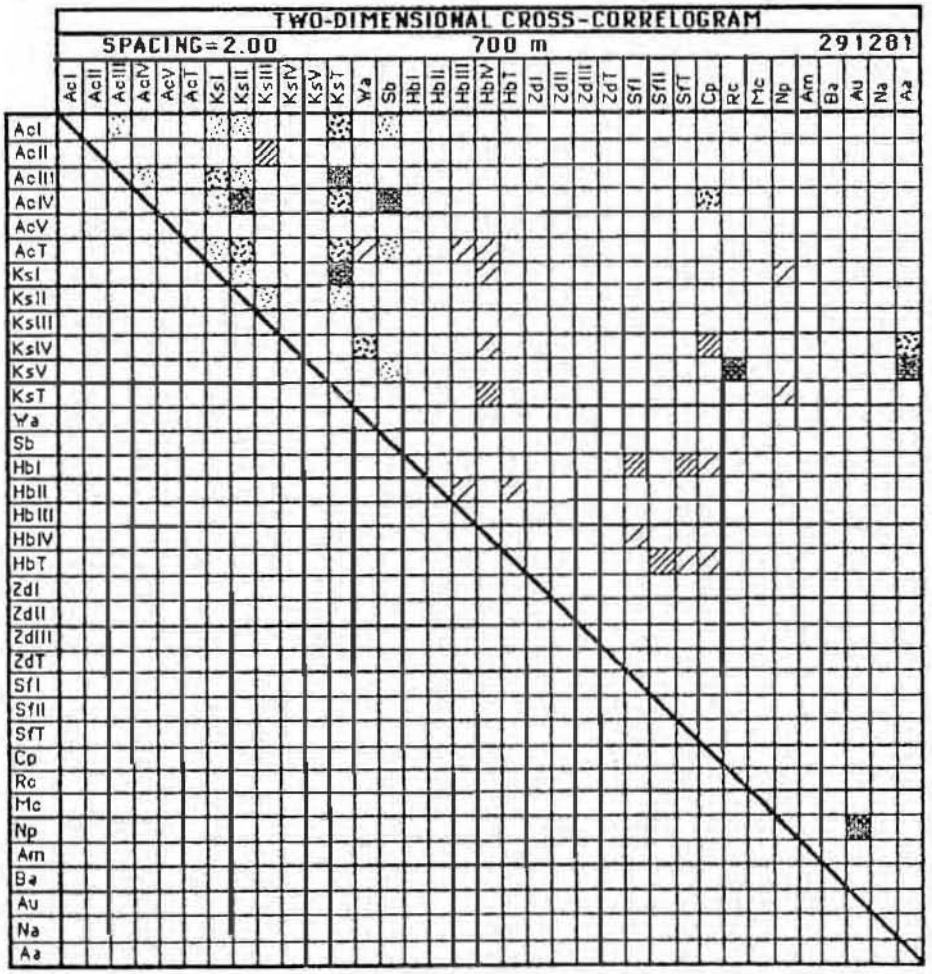

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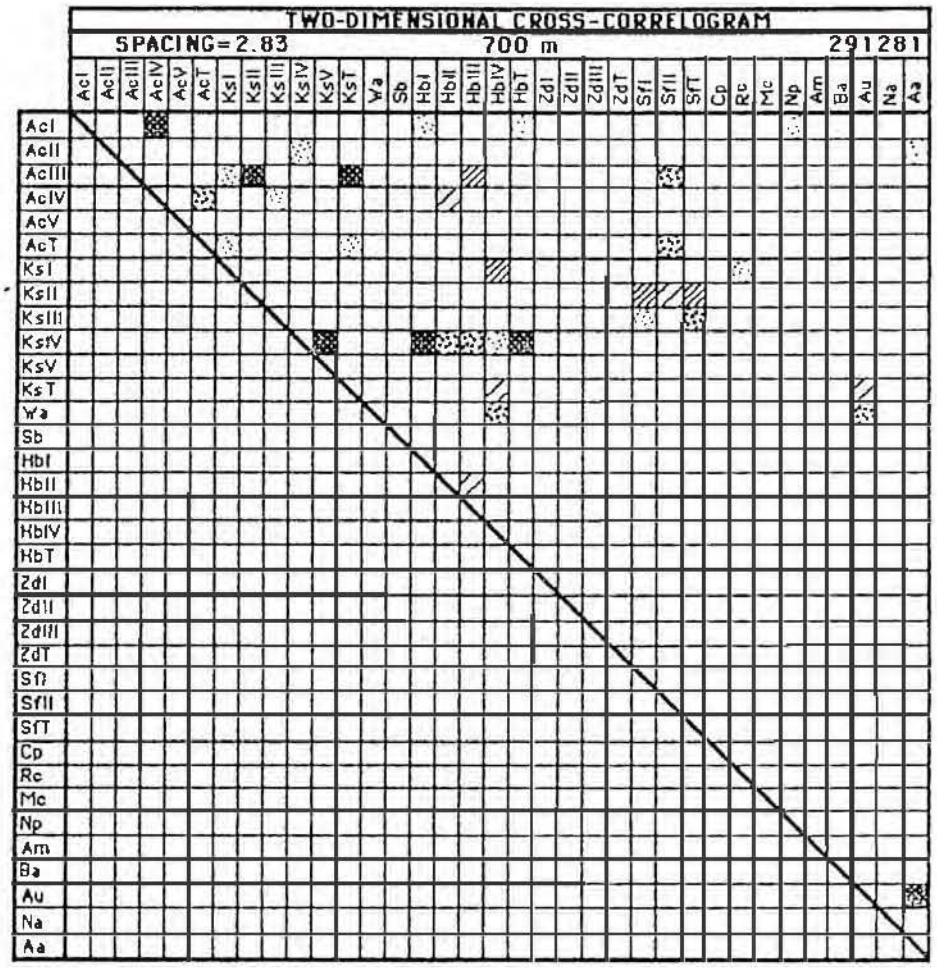


Fig. 6.1 (continued)

indicators for those associations.

Anapella

200381

100 m: The two largest groups have a strong positive association at zero spacings. At medium spacings large and small animals are negatively, and small groups positively, correlated. Correlations are weak at the longest spacings.

200 m: Positive correlations occur betwen small groups and between small and medium animals at zero spacing. Correlations at non-zero spacings are usually negative and involve small and large animals.

300 m: Overall correlations are weak.

400 m: As above.

500 m: As above.

600 m: Small and medium animals have a weak positive correlation at spacing 0. At spacing 1.00 most groups are positively correlated but at other spacings correlations are weak.

700 m: Small groups are positively associated at spacing 0 but interactions are otherwise negligible.

270681

Overall interactions are markedly stronger in winter than in the previous season.

100 m: Strong positive associations occur between small groups and between large groups at zero spacing; groups III and V are similarly related. The small group and III/V group relationships continue at all but the largest spacing.

200 m: Small animals are positively correlated with large animals at spacing 0, as are group III and V. The former relationship continues at other spacings.

300 m: At zero spacing a weak positive correlation and a weak negative correlation occurs between small groups and groups II and V respectively. At non-zero spacings, associations are generally negative and involve group III with most other groups. Associations are negligible at the longest spacings.

400 m: Associations are generally weak at all but the zero spacing where group II is positively associated with group II and V.

500 m: Although no significant correlations are evident at spacing 0, the larger groups are negatively associated with the smaller groups at moderate spacings.

600 m: As above but strong correlations occur only at spacing 1.00 and 2.83.

700 m: As for the 500 m station except that correlations are positive.

290981

100 m: The larger groups are positively, and groups II and III negatively, associated at spacing 0. At short spacings the group II/III relationship continues with increased strength.

200 m: Small groups have a strong positive correlation at spacing 0. At short spacings associations the smallest and largest groups are negatively correlated.

300 m: Correlations are generally weak.

400 m: As above although small and large animals are negatively associated at moderate spacings.

500 m: Correlations are weak.

600 m: As above although small groups are positively associated at moderate spacing.

700 m: At zero spacing the largest groups have a strong positive correlation while groups I and III are negatively correlated. Group II is positively associated with groups III and V at spacing 1.00; otherwise correlations are weak.

291281

100 m: The smallest groups have a weak positive correlation at spacing 0 and associations at other spacings are also relatively weak.

200 m: The small groups show a positive association with group V at zero spacing. Correlations at other spacings are weak and inconsistent.

300 m: At spacing 0 a strong positive relationship between the smallest groups is evident; otherwise correlations are weak.

400 m: At zero and short spacings the smallest groups are positively correlated. At zero and most other spacings there are negative correlations between small and large animals.

500 m: At all spacings the smallest groups are positively related. There is also a weak negative relationship between groups III and V at spacing 0 but otherwise correlations are weak and inconsistent.

600 m: The smallest, and also the largest (weak), groups are positively correlated at zero spacing. At medium spacings the strongest correlations involve group IV with smaller animals.

700 m: Correlations are weak.

Summary

In most seasons significant correlations are minimal towards the middle of the beach transect.

In autumn, only the top and bottom two stations show strong correlations. At the top of the beach positive associations are found among small animals and among large animals; at

the lower end of the beach small animals are positively associated.

Significant correlations in winter are largely confined to the upper half of the transect, where small animals and also large animals show positive associations amongst themselves.

In spring the correlations are strongest at the top two stations and at the last station. In each case positive associations occur among the small and also the large animals while animals of intermediate size are negatively correlated.

In summer significant positive correlations occur between small animals at most beach stations.

Katelysia

200381

100 m: Correlations are weak.

200 m: At zero spacing small groups have a strong positive correlation. Associations are negligible at non-zero spacings.

300 m: Correlations are negligible apart from a strong positive association between groups III and V at long spacings.

400 m: Correlations are weak.

500 m: As above.

600 m: No significant correlations exist at zero spacing. At non-zero spacings groups II and III are positively associated with larger groups.

700 m: At zero and short spacings the two smallest groups have strong positive correlations; otherwise correlations are negligible.

270681

100 m: Correlations are negligible.

200 m: As above.

300 m: Small animals are positively associated at zero spacings but at other spacings correlations are negligible.

400 m: At spacing 0 groups II and III are positively correlated, as are groups II and V at long spacings.

500 m: No significant correlations occur at spacing 0. At medium spacings group II is negatively correlated with larger animals while those associations are positive at larger spacings.

600 m: Small and large animals have a weak positive correlation at spacing zero and a weak negative correlation at larger spacings.

700 m: Positive correlations between group II and groups IV (strong) and V (weak) occur

at spacing 0. These associations continue at short spacings.

290981

100 m: Small animals have a strong positive correlation at zero spacings but at other spacings correlations are negligible.

200 m: Correlations are negligible.

300 m: No significant correlations are evident at spacing 0. At short spacings, however, small animals show a strong positive association while groups I and V have a weak negative correlation.

400 m: No significant correlations occur at spacing 0. At short spacings group II shows a weak positive relationship with group I and group V.

500 m: There is a weak negative correlation between groups III and V at spacing zero. At short spacings, small animals are positively related.

600 m: Correlations are weak.

700 m: At spacing 0 small groups are positively associated. At other spacings larger animals show weak positive relationships.

291281

100 m: Correlations are negligible.

200 m: As above.

300 m: As above.

400 m: Groups of medium size are positively correlated at zero and short spacings but at other spacings correlations are negligible.

500 m: Groups of medium size are positively correlated at zero spacing but at other spacings correlations are weak.

600 m: As for 400 m; in addition, small animals have a weak negative correlation at spacing 0.

700 m: Small animals show a strong positive correlation at zero and short spacings. At spacing 1.00, groups III and IV have a similar relationship.

Summary

In autumn, small animals are positively associated at the 200 m and 700 m stations while at 600 m, similar associations involve larger animals.

Winter associations are dominated by positive correlations between small and large animals over most of the beach. These correlations are negligible at the top 2 stations and are negative at 500 m.

At either end of the beach in spring, small animals are positively associated. At 400 m small and large groups are similarly correlated while at 500 m there is a negative

correlation between medium and large animals.

Most correlations in summer are postive and are among medium sized animals in the lower half of the beach. As in all seasons, small animals are positively related at the 700 m station.

Hydrococcus

200381

100 m: At zero and short spacings groups II and III (strong) are positively correlated with group IV.

200 m: At spacing 0 all groups show a weak positive relationship with group IV and groups II and III are also positively correlated. Associations are weak at other spacings.

300 m: The largest groups have a strong positive relationship at zero and short spacings. Also, group I has a weaker relationship of similar sign with large animals at short spacings.

400 m: Group II shows a strong positive correlations with larger groups at spacing 0 but at most other spacings, correlations are weak.

500 m: There are no significant associations at spacing 0; the strongest correlations occur at spacing 1.00 where groups II and III are positively correlated with larger animals.

600 m: Correlations are weak.

700 m: Correlations among all but group IV are positive at zero spacing while at non-zero spacings correlations are weak.

270681

100 m: At spacing 0 all groups show strong positive correlations with other groups. These weaken after short spacings, particularly among the larger animals.

200 m: As above, except that group I is not involved in any significant associations (other than weak correlations with large animals at spacing 1.00).

300 m: At spacing 0, small and medium sized animals are positively correlated with the largest group and the small and medium animals have a strong correlation of similar sign. Correlations are weak at other spacings.

400 m: Group III is negatively and positively correlated with group I and II respectively at zero spacing. The relationship between groups II and III continues at short spacings.

500 m: At zero spacing the largest groups have a weak positive correlation. At other spacings group II is associated with larger animals.

600 m: Group IV is positively correlated with groups II and III at spacing 0. At non-zero spacings most correlations are positive and are between group III and smaller groups.

700 m: At zero and short spacings, correlations are positive, involve most groups and are strongest among the smaller animals.

290981

100 m: Strong positive correlations exist among all groups at spacing 0. These associations weaken quickly and become negligible at short spacings.

200 m: Correlations are weak.

300 m: Group I is positively associated with the largest groups at zero spacing and also at longer spacings.

400 m: The largest groups show a strong positive correlation at spacing 0. Small animals are weakly associated with larger animals at non-zero spacings.

500 m: As above although at spacing 1.00, weak negative correlations occur between the smallest, and between the largest, groups.

600 m: Weak positive correlations exist betwen group III and smaller animals at zero spacing. Correlations are also weak at other spacings.

700 m: Positive (mostly strong) correlations exist among all groups at spacing 0. These associations weaken quickly and become negligible at short spacings.

291281

100 m: Strong positive correlations exist among all groups at spacing 0. These associations weaken quickly and become negligible at short spacings.

200 m: At zero spacing group I has strong positive correlations with the other groups. For the smallest groups this relationship continues at short and long spacings while at medium spacings group III is negatively associated with smaller and larger animals.

300 m: Correlations are generally weak although the largest groups show a positive relationship at spacing 0.

400 m: Correlations are generally negligible although the smallest groups show a strong positive relationship at spacing 0.

500 m: Correlations are generally weak although at spacing 0 small and large animals have a strong positive relationship.

600 m: Positive correlations exist among all groups at spacing 0; these are strong except for those involving group IV which are moderate. These relationships slowly diminish with increasing spacing.

700 m: Strong positive correlations exist among most groups at spacing 0 and these decrease rapidly after spacing 1.00.

Summary

Significant correlations occur at most stations in all seasons. Strong correlations at

zero spacings are often associated with negligible correlations at other spacings.

In autumn, large animals at the first station, and small animals at the last station, tend to be positively associated. Large animals are generally involved in the significant correlations high on the beach; towards the middle of the beach small and large animals are positively associated. Correlations are weak at 500 m and 600 m.

At both ends of the winter transect all groups show positive associations (less so for small animals high on the beach). At the middle station (400 m) the smallest animals are negatively associated with group III. Either side of this station small and large groups tend to be positively associated.

In spring the first and last stations show positive correlations among all groups. Towards the centre of the beach positive correlations betwen large animals occur and either side of those stations small animals are positively correlated with larger animals.

The summer transect shows positive associations between most groups high and low on the beach. Correlations at the central station are positive and are between small animals. Above that station large animals are similarly associated while below the central point small and large groups are also positively correlated.

Zeacumantus

200381

100 m: Groups II and III are positively correlated at zero and short spacings.

200 m: At spacing 0 groups I and II and groups II and III are positively asociated. These associations are weak at other spacings.

300 m: Correlations are weak.

400 m: As above.

500 m: No significant correlations occur at spacing 0 but at intermediate spacings groups I and III show a positive relationship.

600 m: Correlations are weak.

700 m: At zero spacing groups I and II have a strong positive association; otherwise correlations are negligible.

270681

100 m: Correlations are weak.

200 m: Strong positive correlations exist between all groups at zero and short spacings.

300 m: Groups I and III show a weak positive association at zero spacing but correlations are negligible at other spacings.

400 m: Correlations are negligible.

500 m: At spacing zero groups II and III are positively correlated. At other spacings

group I is positively correlated with other groups.

600 m: Correlations are negligible.

700 m: Correlations are negligible.

290981

100 m: Groups I and II have a strong positive correlations at spacing 0 but otherwise correlations are negligible.

200 m: Groups I has strong positive correlations with groups II and III at spacing 0. At spacing 1.0 all groups are similarly associated but longer spacings show weak correlations.

300 m: Correlations are weak.

400 m: The two largest groups show a weak negative correlation at spacing 0; otherwise correlations are negligible.

500 m: Apart from a strong positive correlation between groups I and II at medium spacings, correlations are negligible.

600 m: Correlations are negligible.

700 m: As above.

291281

100 m: All groups are positively correlated at spacing 0 but these associations diminish rapidly at non-zero spacings.

200 m: At zero spacing groups I and II and groups II and III are positively associated. Correlations are negligible at non-zero spacings.

300 m: As above.

400 m: Correlations are weak.

500 m: Apart from a strong positive correlation between groups I and II at spacing 0, correlations are negligible.

600 m: Correlations are negligible.

700 m: As above.

Summary

Significant correlations are generally resricted to the top 300 m of the beach. They are strongest in summer when they involve all groups and are weakest in winter when strong correlations are restricted to the 200 m station.

Salinator

Correlations between small and large *Salinator* are weak at all distances in all seasons except for a positive relationship at 200 m in spring.

6.3.3.2 Between species analysis

Anapella and

Katelysia (ie. between *Anapella* and *Katelysia*)

200381

100 m: At zero and short spacings group III *Anapella* and *Katelysia* are negatively correlated. At short spacings small *Anapella* are positively associated with large *Katelysia*.

200 m: Medium and large *Anapella* are positively correlated with small *Katelysia* at spacing 0. At short spacings medium sized animals and also large animals are negatively correlated but group II and III *Anapella* show a strong positive association with large *Katelysia*.

300 m: No significant correlations occur at spacing 0. At other spacings small and large *Katelysia* are positively correlated with large *Anapella*.

400 m: Small *Katelysia* are positively correlated with larger *Anapella* at zero and short spacings. At longer spacings group I *Katelysia* is negatively associated with those *Anapella* groups.

500 m: Group IV *Anapella* and group III *Katelysia* are positively related at spacing 0. At other spacings the general pattern is for *Katelysia* to be positively correlated with larger *Anapella*.

600 m: While medium sized animals of each species are positively correlated at zero spacing, the small groups are negatively correlated. The sign of these associations tends to be reversed at short spacings.

700 m: At zero and short spacings, group I *Anapella* and group II *Katelysia* are negatively, and group II *Anapella* and smaller *Katelysia* , positively correlated.

270681

100 m: Medium *Anapella* and small *Katelysia* are positively correlated at zero spacing. At zero and other spacings small (and total) *Katelysia* are negatively correlated with small and large *Anapella*.

200 m: At spacing 0 medium Anapella and large Katelysia are positively associated. Correlations at short spacings are similar to those at 100 m.

300 m: Group II *Katelysia* is positively correlated with *Anapella* groups II and IV at spacing 0. At short spacings group V *Katelysia* is negatively correlated with group I and IV *Anapella* but positively associated with medium sized *Anapella*. These correlations are of opposite sign at longer spacings.

400 m: At zero and short spacings group IV *Anapella* and group II *Katelysia* are

negatively correlated. That *Katelysia* group is also negatively associated with small *Anapella* at short spacings, as are medium sized animals of each species. Otherwise, correlations between the two species are positive.

500 m: The zero spacing shows a positive correlation between *Anapella* group III and *Katelysia* group II and a negative correlation between group II *Anapella* and group V *Katelysia*. These associations continue at short spacings where there is an additional negative correlation between group II *Katelysia* and small and medium *Anapella*.

600 m: Small animals of each species and also group IV Anapella and group V Katelysia are positively correlated at spacing zero. At short and long spacings, small animals of one species are negatively correlated with larger animals of the other species.

700 m: Group II *Anapella* and group V *Katelysia* are positively related at spacing 0. At short spacings group I of one species are negatively correlated with group V of the other species. At long spacings medium sized animals of each species are positively related.

290981

100 m: Medium *Anapella* are positively associated with small *Katelysia* at spacing 0. At short spacings small animals of each species are positively correlated while at medium spacings group III animals show a negative association.

200 m: Correlations a relatively weak at zero and short spacings but at long spacings small *Anapella* are positively correlated with large *Katelysia*.

300 m: Group I *Anapella* is positively correlated with small *Katelysia* and negatively correlated with large *Katelysia* at zero and short spacings. Negative associations also occur between small *Katelysia* and large *Anapella*.

400 m: At zero and short spacings small animals of each species are generally negatively associated. At longer spacings small animals of one species tend to be positively correlated with larger animals of the other species.

500 m: Correlations are relatively weak at most spacings and are generally positive and between similarly sized groups of each species; however, negative correlations occur between groups having a large size difference at intermediate spacings.

600 m: Small animals of each species are negatively (weak) correlated at zero and short spacings. At long spacings group I *Katelysia* shows negative correlations with small and medium *Anapella* as do large animals of each species.

700 m: Correlations are weak apart from a strong negative correlation between small *Katelysia* and medium *Anapella* at spacing 1.00.

291281

100 m: No significant correlations occur at zero spacing but at spacing 1.00, small

Anapella are negatively correlated with large *Katelysia*. At medium spacings strong positive correlations occur between large animals of each species.

200 m: At spacing 0 group II *Katelysia* is negatively (weak) and positively correlated with group II and III *Anapella* respectively. Most correlations at non-zero spacings involve small *Katelysia* ; at medium spacings those animals are positively correlated with larger *Anapella* while the same groups are negatively associated at long spacings.

300 m: Correlations are relatively weak but generally small *Katelysia* are positively correlated with most *Anapella* groups.

400 m: At spacing 0 group I animals of each species are positively correlated while group I *Anapella* shows a weak negative correlation with group III *Katelysia*. Similar associations occur at short spacings while at long spacings negative correlations between each species are common.

500 m: At spacing 0 small *Anapella* are positively correlated with small and medium *Katelysia* as are medium *Anapella* and large *Katelysia*. Most correlations at other spacings are weak and positive and involve small and medium animals.

600 m: Group II of each species have a strong positive correlation at spacing 0. Correlations at other spacings are generally positive and are between large and small groups of each species.

700 m: Small *Katelysia* and group III *Anapella*, and medium *Katelysia* and *Anapella*, are positively correlated at zero spacing. At medium spacings small *Anapella* groups are negatively correlated with most *Katelysia* groups while at long spacings small *Katelysia* are positively related to small and medium *Anapella*.

<u>Summary</u>

In autumn, negative correlations between the two species are strongest at the first and last stations (between medium and small animals respectively). In the top half of the beach other correlations are positive and are between small *Katelysia* and large *Anapella*. Positive correlations also occur in the lower half of the beach but involve medium sized animals of each species.

At the top of the winter transect, small *Katelysia* animals are positively associated with large *Anapella*, while at the last station, small *Anapella* are positively related to large *Katelysia*. Stations near the middle of the beach show negative correlations between small animals of one species and large animals of the other.

In spring small *Katelysia* are positively correlated with medium *Anapella* at the top of the beach but at the last station those groups are negatively correlated. In the lower half of the beach small animals of each species are negatively correlated.

In the top half of the summer transect, small *Anapella* animals tend to be negatively correlated with *Katelysia* while in the bottom half, similarly sized individuals of each species are positively correlated.

Soletellina

Correlations are generally weak in autumn although in the middle sections of the beach *Soletellina* shows weak negative correlations with medium sized *Anapella*.

In winter the correlations are weak at stations other than 400 m. At that distance *Soletellina* is positively associated with most *Anapella* groups at zero and short spacings.

Strong correlations in spring are mainly confined to the middle reaches of the beach and medium spacings, with *Soletellina* being positively associated with large *Anapella*. Summer is the season of most interaction between the two species and *Soletellina* is then positively correlated with medium and large *Anapella* over zero or short spacings at most stations.

Wallucina

At the 300 m station in autumn, *Wallucina* is negatively correlated with large *Anapella* but below this station correlations are generally positive with medium sized animals.

Winter correlations are weak except in the middle sections of the beach. Negative correlations involve medium and small *Anapella* at 400 m and 500 m respectively. In spring *Wallucina* shows positive associations with medium sized *Anapella* at all but the highest sampling stations.

Summer correlations are relatively weak. They usually involve small *Anapella* and are negative in the top, and positive in the bottom, section of the beach.

Hydrococcus

200381

100 m: At zero and non-zero spacings small *Anapella* are positively correlated with most *Hydrococcus* (particularly the smallest) groups. Negative associations occur between *Hydrococcus* and large *Anapella*.

200 m: Group I *Anapella* and group II *Hydrococcus* have a weak positive correlation at spacing 0; those groups are negatively correlated at spacing 1.41 and again positively associated at spacing 2.00. An alternation of sign also occurs at long spacings for correlations involving medium *Anapella* and large *Hydrococcus*.

300 m: At zero spacing small and large *Hydrococcus* are positively correlated with small and medium *Anapella* while small *Hydrococcus* and large *Anapella* are

negatively correlated. At intermediate spacings group III *Hydrococcus* is negatively related to small and large (similarly for group IV *Hydrococcus*) *Anapella*.

400 m: Most correlations are weak but generally the two species are negatively correlated.

500 m: No significant correlations occur at spacing 0. At short spacings small and medium *Hydrococcus* are negatively correlated with small and medium *Anapella*. At other spacings *Hydrococcus* is positively associated with the larger *Anapella* groups.

600 m: Group II animals of each species are negatively associated at zero spacing while correlations are weak otherwise.

700 m: At spacing 0 small *Anapella* animals are positively correlated with large *Hydrococcus*. Small animals of each species are positively related at short spacings but generally correlations are weak.

270681

100 m: Small *Anapella* have a strong positive correlation with all *Hydrococcus* at zero and short spacings. With increasing spacing these associations diminish, least so with those involving group I *Anapella*.

200 m: All *Anapella* groups are positively correlated with medium and large *Hydrococcus* at spacing 0. Non-zero correlations are similar to those at 100 m.

300 m: Correlations are relatively weak but the general pattern is for small *Anapella* to be positively associated with small and medium sized *Hydrococcus*. An exception occurs at spacing 1.41 where group II *Anapella* and group I *Hydrococcus* have a strong negative correlation.

400 m: At spacing 0 group II animals of each species are negatively correlated as are group IV *Anapella* and group III *Hydrococcus*. At non-zero spacings small *Hydrococcus* tend to be negatively correlated with a range of *Anapella* groups.

500 m: *Anapella* group I and *Hydrococcus* group III are positively, and *Anapella* and *Hydrococcus* group II animals negatively, correlated at spacing 0. At short and long spacings medium and large *Hydrococcus* are negatively correlated with medium *Anapella* while small animals of each species are positively associated.

600 m: At zero spacing group I animals of each species, and also group II *Anapella* and group III *Hydrococcus*, are positively related. *Hydrococcus* is generally negatively correlated with small and medium *Anapella* at medium spacings and large animals of each species are positively correlated at long spacings.

700 m: At zero spacing small animals are positively correlated, as are small and medium *Hydrococcus* with medium *Anapella*. Correlations are generally weak at non-zero

spacings.

290981

100 m: Medium *Anapella* and large *Hydrococcus* are positively associated at spacing zero. Most correlations at other spacings are negative and involve large *Hydrococcus* and small and medium *Anapella*.

200 m: No significant correlations occur at spacing 0 and other spacings show weak positive associations between the two species.

300 m: Small *Anapella* are positively correlated with small and medium *Hydrococcus* at zero and short spacings while small *Hydrococcus* and large *Anapella* are negatively related.

400 m: Correlations at zero, short and medium spacings are mainly positive and between small *Anapella* and a range of *Hydrococcus* groups.

500 m: Small *Anapella* are positively correlated with small and medium sized *Hydrococcus* at zero spacing but these groups show a weak negative relationship at medium spacing. At short spacings larger animals of each species are positively correlated while at longer spacings their association is negative.

600 m: At spacing 0 small *Hydrococcus* are positively correlated with small and large *Anapella*. Long spacings have weak correlations but at intermediate spacings there is a negative correlation between group III *Hydrococcus* and large *Anapella* and a positive relationship between that *Hydrococcus* group and medium *Anapella*.

700 m: Small and large *Hydrococcus* are positively correlated with small *Anapella* at spacing 0. At medium spacings group III *Hydrococcus* has positive correlations with small and large *Anapella*.

291281

100 m: At zero and short spacings group I *Anapella* have a strong positive correlations with all *Hydrococcus* goups. Also at zero spacing, *Anapella* groups II and III are similarly associated with large *Hydrococcus*. Correlations are weaker at longer spacings but generally small animals of each species are positively correlated while *Hydrococcus* is negatively related to medium and large *Anapella*.

200 m: At spacing 0 small *Hydrococcus* animals are positively correlated with small and medium *Anapella*. At medium spacing small *Hydrococcus* have a negative association with small and large *Anapella*.

300 m: At spacing zero small *Anapella* are positively related to small and medium *Hydrococcus*. At non-zero spacings correlations are relatively weak.

400 m: Small *Anapella* are positively correlated with large *Hydrococcus* at zero and

short spacings and also with small *Hydrococcus* at long spacings.

500 m: Small animals of each species are positively correlated at spacing 0. These associations continue at other spacings with larger animals also becoming involved.

600 m: Correlations are weak.

700 m: At zero spacing small *Anapella* have a weak negative correlation with large *Hydrococcus* and medium animals of each species are positively correlated. At short spacings small and medium *Anapella* are positively related to small and large *Hydrococcus*.

Summary

Most negative correlations between the two species occur in autumn. In that season small and medium animals of each species are negatively associated between 300 m and 600 m. High on the beach those groups have positive correlations while at the last station small *Anapella* are positively correlated with large *Hydrococcus*.

Over most of the winter transect small animals of each species are positively related. High on the beach all *Hydrococcus* groups are involved. Exceptions occur in the middle of the beach where small and medium animals are negatively associated.

High on the beach in spring, correlations (positive) are relatively weak, particularly between small animals. Generally correlations are positive and involve small animals although at 300 m small *Hydrococcus* are negatively correlated with large *Anapella*.

Correlations are mainly positive throughout the beach in summer and generally involve small animals. At 700 m, however, small *Anapella* and large *Hydrococcus* are negatively related.

Zeacumantus

200381

100 m: At zero and short spacings *Zeacumantus* is positively correlated with small *Anapella* and negatively correlated with medium and large *Anapella*, although most correlations are weak.

200 m: Small and medium *Zeacumantus* are positively associated with small *Anapella* at spacing 0. At short spacings those *Zeacumantus* groups have a negative association with medium and large *Anapella*. Thse associations continue at long spacings but are weak.

300 m: Large *Zeacumantus* and medium *Anapella* are negatively correlated at zero and long spacings. There is also a weak negative correlation between group II animals at short spacings. Large animals of each species have a positive correlation at long spacings.

400 m: At spacing 0 (and short spacings) group I animals of each species are positively

correlated. Also at spacing 0, group I and III *Zeacumantus* are similarly associated with medium *Anapella*. Correlations are weak at other spacings apart from a strong negative correlation between large *Anapella* and medium *Zeacumantus* at long spacings.

500 m: No significant associations occur at spacing 0. At other spacings most correlations are negative and involve a range of *Zeacumantus* groups and small *Anapella*.

600 m: Correlations are negligible.

700 m: Correlations are weak.

270681

100 m: At all spacings small and medium *Zeacumantus* are positively correlated with small *Anapella*.

200 m: Similar to above.

300 m: Similar to above but at medium and long spacings large *Zeacumantus* have a negative association with large and small *Anapella* respectively.

400 m: A range of *Zeacumantus* groups are positively correlated with small *Anapella* at spacing 0, as are medium *Zeacumantus* and large *Anapella*. Correlations are weak at other spacings.

500 m: At zero spacing medium and large *Zeacumantus* show a strong positive correlation with large *Anapella*. Those *Zeacumantus* groups are negatively correlated with small *Anapella* at short spacings.

600 m: Correlations are negligible.

700 m: Correlations are negligible apart from a strong positive association between group I *Zeacumantus* and group II and IV *Anapella* at the longest spacing.

290981

100 m: Small and medium *Zeacumantus* have a positive association with small *Anapella* at zero and short spacings.

200 m: Generally as above although at 200 m the correlations are stronger at long spacings than they are at 100 m.

300 m: As for 100 m but with weak negative correlations between the two species at long spacings.

400 m: At zero spacing group III animals of each species are negatively correlated and group II *Zeacumantus* is positively correlated with medium and large *Anapella*. At longer spacings a range of *Zeacumantus* groups are negatively correlated with a range of *Anapella* groups.

500 m: At spacing 0 small *Zeacumantus* and medium *Anapella* are negatively

correlated; associations between these groups are positive at non-zero spacings. Medium *Zeacumantus* and small *Anapella* show negative associations at those spacings.

600 m: Correlations are negligible.

700 m: As above.

291281

100 m: At zero and short spacings all *Zeacumantus* groups have a strong positive correlation with small *Anapella*.

200 m: Similar to above although group II *Zeacumantus* and large *Anapella* show a strong positive relationship at spacing 0. Also, at medium spacings small *Zeacumantus* has weak negative correlations with small and medium *Anapella*.

300 m: All *Zeacumantus* groups are positively correlated with small *Anapella* at zero and short spacings. At medium spacings *Zeacumantus* is negatively correlated with small and large *Anapella* but those groups are positively correlated at longer spacings.

400 m: At zero spacing small animals of each species show a weak positive relationship while group I *Zeacumantus* and group IV *Anapella* are negatively correlated. Most correlations at other spacings are positive and involve small and medium animals of each species.

500 m: At spacing 0 small *Zeacumantus* and *Anapella* have a positive correlation but the association between these animals is negative at short spacings.

600 m: Correlations are negligible.

700 m: As above.

Summary

In all seasons the top half of the beach is characterised by small and medium *Zeacumantus* being positively correlated with small *Anapella*. In autumn those stations also show negative correlations between *Zeacumantus* and medium/large *Anapella*. Negative correlations also occur at 400 m in spring and summer but involve smaller *Anapella*.

At 500 m negative associaitons occur in spring and summer, involving small and medium *Anapella* respectively. In winter large animals of each species are positively associated at 500 m, as are small animals in summer.

Correlations between the two species are always negligible at 600 m and 700 m.

Salinator

200381

100 m: Group II animals of each species have a weak positive association at spacing 0; otherwise correlations are weak.

200 m: Correlations are negligible at zero and short spacings. At longer spacings large *Salinator* show positive correlations with group III and IV *Anapella*.

300 m: No significant correlations occur at spacing 0. At other spacings most correlations are negative and involve small and medium *Anapella*.

400 m: At zero spacing both *Salinator* groups are positively correlated with group IV *Anapella*. At short spacings *Salinator* is negatively correlated with both small and large *Anapella* while correlations are negligible at longer spacings.

500 m: Correlations are weak.

600 m: Correlations are negligible at spacing zero. At short spacings large *Salinator* are negatively and positively correlated with small *Anapella* and with medium and large *Anapella* respectively.

700 m: Correlations are weak although at short and long spacings *Salinator* and group III *Anapella* show a positive relationship.

<u>270681</u>

100 m: Correlations between the two species are typically negative at all spacings and involve most groups.

200 m: At spacing 0 large *Salinator* are positively correlated with small and large *Anapella*. Correlations are relatively weak at other spacings.

300 m: No significant associations are evident at spacing zero but at short spacings, large *Salinator* show positive correlations with small and large *Anapella*.

400 m: Large *Salinator* show weak negative correlations with small *Anapella* at zero and short spacings while at longer spacings *Salinator* is positively correlated with a range of *Anapella* groups.

500 m: *Salinator* is negatively correlated with small *Anapella* at most spacings.

600 m: Correlations are weak.

700 m: At spacing zero group I animals of each species show a strong positive relationship. At spacing 1.00 large *Salinator* are negatively correlated with small *Anapella* and at other spacings that *Salinator* group is positively correlated with small and large *Anapella*.

<u>290981</u>

100 m: Correlations are relatively weak but at spacing 0 small animals of each species are positively associated.

200 m: At all spacings *Salinator* is positively correlated with small *Anapella*.

300 m: Similar to above although correlations are weaker.

400 m: Correlations are weak.

500 m: Both *Salinator* groups are negatively correlated with small *Anapella* at spacing 0. At long spacings the two species are positively correlated.

600 m: Total *Salinator* numbers are negatively correlated with group III *Anapella* at zero spacing while at short spacings small *Salinator* and small *Anapella* are positively correlated.

700 m: At spacing 0 group I *Salinator* and group III *Anapella* are negatively correlated. Correlations at other spacings are relatively weak.

291281

100 m: *Salinator* is positively related to small and large *Anapella* at spacing zero. At short spacings group I *Salinator* is negatively, and group II positively, correlated with those *Anapella* groups.

200 m: Total *Salinator* numbers show negative correlations with small and large *Anapella* at spacing 0. Correlations are weak at non-zero spacings.

300 m: Correlations are weak.

400 m: There is a strong positive relationship between group II animals from each species at spacing zero but total *Salinator* numbers are negatively correlated with large *Anapella* at that spacing. Most associations at other spacings are positive and are between group I *Salinator* and a range of *Anapella* groups.

500 m: Correlations are negative at all spacings and involve large *Salinator* and small *Anapella*.

600 m: At spacings 0 and 1.00 small *Salinator* and small *Anapella* are positively correlated. At medium spacings group II *Salinator* is negatively correlated with small *Anapella* and positively correlated with large *Anapella*.

700 m: Group II *Salinator* is negatively correlated with small *Anapella*, and positively correlated with medium *Anapella*, at zero spacing. Correlations are weak at non-zero spacings.

Summary

Salinator is positively correlated with small *Anapella* at either end of the autumn transect. Similar associations occur between larger animals at 600 m. Near the middle of the beach *Salinator* is negatively correlated with a range of *Anapella* groups.

In winter the two species are negatively correlated at the top of the beach, as are large *Salinator* and small *Anapella* at the last station. At 200 m and 300 m large *Salinator* are positively related to small and large *Anapella* while at 400 m and 500 m *Salinator* is negatively correlated with small *Anapella*.

In the top half of the spring transect *Salinator* is positively correlated with small

Anapella. Those groups are negatively correlated in the bottom half of the beach.

At the first summer station *Salinator* is positively correlated with small and large *Anapella* but at 200 m that relationship is negative. Small animals are positively related in the middle of the beach but relationships involving large animals of either species are negative there. At the lower end of the beach large *Salinator* and small *Anapella* are negatively correlated but otherwise the two species have a positive association there.

Cylichnina

Autumn correlations are generally weak at spacing 0 but at short spacings *Cylichnina* is often positively correlated with small *Anapella*.

In winter correlations are weak at zero and short spacings except at 100 m, 500 m and 700 m where small *Anapella* and *Cylichnina* are positively correlated.

Correlations are weak in the top half of the beach in spring, and are significant at short spacings only at 700 m where *Cylichnina* is positively associated with small and medium *Anapella*.

In summer *Cylichnina* is generally positively correlated with small *Anapella* although at 200 m and 400 m larger *Anapella* are involved. At 600 m the associations are negative.

Rissopsis

In autumn *Rissopsis* tends to be negatively correlated with small *Anapella* in the middle of the beach but the correlation is positive at the last station.

Negative associations also occur in the middle of the winter transect but elsewhere *Rissopsis* and small *Anapella* show a positive relationship.

At the last two spring stations small and medium *Anapella* are negatively correlated with *Rissopsis* but at other distances those associations are mainly positive.

Correlations are weak below 400 m in summer. In the top half of the beach *Rissopsis* is generally positively correlated with small *Anapella* except at 200 m where group II *Anapella* and *Rissopsis* are negatively correlated at spacing 0.

Microdiscula

Significant correlations are restricted to the top half of the beach in autumn, are mainly positive and involve small *Anapella*. At 300 m, however, *Microdiscula* is negatively associated with small *Anapella* at short spacings and large *Anapella* at long spacings.

In winter correlations are weak at short spacings except at the first and last stations where *Microdiscula* is positively correlated with small *Anapella* (and large *Anapella*

at 700 m).

High on the spring beach *Microdiscula* is negatively correlated with small and large *Anapella*. At the middle and bottom of the transect, *Microdiscula* and group III *Anapella* are positively associated.

Correlations are restricted to the top stations in summer and are strongest at 100 m where *Microdiscula* and group I *Anapella* have a strong positive association.

Nassarius

Autumn correlations are negligible at short spacings except at 200 m and 300 m where *Nassarius* is positively correlated with group III *Anapella*.

At most stations in winter, *Nassarius* shows strong positive correlations with large *Anapella*. High on the beach *Nassarius* is also positively correlated with small *Anapella*.

At spring stations other than 600 m and 700 m, *Nassarius* and small *Anapella* are positively correlated at zero or short spacings.

Summer associations are similar to those of spring.

Agatha

At 200 m in autumn, small *Anapella* are negatively associated with *Agatha* while at 300 m, group III *Anapella* shows a positive correlation with *Rissopsis*. At 100 m and 400 m *Agatha* and large *Anapella* are positively correlated at short spacings.
In winter significant positive correlations occur at most stations and generally involve medium or large *Anapella*.

Spring correlations are confined to the 100 m and 400 m stations , are positive and involve medium and large *Anapella*.

Summer associations are negligible except at 100 m where there is a weak positive correlation between *Agatha* and the smallest *Anapella* group.

Bembicium

Autumn correlations are restricted to the top half of the beach, are positive and involve small *Anapella*.

As in the previous season, winter correlations are negligible below 400 m. In the top half of the beach most associations are negative and involve small *Anapella*.

High on the spring transect *Bembicium* is positively associated with group I and II *Anapella* but shows negative correlations with groups III and IV.

Summer correlations are relatively weak at all stations apart from a strong positive correlation between *Bembicium* and group III *Anapella* at 100 m.

Austrocochlea

In autumn, correlations are weak at most stations but generally *Austrocochlea* is negatively correlated with small *Anapella* in the top half, and positively correlated with small/medium *Anapella* in the bottom half, of the beach.

Austrocochlea and *Anapella* are positively correlated at most stations in winter. The associations involve small *Anapella* in the top half of the beach and large *Anapella* in the bottom half.

Spring correlations are weak except at 400 m and 600 m where they are positive and involve large and medium *Anapella* respectively.

Significant correlations occur at most stations in summer, are positive and typically involve group II or III *Anapella*.

Notoacmea

Autumn correlations are weak at short spacings although at 200 m and 300 m *Notoacmea* is negatively correlated with small *Anapella*. At 600 m those groups are positively correlated.

Correlations are weak in winter apart from positive correlations involving group II *Anapella* at 300 m and 600 m.

Spring correlations are also weak but at 300 m and 400 m they are positive and involve small *Anapella*.

Summer correlations are similar to those in spring but they occur at 100 m, 400 m and 500 m.

Anthopleura

High on the beach in autumn, correlations between *Anthopleura* and small *Anapella* are negative. At most stations *Anthopleura* shows a strong positive relationship with large *Anapella*.

In winter *Anthopleura* and large *Anapella* are positively correlated at most stations. At 300 m small *Anapella* are involved in negative associations.

Overall, correlations are weaker in spring than in other seasons. The strongest (positive) correlations involving large *Anapella* occur at 200 m and 300 m. At 400 m and 500 m small *Anapella* are negatively correlated with *Anthopleura*.

At most summer stations *Anthopleura* and large *Anapella* have a strong positive relationship. Negative correlations are minimal in this season.

Katelysia and

Wallucina

Autumn correlations are weak except at 500 m and 700 m where *Wallucina* shows

strong positive correlations with large and small *Katelysia* respectively.

Correlations are negligible in the upper half of the beach in winter. At 500 m there is a strong positive association involving medium sized *Katelysia* but at other distances correlations are negative and involve smaller animals at the lowest stations.

In spring correlations are negligible although at 500 m and 600 m there are weak negative associations.

Significant positive correlations occur at most stations in summer. The strongest associations occur in the middle of the beach between *Wallucina* and small *Katelysia*.

Soletellina

Significant positive correlations occur at most autumn stations but are strongest in the top half of the beach. Only at 300 m, however, are significant correlations evident at zero spacing (*Katelysia* juveniles).

In winter significant associations again occur at most stations but they are not strong at zero and short spacings.

Strong positive correlations are evident at 300 m, 400 m and 700 m in spring. These involve large *Katelysia* at 300 m and smaller animals at the other stations.

In summer zero spacing correlations occur only at 300 m and 600 m. At 300 m, group V *Katelysia* are positively correlated with *Soletellina* while at 600 m there is a negative association involving *Katelysia* juveniles.

Hydrococcus

<u>200381</u>

100 m: Large *Katelysia* are positively associated with small and medium *Hydrococcus* at zero and short spacings.

200 m: No significant correlations occur at zero spacing. At spacing 1.00 small animals of each species are positively associated but otherwise correlations are weak.

300 m: No significant correlations occur at zero spacing. At short spacings large *Hydrococcus* are negatively related with group III *Katelysia*.

400 m: Small animals of each species have a strong positive relationship at spacing 0. At short spacings medium *Hydrococcus* and small and large *Katelysia* are negatively correlated.

500 m: Correlations are weak.

600 m: Small animals are positively correlated at zero and short spacings while these associations are negative at longer spacings.

700 m: Similar to above with the addition of positive correlations between large *Hydrococcus* and small *Katelysia* at long spacings.

270681

100 m: Correlations are weak.

200 m: As above.

300 m: No significant correlations occur at zero spacing. At other spacings small animals have a positive correlation while small *Hydrococcus* and large *Katelysia* are negatively related at spacing 1.00.

400 m: Group III animals of each species have a positive correlation at spacing 0. At short spacings small animals have a similar relationship but small Hydrococcus are negatively correlated with large *Katelysia*.

500 m: Correlations are weak.

600 m: Group III animals of each species have a positive correlation at spacing 0. At short spacings small animals have a similar relationship while large *Hydrococcus* are negatively correlated with large *Katelysia*.

700 m: At spacing zero group II *Katelysia* and *Hydrococcus* are positively asssociated. Most correlations at other spacings are negative and involve small *Hydrococcus* and medium or large *Katelysia*.

290981

100 m: Correlations are weak.

200 m: As above.

300 m: At zero and short spacings small *Katelysia* are positively related to a range of *Hydrococcus* groups.

400 m: At spacing 0 small animals are positively correlated while larger animals are negatively associated. Correlations between these groups are generally positive at non-zero spacings.

500 m: At zero and short spacings small *Katelysia* are positively related to a range of *Hydrococcus* groups. The two species are negatively correlated at longer spacings.

600 m: At zero and short spacings medium and large *Katelysia* are positively related to a range of *Hydrococcus* groups. Those associations are negative at other spacings.

700 m: Medium sized groups have a positive relationship at spacing 0. Correlations are weak at short spacings.

291281

100 m: Correlations are weak.

200 m: As above.

300 m: As above.

400 m: Large animals are positively correlated at spacing 0. At short spacings small

Hydrococcus show a strong positive association with medium *Katelysia*.

500 m: At spacing 0 total *Hydrococcus* numbers have a weak positive correlation with the smallest *Katelysia* group. Most correlations at short spacings are positive and between small animals of each species.

600 m: Small/medium *Hydrococcus* and large *Katelysia* have negative correlations at most spacings.

700 m: The two species (a range of groups) are negatively correlated at most spacings, although no significant correlations occur at spacing 0.

Summary

In all seasons correlations between the two species are weak at the top three stations.

Most correlations in autumn are positive and involve small animals of each species.

The winter associations are similar although larger animals are involved at 400 m and 600 m.

In spring most *Hydrococcus* groups are positively associated with *Katelysia* in the lower half of the beach. The *Katelysia* groups involved in these associations are larger at the lowest stations. In the middle of the spring beach, larger animals are negatively correlated.

Large animals are positively associated in the middle of the summer beach and small groups are similarly associated at 500 m. In the lower two stations, however, the two species show a general negative relationship.

Zeacumantus

200381

100 m: Correlations are weak.

200 m: Correlations are weak except at spacing 0 where the smallest groups of each species have a strong negative correlation.

300 m: At zero spacing small and medium *Zeacumantus* are positively correlated with small *Katelysia*; also at that spacing, small *Zeacumantus* show are weak negative association with medium *Katelysia*.

400 m: Large animals are positively correlated at spacing 0. At other spacings small animals are similarly related.

500 m: At zero spacing medium and large *Zeacumantus* are positively associated with small and medium *Katelysia* respectively. Similar relationships are evident at non-zero spacings.

600 m: Correlations are weak although medium *Zeacumantus* and small *Katelysia* are positively related at spacing 0.

700 m: Small and medium *Zeacumantus* show negative correlations with small *Katelysia* ; otherwise correlations are negligible.

270681

100 m: Medium *Zeacumantus* and small *Katelysia* have a weak negative correlation at spacing zero. At short spacings small animals of each species have similar associations.

200 m: Correlations are weak apart from a strong negative correlation between small animals at short spacings.

300 m: No significant correlations occur at spacing zero. At spacing 1.00 large *Zeacumantus* and small *Katelysia* show a strong positive correlation.

400 m: At spacing 0 positive correlations occur between small *Zeacumantus* and small *Katelysia* , and between large *Zeacumantus* and medium *Katelysia* . Correlations are weak at other spacings.

500 m: No significant correlations occur at spacing zero. At spacing 1.00, however, medium *Zeacumantus* is positively correlated with small and medium *Katelysia* . Large *Zeacumantus* are also positively associated with medium *Katelysia* but is negatively correlated with small *Katelysia* .

600 m: Correlations are negligible.

700 m: Correlations are weak.

290981

100 m: At zero spacing small *Katelysia* show negative and positive correlations with small and medium *Zeacumantus* respectively. Correlations are negligible at other spacings.

200 m: Small and medium *Zeacumantus* show positive relationships with large *Katelysia* at most spacings. At short spacings large *Zeacumantus* and small *Katelysia* have a strong positive correlation.

300 m: At zero and short spacings *Zeacumantus* is positively correlated with small *Katelysia* and negatively correlated with large *Katelysia* .

400 m: Medium and large *Zeacumantus* are positively associated with small and medium *Katelysia* at zero and short spacings.

500 m: At most spacings small, and also medium, animals of each species show positive relationships.

600 m: Correlations are negligible.

700 m: As above.

291281

100 m: Correlations are weak.

200 m: As above, although at medium spacings small animals show positive correlations.

300 m: No significant correlations occur at spacing zero.

400 m: Correlations are weak.

500 m: At spacing zero small *Katelysia* are positively correlated with small and medium *Zeacumantus*. Correlations are weak otherwise.

600 m: Correlations are negligible.

700 m: As above.

Summary

Near the top end, and at the bottom, of the autumn beach, small animals are negatively correlated. Correlations at other stations are positive. The significant associations involve large animals near the middle of the beach and smaller animals away from the centre.

In winter small animals are negatively correlated at the top of the beach as are large *Zeacumantus* and small *Katelysia* at 500 m. In the middle sections of the beach correlations are positive and involve larger animals. Associations are weak at 600 m and 700 m.

Small animals of each species are negatively correlated at the top of the spring beach, as are large *Katelysia* and most *Zeacumantus* at 300 m. Correlations at other stations are positive and generally involve small and medium animals.

In summer correlations are weak over most of the beach with the strongest being positive and occuring between small animals at 500 m.

Salinator

200381

100 m: No significant correlations occur at spacing 0. At short spacings group I *Salinator* is positively correlated with medium and large *Katelysia* while group II *Salinator* shows a weak negative correlation with medium *Katelysia*.

200 m: Correlations are weak.

300 m: Group II animals of each species are positively associated at zero spacing although correlations are generally weak.

400 m: Correlations are negligible.

500 m: Correlations are weak although both *Salinator* groups are positively correlated with large *Katelysia* at short spacings.

600 m: Correlations are weak.

700 m: At zero spacing group I animals are negatively correlated while at short spacings, group II *Salinator* shows positive correlations with small and medium *Katelysia*.

270681

100 m: Correlations are weak but at short and medium spacings group I animals are positively associated.

200 m: Correlations are negligible.

300 m: There is a strong positive correlation between group I *Katelysia* and group I *Salinator* at spacing 0. Correlations are weak otherwise.

400 m: Correlations are weak at short spacings apart from a positive correlation between large *Salinator* and medium *Katelysia*.

500 m: At spacing zero group I *Salinator* and group IV *Katelyia* show a strong positive association. At medium spacing both *Salinator* groups are negatively correlated with small *Katelysia*.

600 m: Group II *Salinator* shows positive relationships with medium and small *Katelysia* at zero and short spacings respectively.

700 m: At spacing 0 there are strong positive correlations between small *Salinator* and small *Katelysia*. Correlations are weak at non-zero spacings but generally *Salinator* is negatively correlated with medium *Katelysia*.

290981

100 m: Correlations are weak.

200 m: At spacing 0 small and large *Salinator* have a strong positive correlation with small and large *Katelysia* respectively. At short spacings large *Salinator* and small *Katelysia* show a weak positive relationship.

300 m: Small *Salinator* is weakly negatively correlated with large *Katelysia* at zero spacing. At short spacings *Salinator* and small *Katelysia* are positively correlated.

400 m: Correlations are weak.

500 m: Group I *Salinator* shows strong positive correlations with small and medium *Katelysia*, and negative correlations with large *Katelysia*, at spacing zero. Correlations are weak otherwise.

600 m: At spacing 0 there is a strong positive relationship between group I animals of each species. At other spacings correlations are weak.

700 m: Correlations are weak at all spacings but at zero and short spacings, small animals are positively associated.

291281

100 m: Correlations are weak.

200 m: At zero and short spacings group I *Salinator* is positively associated with large *Katelysia*.

300 m: Both *Salinator* groups are positively correlated with small *Katelysia* at zero and short spacings but correlations are negligible at other spacings.

400 m: Correlations are weak although small animals are negatively correlated at spacings 0 and 1.41.

500 m: At zero and short spacings small *Salinator* animals are positively correlated with small *Katelysia* while large *Salinator* are negatively associated with those *Katelysia* groups.

600 m: *Salinator* shows positive correlations with small and large *Katelysia* at zero and short spacings.

700 m: Correlations are weak but generally small animals are negatively associated.

Summary

At the top of the autumn beach medium/large animals are negatively correlated as are small animals at the last station. At 300 m and 500 m, the two species are positively correlated, with associations involving small animals of one species and large animals of the other.

Strong associations are primarily restricted to the lower half of the beach in winter. At either end of this zone the associations are between small animals and are positive. In the intermediate areas the associations are also positive but generally involve small animals of one species and large animals of the other.

At the top of the spring beach, and throughout the lower half, small animals have a positive correlation. Small *Salinator* are negatively associated with large *Katelysia* near the middle of the beach.

The two species show a general positive relationship towards the top and bottom of the summer transect. Near the centre of the beach, however, *Salinator* is negatively correlated with small *Katelysia*.

Cylichnina

Autumn correlations are weak at zero spacings. At either end of the beach *Cylichnina* shows weak positive relationships with small/medium *Katelysia*. At 300 m there is a strong positive association involving large *Katelysia* but at 400 m that association is negative.

In winter the strongest correlations are positive and occur in the top half of the beach where they involve *Cylichnina* and large *Katelysia*.

Correlations are weak in spring but at 200 m and 600 m *Cylichnina* is positively correlated with large *Katelysia*.

Summer correlations are also weak although small and large *Katelysia* are involved

in negative associations with *Cylichnina* at 400 m and 600 m.

Rissopsis

Correlations are weak at most stations in autumn. Only at 700 m do significant associations occur at spacing 0; these are positive and involve small *Katelysia*.

The winter associations are similar to those of autumn.

Overall interactions between the two species are strongest in spring and significant zero spacing correlations occur at most stations. These are positive and involve large *Katelysia* near the top, medium *Katelysia* near the bottom and small *Katelysia* near the middle of the beach.

Correlations are weak in summer although there is a positive relationship between *Rissopsis* and small *Katelysia* at the 200 m station.

Microdiscula

Autumn correlations are negligible apart from strong positive relationships with large *Katelysia* over short spacings at 100 m and 400 m.

In winter the only strong association occurs at 400 m where *Microdiscula* has a strong positive correlation with large *Katelysia*.

Correlations are weak in spring and summer.

Nassarius

In autumn *Nassarius* is postively correlated with large *Katelysia* in the top half, and with small *Katelysia* in the bottom half of the beach; at 700 m, however, the latter relationship is negative.

In the middle of the winter transect *Nassarius* and large *Katelysia* show a positive correlation. Positive relationships are also evident in the lower half but small animals are involved.

In spring correlations between the two species are positive, strongest in the lower half of the beach and usually involve small *Katelysia*.

The strongest summer associations occur in the middle reaches of the beach. At 300 m they are between *Nassarius* and large *Katelysia* while at 400 m small *Katelysia* are involved.

Agatha

Associations between *Katelysia* and *Agatha* are weak at most stations in all seasons. Exceptions occur at 600 m in winter and at 400 m in summer when *Agatha* shows strong positive correlations with small and medium *Katelysia*.

Bembicium

Correlations between *Katelysia* and *Bembicium* are weak.

Austrocochlea

In autumn the strongest associations occur near the middle of the beach where *Austrocochlea* and large *Katelysia* are positively correlated.

Correlations are weak in winter apart from a strong positive relationship between *Austrocochlea* and group III *Katelysia* at 600 m.

Small *Katelysia* are negatively correlated with *Austrocochlea* at 400 m and 700 m in spring but those groups are positively related at 600 m.

Summer correlations are negligible apart from positive associations involving large *Katelysia* at 100 m and 600 m.

Notoacmea

In autumn *Notoacmea* is positively correlated with large *Katelysia* in the top section of the beach.

Winter associations between *Notoacmea* and *Katelysia* are weak.

Correlations are also weak in spring although *Notoacmea* and small *Katelysia* are negatively related at 400 m.

In summer *Notoacmea* is positively correlated with small *Katelysia* near the middle of the beach.

Anthopleura

In autumn *Anthopleura* shows strong positive relationships with large *Katelysia* at all but the 700 m station. In the middle of the beach *Anthopleura* and small *Katelysia* are negatively correlated.

Associations between the two species are weaker in winter but at 100 m and 400 m, small *Katelysia* are involved in positive associations. Also at 400 m, large *Katelysia* and *Anthopleura* are positively correlated.

In spring *Anthopleura* and large *Katelysia* are positively correlated in the middle sections of the beach. At 300 m small *Katelysia* are negatively associated with *Anthopleura*.

Anthopleura and large *Katelysia* are positively correlated with large *Katelysia* in the middle sections of the summer beach.

Wallucina and

Soletellina

Correlations between *Wallucina* and *Soletellina* are weak. Only in summer, at 300 m, do the two species show strong association (positive).

Hydrococcus

Correlations are weak but generally *Wallucina* is negatively correlated with small

Hydrococcus at short spacings.

Zeacumantus

In autumn, correlations are significant only at 300 m where they are negative and involve large *Zeacumantus* . Associations between the two species are weak in other seasons.

Salinator

In autumn and winter *Wallucina* is positively correlated with large *Salinator* over medium spacings at a number of stations. Correlations are weak but the two species are negatively related at the last station. Associations are also weak in summer although *Wallucina* and *Salinator* are positively correlated at the top, in the middle and at the bottom of the beach.

Cylichnina

Correlations are weak.

Rissopsis

Apart from a positive correlation at the lower end of the autumn transect, correlations between *Wallucina* and *Rissopsis* are weak.

Microdiscula

In autumn *Wallucina* and *Microdiscula* show a positive correlation in the middle of the beach. Associations between the two species are weak in winter. Positive correlations occur at the last and first stations in spring and summer respectively.

Nassarius

Correlations between *Wallucina* and *Nassarius* are negligible apart from a negative relationship in the middle of the autumn beach.

Agatha

Correlations are generally weak.

Bembicium

As above.

Austrocochlea

As above.

Anthopleura

In autumn *Wallucina* and *Anthopleura* are positively correlated at 500 m. The two species are also positively correlated in winter at the last station. In spring positive correlations occur in the lower half of the beach while in summer there are only weak associations between the two species (at 700 m).

Soletellina and

Hydrococcus

In autumn there are significant positive correlations between *Soletellina* and *Hydrococcus* at most stations. At 300 m and 700 m these involve small *Hydrococcus* ; at 100 m and 400 m medium sized, and at 500 m large, *Hydrococcus* are involved.

Correlations between the two species are weak in winter although at 200 m there is a positive correlation with small *Hydrococcus* . At 300 m medium sized *Hydrococcus* have a weak negative association with *Soletellina* .

Correlations are also weak in spring apart from a negative correlation involving large *Hydrococcus* at the 300 m station.

In summer all *Hydrococcus* groups show a strong positive relationship with *Soletellina* at 100 m and there is a negative correlation between the two species at 600 m.

Zeacumantus

In all seasons but winter *Soletellina* and large *Zeacumantus* show positive correlations near the top of the beach. These are particularly strong in summer when medium sized animals are also involved.

Salinator

In autumn and winter *Soletellina* shows positive associations with large *Salinator* near the top of the beach. Positive relationships between the two species occur near the middle of the beach in spring and summer but smaller animals are involved and the correlations are weaker.

Cylichnina

At the 300 m station in autumn *Soletellina* and *Cylichnina* have a weak positive correlation; at 500 m in that season the two species are negatively correlated. In winter *Soletellina* and *Cylichnina* show positive relationships at the lower end of the beach.

Associations are weak in spring and summer.

Rissopsis

Correlations are weak in autumn and winter. In spring the two species have a weak positive correlation at 700 m while in summer there are strong positive associations at the top two stations.

Microdiscula

Correlations are negligible except for a positive relationship at the 100 m station in summer.

Nassarius

In autumn and summer *Nassarius* and *Soletellina* are positively correlated near the top of the beach; otherwise associations are negligible.

Agatha

As above.

Bembicium

In autumn *Bembicium* and *Soletellina* show positive correlations at 200 m and 400 m while in summer there is a positive relationship at 400 m. Correlations are negligible otherwise.

Austrocochlea

In autumn the two species are positively associated at 100 m. Correlations are negligible in winter while in spring and summer there are positive correlations towards the bottom of the beach.

Notoacmea

In autumn *Soletellina* and *Notoacmea* are positively correlated at all but the first and last stations of the beach. Associations are negligible in winter and spring and in summer there is a positive correlation at 500 m.

Anthopleura

Soletellina and *Anthopleura* show a positive association at 300 m in autumn. In winter there are similar associations at 200 m and 400 m. Correlations are negligible in spring and in summer they are positive but confined to the last station.

Hydrococcus and

Zeacumantus

200381

100 m: At spacing 0 a range of groups of each species show strong positive correlations. These continue over most spacings.

200 m: Correlations are weak.

300 m: Correlations are weak but small animals of one species are positively associated with large animals of the other.

400 m: At spacing 0 small *Hydrococcus* and medium *Zeacumantus* are positively correlated while that *Zeacumantus* group is negatively associated with medium *Hydrococcus*. Similar associations occur at short spacings.

500 m: Correlations are weak.

600 m: At spacing zero small *Hydrococcus* show a weak positive relationship with medium *Zeacumantus*.

700 m: There are negative correlations between small/medium *Zeacumantus* and medium *Hydrococcus* at spacing 0.

270681

100 m: At zero spacing large *Zeacumantus* show strong positive correlations with small and large *Hydrococcus*. There are similar associations involving most groups at short spacings.

200 m: At zero and short spacings all *Zeacumantus* groups are positively correlated with medium and large *Hydrococcus*.

300 m: Small *Zeacumantus* are positively related to medium *Hydrococcus* at spacing 0. Also at that spacing small *Hydrococcus* shows positive and negative correlations with medium and large *Zeacumantus* respectively. Correlations are weak otherwise.

400 m: Large *Hydrococcus* and medium *Zeacumantus* have a weak positive association at spacing 0.

500 m: At zero and short spacings medium and large animals from each species are positively related.

600 m: Correlations are negligible.

700 m: Small *Zeacumantus* are positively correlated with large *Hydrococcus* at spacing 0 and with small *Hydrococcus* at short spacings.

290981

100 m: At zero and short spacings medium and large *Zeacumantus* are positively associated with small and medium *Hydrococcus*.

200 m: Group I *Hydrococcus* is positively, and group II *Hydrococcus* negatively, correlated with *Zeacumantus* at zero and short spacings.

300 m: At spacing 0 small *Zeacumantus* and small and medium *Hydrococcus* are positively correlated as are large animals of each species. Similar associations occur at other spacings.

400 m: Correlations are weak except at spacing 0 where small animals of each species are positively related.

500 m: Correlations are weak.

600 m: Correlations are negligible.

700 m: As above.

291281

100 m: At spacing 0 all groups of each species have strong positive correlations. Similar associations occur at spacing 1.00 but correlations are weak at longer spacings.

200 m: At spacing 0 all groups of each species have strong positive correlations.

Correlations are relatively weak at non-zero spacings.

300 m: Medium and large animals are positively associated at zero spacing but correlations are weak at other spacings.

400 m: At spacing 0 large *Zeacumantus* and small *Hydrococcus* show a positive correlation.

500 m: Correlations are weak.

600 m: As above.

700 m: Correlations are negligible.

Summary

Positive correlations occur at most autumn stations and involve a range of groups. Negative associations occur in the middle and at the bottom of the transect.

The winter relationships are similar to those of autumn although negative associations occur only at 300 m.

In spring, significant correlations are restricted to the upper half of the beach. Most associations are positive but small animals are negatively correlated at 200 m.

Correlations are also confined to the upper beach in summer and are always positive in that season. Associations between *Hydrococcus* and *Zeacumantus* are particularly strong at the top two stations.

Salinator

200381

Correlations are weak in autumn apart from negative associations between small *Salinator* and small/medium *Hydrococcus* at the 700 m station.

270681

100 m: *Salinator* is negatively correlated with small and medium *Hydrococcus* at short spacings.

200 m: Correlations are weak.

300 m: *Salinator* is positively correlated with medium and large *Hydrococcus* at spacing 0; otherwise associations are weak.

400 m: Correlations are weak although large *Salinator* and group III *Hydrococcus* are positively related at spacing 0.

500 m: At spacing 1.00 small animals of each species show a strong positive relationship.

600 m: Correlations are weak.

700 m: Small animals show a strong positive relationship at zero and short spacings while large animals are negatively correlated.

290981

100 m: Small animals are positively correlated at spacing 0 and at short spacings large *Salinator* is also positively related to small *Hydrococcus* .

200 m: Correlations are weak.

300 m: Large *Salinator* show a positive correlation with small *Hydrococcus* at zero and short spacings.

400 m: Small animals of each species are positively related at spacing 0 and at short spacings medium *Hydrococcus* are also involved.

500 m: At spacing 0 small and large *Hydrococcus* are negatively correlated with large and small *Salinator* respectively. Correlations are weak at short spacings.

600 m: Correlations are weak although at spacing zero group I animals of each species are positively related.

700 m: Correlations are weak.

291281

100 m: Correlations are weak apart from negative correlations between a range of groups at medium spacings.

200 m: Correlations are weak.

300 m: There is a strong positive correlation between small animals at spacing 0.

400 m: At zero and short spacings large *Salinator* are positively correlated with large and medium *Hydrococcus* respectively.

500 m: Although correlations are weak there is a general negative relationship between the two species at most spacings.

600 m: Correlations are negligible.

700 m: Correlations are weak but at spacing 1.00 small animals are negativelty associated.

Summary

Associations in autumn are weak at all but the 700 m station where small animals are negatively correlated.

In winter negative correlations occur at both the top and bottom stations. Near the middle of the beach large *Salinator* are positively associated with medium/large *Hydrococcus* ; at 500 m similar relationships occur between small animals.

Salinator and *Hydrococcus* show negative correlations at the 500 m station in spring while associations are positive higher on the beach.

In summer the two species show negative correlations at 500 m and 700 m; associations are positive near the middle of the beach.

Cylichnina

In autumn strong asociations between *Hydrococcus* occur only at 100 m where *Cylichnina* is positively associated with small *Hydrococcus*. At 400 m and 500 m there are similar associtaions at short spacings.

Significant zero spacing correlations occur at 200 m, 300 m, 500 m and 600 m in winter. These involve small *Hydrococcus* at 600 m and medium *Hydrococcus* at the other stations.

In spring *Cylichnina* is positively associated with small and medium *Hydrococcus* at 400 m and 600 m respectively.

At 400 m on the summer beach group II *Hydrococcus* is negatively correlated with *Cylichnina* but at 500 m those groups are positively related. Above 400 m medium *Hydrococcus* are positively correlated with *Cylichnina* at short spacings. Similar associations involving all *Hydrococcus* groups occur at 600 m.

Rissopsis

Autumn correlations are weak except for positive associations at 400 m and 500 m involving medium and large *Hydrococcus* respectively.

In the upper half of the winter beach *Rissopsis* is positively correlated with medium and large *Hydrococcus* while at the bottom two stations small animals are involved in similar associations.

In spring only the 200 m and 700 m stations show zero spacing correlations. At 200 m they are positive and include group II and III *Hydrococcus* and at 700 m, group III *Hydrococcus* are positively correlated with *Rissopsis*.

In summer all *Hydrococcus* groups show positive correlations with *Rissopsis* at 100 m. Correlations are weak otherwise apart from a positive correlations between *Rissopsis* and group III *Hydrococcus* at 700 m.

Microdiscula

In autumn and winter *Microdiscula* is positively correlated with large and medium *Hydrococcus* respectively, near the middle of the beach. Correlations in those seasons are otherwise weak.

In spring the only significant zero spacing associations are positive and involve small *Hydrococcus* at 100 m.

In summer there are similar associations at 300 m.

Nassarius

In autumn large *Hydrococcus* are positively correlated with *Nassarius* at 200 m. At 700 m small *Hydrococcus* are negatively correlated with *Nassarius*.

There are strong positive associations between *Nassarius* and large *Hydrococcus* at the winter 200 m station. Small animals are involved in positive relationships at 700 m.

In the middle sections of the spring beach *Nassarius* is positively correlated with large *Hydrococcus* over short spacings. At either end of the transect small *Hydrococcus* are negatively correlated with *Nassarius*, also over short spacings.

In summer there are negative correlations between *Nassarius* and medium *Hydrococcus* at 200 m and 700 m but at 100 m all *Hydrococcus* groups show a positive association with *Nassarius*.

Agatha

Large *Hydrococcus* are positively associated with *Agatha* in the middle of the autumn beach. There is a similar relationship with medium *Hydrococcus* at 500 m.

In winter *Agatha* is positively correlated with large *Hydrococcus* at 200 m.

At the top of the spring and summer transects *Agatha* is positively related to group II and III *Hydrococcus*.

Bembicium

No significant zero spacing correlations occur in autumn but at 100 m, *Bembicium* is positively correlated with large *Hydrococcus*.

Large *Hydrococcus* are positively correlated with *Bembicium* in the middle of the winter beach; otherwise correlations are weak.

In spring small *Hydrococcus* and *Bembicium* are positively associated at 100 m.

In summer medium and large *Hydrococcus* are involved in positive correlations with *Bembicium* at 100 m.

Austrocochlea

Correlations between *Austrocochlea* and *Hydrococcus* are weak in autumn and winter.

In spring, all but the largest *Hydrococcus* groups are positively correlated with *Austrocochlea* at 300 m while group IV *Hydrococcus* is involved in a positive association at 600 m.

At the summer 300 m station *Austrocochlea* is positively correlated with small *Hydrococcus*. Similar associations involving medium/large *Hydrococcus* occur at 700 m; at 600 m medium *Hydrococcus* are negatively associated with *Austrocochlea*.

Notoacmea

Small *Hydrococcus* are positively correlated with *Notoacmea* in the middle of the autumn transect.

In winter group III *Hydrococcus* and *Notoacmea* show a positive relationship in the middle of the beach.

All *Hydrococcus* groups show positive associations with *Notoacmea* near the middle of the spring beach.

In summer *Notoacmea* is positively associated with group III *Hydrococcus* at 200 m and 400 m.

Anthopleura

In autumn small and medium *Hydrococcus* are negatively correlated with *Anthopleura* in the upper half of the beach. At 500 m, however, there is a weak positive association involving small *Hydrococcus*.

Medium and large *Hydrococcus* are negatively correlated with *Anthopleura* at winter stations other than 200 m, 500 m and 700 m. At 200 m large *Hydrococcus* show a positive relationship with *Anthopleura*.

Below the 200 m station in spring small *Hydrococcus* are negatively related to *Anthopleura*; at 100 m there is a similar association between large *Hydrococcus* and *Anthopleura*.

Correlations in summer are weak in comparison to those of the other seasons. At 300 m, however, medium/large *Hydrococcus* are negatively correlated with *Anthopleura* while at 600 m small *Hydrococcus* and *Anthopleura* are also negatively associated.

Zeacumantus and

Salinator

200381

100 m: Correlations are negligible.

200 m: At spacing 0 small *Zeacumantus* and large *Salinator* are positively associated.

300 m: Correlations are weak.

400 m: At spacing 0 there is a weak positive relationship between small *Zeacumantus* and large *Salinator*.

500 m: Correlations are negligible.

600 m: Medium *Zeacumantus* and large *Salinator* show a strong positive correlation at zero spacing; otherwise correlations are weak.

700 m: Small and medium *Zeacumantus* have a strong positive association with small *Salinator* at spacing 0 but correlations are negligible at other spacings.

270681

100 m: At zero and short spacings *Salinator* is negatively correlated with small *Zeacumantus* .

200 m: At spacing 0 large animals of each species are positively correlated.

300 m: Large *Zeacumantus* are positively correlated with small *Salinator* at zero spacing.

400 m: No significant correlations exist at spacing 0 but at short spacings *Salinator* shows negative relationships with small and medium *Zeacumantus* .

500 m: Small and large *Zeacumantus* are positively correlated with large *Salinator* at zero and short spacings respectively.

600 m: Correlations are negligible.

700 m: Correlations are weak.

290981

100 m: Correlations are weak.

200 m: At spacing 0 there is a weak positive relationship between medium *Zeacumantus* and large *Salinator* . At short and medium spacings the two species show strong positive correlations involving a range of groups.

300 m: Correlations are weak.

400 m: As above.

500 m: Correlations are negligible.

600 m: As above.

700 m: As above.

291281

100 m: Correlations are weak.

200 m: Correlations are negligible.

300 m: As above.

400 m: Small *Zeacumantus* are positively related to *Salinator* at zero and short spacings.

500 m: Correlations are weak.

600 m: Correlations are negligible.

700 m: As above.

Summary

In autumn small and medium *Zeacumantus* are positively correlated with *Salinator* at stations other than 100 m, 300 m and 500 m.

At 200 m, 300 m and 500 m on the winter beach, large *Zeacumantus* are

positively correlated with *Salinator*. At 100 m and 400 m smaller *Zeacumantus* have a negative association with *Salinator*.

In spring correlations are weak apart from strong positive associations between the two species at 200 m.

Correlations are also weak in summer except for a positive relationship between small *Zeacumantus* and *Salinator* in the middle of the beach.

Cylichnina

In autumn *Cylichnina* shows a weak negative correlation with small *Zeacumantus* at 300 m. At 500 m medium *Zeacumantus* are involved in positive correlations while at 700 m there are strong positive associations between *Cylichnina* and small and medium *Zeacumantus*.

Correlations are weak in winter apart from a positive association with large *Zeacumantus* at the 500 m station.

Spring and summer associations are similar to those of winter except that smaller *Zeacumantus* are involved.

Rissopsis

Small *Zeacumantus* are positively correlated with *Rissopsis* over short spacings near the middle of the autumn beach.

In winter all *Zeacumantus* groups are positively correlated with *Rissopsis* over zero and short spacings at 200 m. At 700 m small *Zeacumantus* are involved in a strong positive association.

The two species are positively correlated at the top of the spring transect; at 400 m there is a weak negative correlation between *Rissopsis* and medium *Zeacumantus*.

In summer *Zeacumantus* and *Rissopsis* have a positive association at the top station but otherwise correlations are weak.

Microdiscula

In autumn there are weak negative and positive associations between the two species at the top and middle of the beach respectively.

Large *Zeacumantus* are positively correlated with *Microdiscula* at the top and middle of the winter beach.

In spring large *Zeacumantus* are negatively correlated with *Microdiscula* at 300 m while medium *Zeacumantus* are involved in a positive association at 400 m.

Microdiscula shows weak positive associations with large *Zeacumantus* near the top of the summer transect.

Nassarius

Small and medium *Zeacumantus* show strong positive correlations with *Nassarius* at the 700 m station in autumn.

Small and large *Zeacumantus* are positively related to *Nassarius* in the top section of the winter beach.

In spring *Nassarius* is positively correlated with medium *Zeacumantus* near the top of the beach.

At the top summer station medium *Zeacumantus* and *Nassarius* are positively correlated. Similar associations involving large and small *Zeacumantus* occur at 400 m and 600 m respectively. At 200 m there is a weak negative correlation between *Nassarius* and small *Zeacumantus* .

Agatha

In autumn and winter *Agatha* shows weak positive correlations with small *Zeacumantus* at 300 m and 200 m respectively.

Medium *Zeacumantus* and *Agatha* are positively correlated at the top and middle of the spring beach.

Summer associations between *Agatha* and *Zeacumantus* are negligible.

Bembicium

In autumn, spring and summer large *Zeacuamtus* are positively correlated with *Bembicium* near the top of the beach while in winter, medium *Zeacumantus* are negatively related to *Bembicium* in those regions.

Austrocochlea

Correlations between *Austrocochlea* and *Zeacumantus* are weak in autumn.

In winter *Austrocochlea* is positively correlated with large and small *Zeacumantus* at 100 m and 500 m respectively.

Correlations are weak in spring.

Correlations are negligible in summer apart from a positive correlation involving small *Zeacumantus* at 300 m.

Notoacmea

Correlations are weak apart from positive correlations with medium and large *Zeacumantus* near the middle of the beach in autumn and spring.

Anthopleura

In autumn medium *Zeacumantus* are negatively correlated with *Anthopleura* near the top of the beach while large *Zeacumantus* are involved in positive associations near

the middle of the beach.

Anthopleura is positively associated with small *Zeacumantus* near the top of the winter beach.

Spring associations are similar to those of winter except that large *Zeacumantus* are involved.

In summer *Anthopleura* is positively related to medium and large *Zeacumantus* near the top of the beach.

Salinator and

Cylichnina

Correlations between *Cylichnina* and *Salinator* are weak in autumn, apart from a strong positive association involving small *Salinator* at 700 m.

Small *Salinator* and *Cylichnina* are positively related at the winter 600 m station.

At 200 m in spring and summer, large *Salinator* are positively correlated with *Cylichnina* at zero and short spacings respectively.

Rissopsis

Rissopsis and *Salinator* are positively associated over short distances at either end of the autumn transect.

In winter there is a weak negative relationship between the two species at the middle of the beach.

At the 500 m station in spring *Rissopsis* and small *Salinator* show a strong positive association; in that season there is also a weak positive correlation between the species at 700 m.

Correlations are negligible in summer.

Microdiscula

At 300 m in autumn and summer, *Microdiscula* is positively correlated with large and small *Salinator* respectively; otherwise correlations are negligible.

Nassarius

Nassarius shows a strong positive relationship with small *Salinator* at 700 m in autumn and winter.

In spring there is a weak positive association involving large *Salinator* at 400 m.

Correlations are negligible in summer.

Agatha

In autumn, zero spacing correlations are significant only at 400 m, are positive and involve large *Salinator*.

At the winter 400 m station *Agatha* shows a weak negative relationship with *Salinator* while at 600 m large *Salinator* are involved in a positive association.

There is a weak positive correlation between large *Salinator* and *Agatha* at 100 m in spring.

Correlations are negligible in summer.

Bembicium

Bembicium and *Salinator* are positively related at the top of the autumn and summer transects but otherwise correlations are negligible.

Austrocochlea

Correlations are weak in all seasons.

Notoacmea

In autumn *Salinator* and *Notoacmea* are positively related over short spacings at the 100 m station.

Large *Salinator* and *Notoacmea* are positively related at 600 m in winter.

In spring there is a weak negative correlation between *Notoacmea* and small *Salinator* at 600 m.

Correlations are weak in summer.

Anthopleura

Large *Salinator* are positively correlated with *Anthopleura* in the upper half of the autumn beach. There is a weak negative association between those groups at 400 m.

Correlations are weak in winter apart from positive correlations with small and large *Salinator* at 100 m and 700 m respectively.

In spring *Anthopleura* and small *Salinator* are positively correlated at 100 m while at 200 m and 500 m, large *Salinator* are involved in similar associations.

Anthopleura and large *Salinator* are positively related at 100 m, 600 m and 700 m in summer.

Cylichnina and

Rissopsis

Correlations between *Cylichnina* and *Rissopsis* are weak in all seasons apart from a positive association at the top of the winter beach.

Microdiscula

In winter the two species are positively correlated at the middle of the beach. In summer there are strong correlations over zero and short spacings at 300 m.

Nassarius

Correlations between *Cylichnina* and *Nassarius* are weak.

Agatha

In autumn and winter *Cylichnina* and *Agatha* are positively associated at 300 m and 200 m respectively.

Bembicium

Correlations are negligible.

Austrocochlea

Correlations are negligible at zero spacings but in seasons other than winter, *Cylichnina* and *Austrocochlea* are positively asociated over short spacings in the lower half of the beach.

Notoacmea

Correlations are weak.

Anthopleura

In autumn *Cylichnina* and *Anthopleura* are positively associated over zero and short spacings in the middle sections of the beach; otherwise correlations are negligible.

Rissopsis and

Microdiscula

Correlations are negligible.

Nassarius

Correlations are weak.

Agatha

Correlations are weak apart from a positive association at 400 m in summer.

Bembicium

In spring and summer *Rissopsis* and *Bembicium* are positively correlated at the top of the beach.

Austrocochlea

Rissopsis and *Austrocochlea* are positively correlated at the top of the summer beach; otherwise associations are negligible.

Notoacmea

As above.

Anthopleura

In winter *Rissopsis* and *Anthopleura* are positively associated at 200 m and 500 m but correlations are negligible in other seasons.

Microdiscula and

Nassarius

The two species are positively associated at the top of the summer beach.

Agatha

Correlations are negligible.

Bembicium

As above.

Austrocochlea

As above.

Notoacmea

As above.

Anthopleura

As above.

Nassarius and

Agatha

Correlations are negligible.

Bembicium

As above.

Austrocochlea

Nassarius and *Austrocochlea* are positively correlated at the top of the autumn and winter beaches.

Notoacmea

Correlations between *Nassarius* and *Notoacmea* are negligible apart from a strong positive relationship at 400 m in summer.

Anthopleura

Correlations between *Nassarius* and *Anthopleura* are negligible apart from a strong positive relationship at 400 m in autumn.

Agatha and

Bembicium

In autumn *Agatha* and *Bembicium* show a positive relationship at 300 m but correlations in other seasons are negligible.

Austrocochlea

In autumn and summer *Agatha* and *Austrocochlea* show positive relationships near the middle of the beach but correlations in other seasons are negligible.

Notoacmea

In autumn *Agatha* and *Notoacmea* are positively related in the middle sections of the beach. Similar associations in winter and summer are confined to the central station while in spring there are negligible correlations.

Anthopleura

In autumn and winter there are weak positive relationships between the two species near the top of the beach.

Bembicium and

Austrocochlea

Correlations are weak apart from a strong positive relationship at the top of the summer transect.

Notoacmea

Correlations are weak apart from positive associations at the top of the autumn and summer beaches.

Anthopleura

Correlations are weak.

Austrocochlea and

Notoacmea

In winter and summer the two species are positively correlated at 400 m and 100 m respectively.

Anthopleura

In winter and spring *Austrocochlea* and *Anthopleura* are positively correlated near the middle of the beach.

Notoacmea and

Anthopleura

In autumn *Notoacmea* and *Anthopleura* are positively associated near the middle of the beach but otherwise correlations are negligible.

6.4 Discussion

6.4.1 Planar autocorrelation

Planar autocorrelations within *Anapella* and *Katelysia* size classes are strongest in winter and spring, probably reflecting attractions associated with reproduction. This contrasts with the relative strengths of the serial autocorrelations shown by the bivalves: while serial autocorrelations among *Anapella* are minimal, *Katelysia* autocorrelations are strongest in spring and summer. Thus, the serial associations lag behind the two-dimensional correlations by one season.

Juveniles of both species show positive autocorrelations over short distances but the associations are markedly stronger within the *Anapella* juvenile classes. In that species, the attractions are sufficiently strong to produce a 'hole' effect where the attractions of neighbouring animals leaves a deficiency in outlying areas and consequently a negative correlation at those spacings. Juvenile *Anapella* autocorrelations are typically positive; in contrast, *Katelysia* juveniles show negative relationships in the seasons of strongest interaction. In those seasons large *Katelysia* also show negative autocorrelations at the 700 m station.

The autocorrelation patterns of *Anapella* allow that species to be divided into a number of functional size groups. The 3 mm size class shows behaviour that is intermediate between the juveniles and the larger classes. With increasing size of animals, the autocorrelations tend to occur over longer spacings, suggesting that the range of attraction is proportional to the body size. This pattern is not as clearly defined among *Katelysia*, which shows weaker interactions overall. In that species, animals near 10 mm in size have positive associations in all seasons, probably indicating attractions among recently matured animals. It appears that 3 mm and 10 mm represent critical sizes in the life histories of *Anapella* and *Katelysia* respectively.

Anapella and *Katelysia*, then, show quite different patterns of spatial interaction. While *Anapella* interacts strongly within its size classes over short distances, there is little interaction over the transect. *Katelysia*, on the other hand, exhibits considerable interaction along the beach but relatively little in localised areas. *Katelysia* adults interact in both serial and planar dimensions over winter and spring, probably for reproduction. The resultant juveniles segregate over short planar distances, and by summer those interactions become evident over serial distances. *Anapella* juveniles never show segregation and are typically strongly positive. Unlike *Katelysia*, however, these interactions do not extend into the serial dimension. The correlations probably reflect the contrasting dependencies on the tidal gradient shown by *Anapella* and

Katelysia.

The anemone, *Anthopleura*, could be expected to show autocorrelation patterns similar to those of its principal hosts, *Anapella* and *Katelysia* - this is not the case, however. The planar autocorrelations within *Anthopleura* are strongest in summer and autumn, in direct contrast to the bivalves. Also, the interaction ranges tend to be inversely proportional to body size. These patterns appear to reflect a combination of the breeding and settlement behaviour of *Anthopleura*. The strongest interactions occur in the reproductive season and among large animals, suggesting they may be related to reproduction behaviour.

The apparent inverse relationship between size and interaction range can be attributed to the discrete distribution of *Anthopleura* hosts. *Anthopleura* can only occupy discrete positions within the continuous sampling grid and the attraction between animals (possibly associated with reproduction) leads to a number of animals coming to lie within a single cell of the sampling grid, rather than being continuously distributed between the cells. Strong attraction between large *Anthopleura*, therefore, concentrates animals into a given cell and reduces the apparent range of attraction.

Wallucina shows little seasonal variation in autocorrelation patterns. There are only weak relationships among juveniles but the largest animals frequently show interactions. There are suggestions that the range of interaction is proportional to body size. In all seasons, the associations are weak near the high areas of the beach while in autumn and winter, negative correlations occur at the 700 m station. It appears that resources are limiting for *Wallucina* at the bottom of the beach during the reproductive seasons.

As with the major bivalves, planar autocorrelations within *Hydrococcus* are strongest in winter, prior to the major recruitment season, and extend over ranges proportional to body size. The autocorrelations are positive and appear to be weaker near the beach ridges, close to the 300 m and 500 m stations. The strength of the attractions within the various size classes are sufficient to produce a hole effect, similar to that exhibited by *Anapella* juveniles. The strong attractions shown by *Hydrococcus*, prior to the main breeding season, weaken in autumn. In that season the serial correlations suggest a serial segregation of animals. Thus it appears that the gastropods come together for reproduction and then segregate along the transect as the densities increase the following season.

The other deposit feeding gastropod, *Salinator*, shows comparatively little consistency in its autocorrelations. Interactions are strongest near the top of the

transect, however, and extend down the beach following winter, probably reflecting recruitment during spring and summer.

Of all species in Pipe Clay Lagoon, *Zeacumantus* shows the clearest trend for the range of significant interactions to be proportional to body size. Like *Hydrococcus* , the autocorrelations are positive and are strong enough to produce a hole effect. As with previous species, *Zeacumantus* interactions are strongest in winter. In contrast to those species, however, this is not the reproductive season for *Zeacumantus* . In fact, the autocorrelations are weakest in the summer, when reproduction probably occurs. This may indicate a very long incubation period.

Other algivores, *Rissopsis* and *Microdiscula* , also exhibit strong autocorrelations in the cooler months. In winter and spring, *Rissopsis* autocorrelations extend over much of the beach but in summer they are confined to the top sections of the beach; in autumn the interactions are restricted to the lower half. The summer interactions probably lead to the autumn recruitment of *Rissopsis* in the top sections of the beach. Similarly, the autumn interactions in the lower half of the beach precede the major recruitment in the following seasons with interactions and recruitment continuing over winter and spring.

Microdiscula autocorrelations also differ between the top and lower halves of the beach. While the interactions are positive in the top half, the evidence suggests that *Microdiscula* avoid each other in the lower sections. The segregation among *Microdiscula* occurs away from its preferred zone and suggests there may be competition for limited resources in the lower half of the beach. The planar autocorrelations are strongest in winter and weak in autumn and summer. The autumn recruitment of *Microdiscula* , therefore, does not appear to be associated with a prior attraction of animals. Of course, the extremely small size of *Microdiscula* makes it doubtful that all interactions could be detected at the scale of the sampling.

Negative autocorrelation coefficients occur among *Cylichnina* in summer suggesting an active avoidance between those animals. Summer is the season of recruitment for *Cylichnina* and the negative correlations during the recruitment season contrast with those of previous species. In autumn, however, the associations are positive while in other seasons the interactions are relatively weak.

Cylichnina is an extremely mobile animal compared to all other species in the assemblage and quadrat sampling could not be expected to reflect dispersion patterns intrinsic to that species. Instead, the patterns detected are more likely to be artifacts of interspecific interactions. The negative correlations, for example, could be related to a

shortage of food, in the form of juveniles of its major prey species during those seasons. The remaining species do not exhibit significant planar autocorrelation.

6.4.2 Planar intraspecific cross-correlation

In all seasons, positive cross-correlations occur between small and between large *Anapella* groups. Summer is the season of greatest overall interaction. The correlations are weakest in the middle reaches of the beach, where *Anapella* reaches its greatest densities. This suggests that each end of the transect represents a critical zone for *Anapella*. Segregation between *Anapella* classes occur only in spring, and involve medium sized animals. The segregation could be due to intraspecific competition for limited resources following the previous season's density increases, although migration and passive resettlement may also play a role.

Small *Katelysia* groups also show positive correlations, but significant associations are confined to the bottom of the beach. In contrast to *Anapella*, *Katelysia* interactions are strongest in winter. Small animals are negatively associated with medium or large animals only at the 500 m beach ridge station in winter and spring. This suggests that juveniles avoid adults in stressed regions of the beach during the peak densities and probably reflects competition for limited resources. The general absence of negative correlations between juvenile and adult animals at other stations indicates that the ingestion of larvae by the suspension feeding adults probably does not occur.

There is considerable interaction between most *Hydrococcus* size groups in all seasons, particularly at either end of the beach. As with *Anapella*, this indicates that each end of the beach represents a critical zone. In the middle of the beach small and large animals tend to be positively related. The exception occurs in winter when those groups are negatively correlated. Thus, while similarly sized animals are strongly attracted to each other in winter, animals of quite different sizes appear to avoid each other. Again, this may reflect competition for limited resources during a season of high densities and relatively poor nutrient supply.

Significant correlations occur between all *Zeacumantus* groups in the top sections of the beach. These are weakest in winter, in direct contrast to the relative strengths of the planar autocorrelations but in keeping with the summer reproduction patterns shown by *Zeacumantus*. The discrepancies between the auto- and cross-correlations suggest that reproduction may occur within a range of size groupings. Other species have more clearly defined cohorts than *Zeacumantus* and reproduction is likely to be restricted to single size groupings.

6.4.3 Planar interspecific cross-correlation

Anapella and *Katelysia* show cross-correlations that vary with both the position on the beach and the season. The two species appear to avoid each other in all seasons. In autumn this occurs at either end of the transect, while in winter the avoidance is apparent in the middle of the beach. The negative correlations in autumn involve similarly sized (usually small) animals of each species. In winter, however, small animals of one species are segregated from large members of the other in the middle of the beach. In spring and summer, small animals of each species are negatively associated at the bottom and top of the respective transects.

Thus, it appears that juveniles of both species tend to avoid juveniles and adults of the other species near the middle of the winter beach, where the combined recruitment of the two species is greatest. In other seasons, the juveniles avoid each other at the extremes of the zones of distribution. In all cases, the avoidance suggests a resource limitation, dependent on the combined densities of the two species. Alternatively, the adult-juvenile segregation may reflect larval mortality resulting from ingestion of larvae by feeding adults. The general absence of negative adult-juvenile correlations within the same species, however, suggests that this is unlikely, unless the feeding adults are able to distinguish between conspecific and aspecific larvae.

Away from the areas of segregation, *Anapella* and *Katelysia* are positively associated, as would be expected for two species having similar resource requirements. In autumn and winter these associations often involve small animals of one species and large animals of the other. In summer similarly sized animals from each species are positively related.

Wallucina exhibits spatial segregation with *Anapella* and, to a lesser extent, with *Katelysia*. In autumn and winter there appears to be avoidance between *Wallucina* and non-juvenile *Anapella* near the middle of the beach. In spring, however, those groups are positively related over most of the beach. Negative correlations occur again in summer and involves small *Anapella* in the top sections of the beach. Positive associations occur between *Wallucina* and *Katelysia* in autumn and summer but in winter and spring, *Wallucina* and juvenile *Katelysia* appear to segregate in the lower half of the beach. *Wallucina* has similar resource requirements to *Anapella* and *Katelysia* and appears to be an inferior competitor, being excluded by the more dominant species.

According to the working hypothesis, the deposit feeding *Soletellina* could be expected to show segregation with the suspension feeding bivalves. However, *Soletellina*

is positively correlated with medium and large *Anapella* in the middle of all but the summer transects. In summer, which is the season of strongest interaction between *Soletellina* and *Anapella*, those groups are positively related over most of the beach. Although *Soletellina* shows weak correlations with *Katelysia* in autumn and winter, the relationships are similar to those between *Soletellina* and *Anapella*. An exception occurs in summer when *Katelysia* juveniles and *Soletellina* segregate at the bottom of the transect.

In most seasons, small *Hydrococcus* and small or medium *Anapella* are negatively correlated in the middle sections of the beach, as expected under the working hypothesis. In summer the segregation occurs further down the beach and involves large *Hydrococcus* and small *Anapella*. Away from the middle of the beach, small members of each species are often positively correlated. While the correlations between *Katelysia* and *Hydrococcus* are generally positive, negative associations occur between large animals of each species in the middle of the spring beach; the two species are negatively correlated near the bottom of the summer beach.

Similarly, large *Salinator* are negatively correlated with small *Anapella* in the lower half of the beach. In winter and summer negative correlations also occur at the top of the beach. In autumn and spring, however, the two species are positively related in the upper half of the transects. Negative correlations between *Salinator* and *Katelysia* occur in autumn when small animals segregate at the bottom of the beach and large animals segregate at the top. Also, the two species segregate near the middle of the beach in spring and summer. In winter, correlations are generally positive in the lower half.

Interactions between the suspension feeding bivalves and algivorous gastropods could arise if similar food types occur in their respective diets. For example, substrate distrubance may lead to microalgae being suspended in the water column and thus being available to the suspension feeders.

In all seasons small or medium *Zeacumantus* are positively related to small *Anapella*. However, in autumn *Zeacumantus* and larger *Anapella* segregate in the top sections of the beach. Segregation also occurs in the middle of the summer beach, between *Zeacumantus* and small *Anapella*. In seasons other than summer, small *Zeacumantus* and *Katelysia* are negatively correlated near the top of the beach. *Zeacumantus* and large *Katelysia* are also segregated near the top of the spring beach. Otherwise the two species tend to be positively related. Correlations between these two species are weak in summer.

Rissopsis and small *Anapella* appear to segregate in the middle of the autumn and

winter beaches. In spring and summer the segregation is transferred to the bottom and top of the transects respectiviely. Otherwise the two species have positive associations. No segregation occurs between *Katelysia* and *Rissopsis*, and small *Katelysia* are generally involved in positive correlations in the lower half of the beach.

In most seasons *Microdiscula* and small *Anapella* are positively correlated in the top half of the beach. Negative correlations occur in the middle of the autumn beach and in spring, *Microdiscula* and large *Anapella* segregate. *Katelysia* and *Microdiscula* show little interaction.

While *Katelysia* and *Bembicium* show negligible interaction, due to their disparate zonations, *Bembicium* and *Anapella* frequently interact near the top of the beach. The associations are usually positive and involve small *Anapella* ; in winter, however, those groups segregate. Also, negative correlations occur between *Bembicium* and medium *Anapella* in spring.

Austrocochlea and medium or large *Anapella* frequently have positive associations at stations other than the first; in summer small *Anapella* are involved. Similar correlations occur between *Austrocochlea* and *Katelysia* in autumn and winter. Negative correlations between *Austrocochlea* and the bivalves are uncommon. In autumn they involve small *Anapella* in the top half , and in spring they involve small *Katelysia* in the bottom half, of the beach.

Correlations between *Notoacmea* and the major bivalves are weak but tend to be positive in the middle and upper sections of the beach. Negative correlations occur only in autumn and involve small *Katelysia* in the bottom section of the transect.

The less common algivorous gastropods often show segregation with the suspension feeding bivalves. This could reflect a resource overlap with the suspension feeders limiting the avaliability of at least part of the gastropod food supplies. Only the comparatively poor competitors are affected while the dominant gastropods are apparently buffered against the resource intrusion.

Cylichnina tends to be positively correlated with small *Anapella* and medium or large *Katelysia* at either end of the transect. Negative correlations occur near the bottom of the transect in summer. Also, *Katelysia* and *Cylichnina* show segregation in the middle of the summer and autumn transects. Typically, non-juvenile *Katelysia* are involved in significant correlations while the opposite is true for *Anapella*. These corrrelations support the observations of the serial analysis, which suggested that juvenile *Anapella* were a more likely food source for *Cylichnina* than juvenile *Katelysia*. At the bottom of the summer transect, the numbers of *Anapella* juveniles

appear to be sufficiantly low to result in depauration through *Cylichnina* predation and a consequent segregation between the species.

Nassarius generally exhibits positive correlations with large *Anapella* and *Katelysia*. The correlations are strongest in areas of the beach where the two bivalves reach their respective greatest densities. Thus, *Anapella* and *Nassarius* tend to be related at all but the lowest stations while correlations with *Katelysia* are strongest in the middle and lower sections of the beach. *Nassarius* also exhibits positive correlations with small bivalves but this is probably an indirect correlation.

These correlations support the field observations which showed that large *Anapella* and large *Katelysia* are common food sources for *Nassarius*. The correlations also represent confirmation of the usefulness of the analytical methods.

Agatha is often positively correlated with medium and large *Anapella* in the top sections of the beach but *Agatha* and *Katelysia* have little interaction. As was found with the series analysis, there is insufficient evidence to support the suggestion of a host-parasite relationship between *Agatha* and either bivalve.

Anthopleura is positively correlated with large *Anapella* and/or *Katelysia* over most of the beach. The correlations involving *Katelysia* occur most often in the middle of the beach. In the main seasons of reproduction for those bivalves, *Anthopleura* and juvenile bivalves are negatively correlated in the middle and upper sections of the beach. The correlations support field observations which indicated that large *Anapella* and *Katelysia* are the principal substrates for the anemone. The negative correlations with juvenile bivalves are also in agreement with the findings of those animals in the gut of *Anthopleura*, and suggest that the juveniles bivalves do form part of the food spectrum of the anemone.

Wallucina and *Hydrococcus* show evidence of weak segregation over most of the beach, as would be expected according to the trophic group amensalism hypothesis. In contrast, the other deposit feeding gastropod - *Salinator* - is often positively associated with *Wallucina* in autumn and winter. Clearly, *Hydrococcus* has the dominant role in the trophic group amensalism.

Large *Zeacumantus* also appear to segregate with *Wallucina*, but only in autumn, near the middle of the beach. Both species are at the extremes of their zones in those areas, and could be particularly sensitive to interspecific interactions there.

Wallucina is usually positively related with *Agatha* in the lower sections of the beach but it is not possible to suggest host-parasite relationships between those species.

The remaining bivalve, *Soletellina*, exhibits considerably more interspecific

interaction than *Wallucina*. Although *Soletellina* and *Hydrococcus* interact positively over most of the autumn beach, in other seasons the two species segregate in the middle and lower sections. This is probably evidence of competitive exclusion between two species utilising similar resources. Correlations between *Soletellina* and the other deposit feeding gastropod, *Salinator*, are positive, however, and are strongest in the upper half of the beach in autumn and winter. It appears that, while *Soletellina* and *Salinator* may share similar resources, the competition between the two species is not sufficient to cause a spatial segregation on the tidal flat.

Interactions between *Soletellina* and the algivorous gastropods, *Zeacumantus*, *Rissopsis*, *Bembicium*, *Notoacmea* and *Austrocochlea*, tend to be positive near the top of the beach but are weak in autumn and/or winter. These associations are likely to artifacts of the correlations between *Salinator* and *Soletellina*, which occur in similar areas of the beach and in similar seasons.

In contrast, *Cylichnina* and *Soletellina* are positively correlated in autumn and winter in the middle and lower reaches of the beach respectively. Segregation occurs near the bottom of the autumn transect. Again, however, these correlations could be reflections of the underlying associations between *Soletellina* and the major bivalves. Those species tend to be positively related in the middle and lower sections of the beach, although segregation occurs at the bottom of the summer beach. Similar patterns of association occur between *Cylichnina* and the major bivalves, suggesting the correlations involving *Soletellina* are indirect.

In summer and autumn, *Soletellina* and *Anthopleura* are positively associated in the middle and at the bottom of the beach; otherwise the correlations between those two species are weak. As before, the positive correlations shown between *Soletellina* and large *Anapella* may account for this.

The two deposit feeding gastropods, *Hydrococcus* and *Salinator*, appear to segregate at the bottom of the beach. In winter, segregation also occurs at the top. Elsewhere on the beach, the two species are usually positively related. Thus, it appears that either end of the beach represents a critical zone for deposit feeders, including *Soletellina*. The areas of the beach, particularly the lower end, show the highest densities of deposit feeders. Competition for limited resources probably leads to competitive exclusion, which is enhanced in the coldest months and extends to the upper end of the transect.

Salinator and *Zeacumantus* interactions are weak, particularly in spring and summer. In seasons other than winter, the two species tend to be positively related in the middle sections of the beach. This contrasts with the serial relationships which show

spatial segregation along the transect in summer and autumn. Only in winter, and in the top half of the beach, do *Salinator* and (small) *Zeacumantus* appear to segregate. The two species reach their highest abundances in the top sections of the beach and, although their modes of feeding differ, they may have overlap food resources. The winter conditions that appear to stress *Salinator* and *Hydrococcus* coexistence could also account for the winter planar segregation between *Salinator* and *Zeacumantus* .

Planar correlations between *Hydrococcus* and *Zeacumantus* are positive over most of the transects. These associations are particularly strong near the top of the summer beach. At occasional stations, negative correlations do occur. Thus, there is evidence of segregation in the middle and at the bottom of the beach in autumn and winter, and in spring, negative associations are evident at the top of the beach. The former segregations do not appear strong enough to affect the serial correlations between the species, as no serial segregation was evident. It is possible, however, that the negative correlations in the middle of the beach may at least partly account for the abrupt decrease in *Zeacumantus* densities there. In spring, the two species show both serial and planar segregations, suggesting competitive exclusion. The relationships change from segregation in spring to strong positive associations in summer, indicating that spring is a particularly critical season.

Cylichnina and small or medium *Hydrococcus* are positively associated at most stations in all seasons. The strongest correlations occur in the middle sections of the beach. In summer, however, the two species appear to segregate in that region, possibly due to the predatory pressure following the summer *Cylichnina* recruitment. The relationships between *Cylichnina* and small *Salinator* are always positive but are restricted to either end of the transects. Juveniles of both *Hydrococcus* and *Salinator* are thus likely candidates for *Cylichnina* prey.

Rissopsis is positively correlated with a range of *Hydrococcus* groups at both ends of the transects. Similar relationships exist between *Rissopsis* and *Salinator* , although the correlations are weaker. Also, *Rissopsis* and *Salinator* are negatively correlated in the middle of the winter beach. The segregation is likely to be due to factors similar to those attributed to the winter segregation between *Zeacumantus* and the deposit feeders. The correlations could also be indirectly due to the positive associations between *Zeacumantus* and *Rissopsis* .

Hydrococcus and *Salinator* tend to be positively correlated with the remaining algivorous gastropods. The associations are strongest in the major zones of the latter species and weaken in winter and/or spring. These patterns suggest that the species tend

to casually occur together in their respective zones and that the influx of deposit feeding recruits temporarily swamps the casual relationships.

In all seasons except summer, *Nassarius* and large *Hydrococcus* are positively correlated at the top of the beach. In summer there are negative correlations in that region. In seasons other than winter *Nassarius* and small or medium *Hydrococcus* are negatively correlated at the bottom of the beach; in winter the correlations are positive there. *Salinator* and *Nassarius* are positively related at the top of the autumn and winter transects. The existence of significant correlations between *Nassarius* and the deposit feeding gastropods are unexpected. Indirect correlations could arise through the gastropods being correlated with the large bivalves, which are *Nassarius* prey. However, the sign of the *Nassarius* / gastropod correlations are often opposite to the sign of the *Nassarius* / bivalve correlations.

In all seasons, *Agatha* is positively correlated with medium or large *Hydrococcus* near the top of the beach. *Agatha* and large *Salinator* show positive correlations in the lower sections of the autumn and winter beaches; otherwise asociations between those species are weak.

Hydrococcus and *Anthopleura* typically exhibit negative correlations at most stations. This could be expected on the basis of the field observations which found *Hydrococcus* in the gut cavity of the anemone. *Salinator* and *Anthopleura*, however, tend to be positively associated at either end of the beach. Only in autumn, in the middle of the beach, are (small) *Salinator* and *Anthopleura* negatively related. The comparatively low densities of *Anthopleura* at the ends of the beach probably allow *Salinator* to escape predation there.

Large *Zeacumantus* are positively correlated with other algivorous gastropods in various seasons. Thus, *Zeacumantus* and *Austrocochlea* are positively asociated at either end of the winter beach. *Bembicium* and large *Zeacumantus* are positively correlated at the top of the beach in all seasons but winter, when the relationship is negative. Similarly, *Microdiscula* and *Zeacumantus* show positive associations in that region in all seasons but autumn. Also, negative correlations between *Microdiscula* and *Zeacumantus* exist in the middle sections of the spring beach. Large *Zeacumantus* and *Notoacmea* are positively related near the middle of the beach in autumn and spring. These associations probably arise due to the species sharing a common resource. There is apparently no competitive exclusion among the algivores.

Cylichnina, *Nassarius* and *Agatha* are usually positively correlated with small or medium *Zeacumantus* in the upper regions of the beach. *Cylichnina* and

Nassarius are likely predators of small and medium *Zeacumantus* respectively and the planar correlations could be evidence of predator/prey relationships.

The relationships involving *Agatha*, however, are relatively weak. The series analysis showed that the associations between *Zeacumantus* and *Agatha* were strong enough to affect the zonations of the two species, and suggeted that *Zeacumantus* was a likely host for *Agatha*.

The planar correlations do not dispute this suggestions but they do indicate that attractions are relatively weak in two dimensions. The relatively high densities of *Zeacumantus* would make for a high host/parasite ratio and it would not be critically important for the parasites to search for hosts on a scale of centimetres. It would, however, be important for the parasites to maintain a similar zonation to their hosts, to maximise the contact likelihood. Thus, strong serial, and relatively weak planar, correlations between *Zeacumantus* and *Agatha* do not necessarily dismiss the suggested host/parasite relationship.

Zeacumantus and *Anthopleura* also tend to be positively associated in the upper sections of the beach, although medium *Zeacumantus* are involved in negative correlations near the top of the autumn transect. Small *Zeacumantus* were observed in the gut of *Anthopleura* but it appears that predation by the anemone is not strong enough to significantly exclude *Zeacumantus* from areas of the beach.

The other algivorous gastropods tend to be positively related in the upper sections of the beach in summer and spring, with weak associations in the other seasons. None of the remaining species show strong or consistent relationships but when the correlations are significant, they tend to be positive.

CHAPTER 7

CAGING MANIPULATION EXPERIMENTS

7.1 Introduction

Caging experiments in soft substrates have become common in the last decade (Woodin 1974; Reise 1977, 1983; Virnstein 1977, 1978; Dayton and Oliver 1980; Hulberg and Oliver 1980; Wiltse 1980) and have provided important insights into the controlling factors in the marine benthos. Cages have generally been use to allow the addition or exclusion of various species, commonly predators. Problems associated with habitat modifications produced by the cages themselves have been discussed by Virnstein (1978), Hulberg and Oliver (1980) and Gallagher *et al* (1983). They caution that many experimental effects may actually be due to sedimentary modifications, such as sedimentary buildup against the walls of the cages. This is particularly pronouced in high wave energy substrates but not in low energy regimes such as those at Pipe Clay Lagoon.

Caging manipulation experiments are potentially more powerful tests of species interactions than correlation analyses. Unfortunately, they demand prior knowledge of the community (in order to know what to manipulate) and are therefore not suited to poorly studied communities. The Pipe Clay Lagoon assemblage was poorly known prior to the present study and the caging experiments described here were based on the survey sampling of the previous chapters. The constraints imposed by sorting time meant the caging experiments were designed and set up prior to the completion of the survey work. They are thus based on incomplete information gained during the early sorting and could not anticipate many of the species interactions indicated by the analysis of the survey data. Nevertheless, they do provide tests of many of the more obvious intra- and interspecific correlations.

The caging experiments described here can be divided into three basic types: the first constitute a series of control experiments, the second a series of translocation experiments and the third a series of species addition experiments. Also, pitfall trap and substrate disturbance experiments were conducted.

The experiments use survivorship as a measure of the manipulation effects. In contrast, the correlation analyses detect both survivorship and local migration. The caging experiments, therefore, examine only the most powerful interactions between animal groups. Also, the confinement of animals inside cages would prevent competitive exclusion effects from being manifested through migration, which could occur under

natural conditions. The experiments are best regarded as a corollary to the correlation analyses, rather than as an independent examination of species interactions.

Due to the time constraints, the experiments could not be repeated at various times through the year, nor could they be conducted for all species at all stations. The experiments were therefore conducted at the top, in the middle and at the bottom of the beach as much as possible. Addition experiments were conducted in regions of high, medium and low natural densities of the added species. In this way, attempts were made to examine the role of the most common species, and to test the validity of the conclusions drawn from the correlation analyses of Chapters 5 and 6.

7.2 Methods

7.2.1 Introduction

The design of the caging experiments was determined by the constraints of sorting time. As described in Section 2.2, the removal of the molluscan fauna from the substrate samples was very time consuming. This placed restrictions on both the number of experiments and the number of replicates within each experiment. Also, the time required for the sorting of the survey transects meant that the caging experiments had to be started before those transects were analysed. Thus, although the caging experiments are used to test conclusions drawn from the survey analysis, no *a priori* designs to test specific conclusions were possible.

Despite these limitations, the c. 80 experimental setups (in addition to the backgrounds and controls) cover a wide variety of possible intra- and interspecific associations; the influence of position within the tidal regime can also be tested.

All caging experiments were conducted using cages constructed from plastic freezer jars (diameter 11 cm; height 15 cm). The bottom was removed from each jar and the centre was removed from the lid, leaving only the thread. The removed portion of the lid was replaced with 500 µm stainless steel mesh (the same mesh size as the sieves used in the survey work) heat-welded into the plastic. Seven 3.5 cm diameter holes were cut in the jar body just below its top and were replaced by similar mesh in the same manner.

The result was a bottomless cage that could be forced into the substrate down to the anoxic layer (depth c. 5 cm). The bottom of the side holes were then level with the substrate surface. This allowed the free movement of sediment through the cages and no significant build up (or loss) of sediment ever occurred, either inside or outside the cages. The lid of each cage could be removed to allow manipulation or inspection. Labels were engraved on each cage and lid and for convenience the lid was also labelled with a marker pen (this label needed periodic renewal).

The cages proved to be extremely robust and remained intact for up to 14 weeks on the tidal flat without significant damage. No cages were lost in approximately 15,000 cage-days.

Almost all experiments were conducted at the 100 m-interval stations, within a 10 m band either side of the midline of the transect. To avoid the possibility of using adulterated substrate, cages were placed in those areas that had been undisturbed by transect sampling for the longest period, generally a minimum of 9 months (see Section 2.2).

The cages were randomly (blindly) placed in the substrate; each replicate cage was placed approximately 1 m (arm's length) from the others. As with the transect quadrats,

the placing was rejected only if the cages contained a feeding aggregation of *Nassarius* . Each caging experiment was restricted to 3 replicates. All cage and background samples were returned to frozen storage before being sorted using the methods of the survey analysis (Section 2.2). The samples typically required 2 hrs to sort.

In addition to the caging experiments, pitfall traps were placed in the substrate for one tidal period (170482-180482) at each 100 m station. The traps were open topped food cans buried flush with the surface of the sediments. After collection, the pitfall samples were treated in a similar manner to the caging samples.

A description of the each caging experiment follows.

7.2.2 Description of the caging experiments

The experiments are identified with the position on the tidal flat and the starting and collection dates; for the BACKGROUND samples the date is the sampling date. Also included is a code label (CX...) for convenience. All labelled 'experiments' (CX...) constitute 3 cages or samples.

CX1 - CX7

BACKGROUND 151282

Background samples were taken by forcing uncapped cages into the substrate in the usual manner (i.e. random placing) and removing the contained substrate down to the anoxic layer.

CX1: BACKGROUND 151282 100 m

CX2: BACKGROUND 151282 200 m

CX3: BACKGROUND 151282 300 m

CX4: BACKGROUND 151282 400 m

CX5: BACKGROUND 151282 500 m

CX6: BACKGROUND 151282 600 m

CX7: BACKGROUND 151282 700 m

CX8 - CX14

BACKGROUND 290183

CX8: BACKGROUND 290183 100 m

CX9: BACKGROUND 290183 200 m

CX10: BACKGROUND 290183 300 m

CX11: BACKGROUND 290183 400 m

CX12: BACKGROUND 290183 500 m

CX13: BACKGROUND 290183 600 m

CX14: BACKGROUND 290183 700 m

CX15 - CX21

BACKGROUND 230383

CX15: BACKGROUND 230383 100 m

CX16: BACKGROUND 230383 200 m

CX17: BACKGROUND 230383 300 m

CX18: BACKGROUND 230383 400 m

CX19: BACKGROUND 230383 500 m

CX20: BACKGROUND 230383 600 m

CX21: BACKGROUND 230383 700 m

CX22 - CX29

BACKGROUND 190583

CX22: BACKGROUND 190583 50 m

CX23: BACKGROUND 190583 100 m

CX24: BACKGROUND 190583 200 m

CX25: BACKGROUND 190583 300 m

CX26: BACKGROUND 190583 400 m

CX27: BACKGROUND 190583 500 m

CX28: BACKGROUND 190583 600 m

CX29: BACKGROUND 190583 700 m

CX30 - CX36

BACKGROUND 170783

CX30: BACKGROUND 170783 100 m

CX31: BACKGROUND 170783 200 m

CX32: BACKGROUND 170783 300 m

CX33: BACKGROUND 170783 400 m

CX34: BACKGROUND 170783 500 m

CX35: BACKGROUND 170783 600 m

CX36: BACKGROUND 170783 700 m

CX37 - CX43

CONTROL 141282-280183

Control cages were placed in position without any manipulation of the contained biota.

CX37: CONTROL 141282-280183 100 m

CX38: CONTROL 141282-280183 200 m

CX39: CONTROL 141282-280183 300 m

CX40: CONTROL 141282-280183 400 m

CX41: CONTROL 141282-280183 500 m

CX42: CONTROL 141282-280183 600 m

CX43: CONTROL 141282-280183 700 m

CX44 - CX50

CONTROL 140283-210383

CX44: CONTROL 140283-210383 100 m

CX45: CONTROL 140283-210383 200 m

CX46: CONTROL 140283-210383 300 m

CX47: CONTROL 140283-210383 400 m

CX48: CONTROL 140283-210383 500 m

CX49: CONTROL 140283-210383 600 m

CX50: CONTROL 140283-210383 700 m

CX51 - CX53

CONTROL 260283-040483

CX51: CONTROL 260283-040483 50 m

CX52: CONTROL 260283-040483 300 m

CX53: CONTROL 260283-040483 500 m

CX54 - CX56

CONTROL 210383-060583

CX54: CONTROL 210383-060583 100 m

CX55: CONTROL 210383-060583 400 m

CX56: CONTROL 210383-060583 700 m

CX57 - CX63

LONG TERM CONTROL 270383-170783

CX57: LONG TERM CONTROL 270383-170783 100 m

CX58: LONG TERM CONTROL 270383-170783 200 m

CX59: LONG TERM CONTROL 270383-170783 300 m

CX60: LONG TERM CONTROL 270383-170783 400 m

CX61: LONG TERM CONTROL 270383-170783 500 m

CX62: LONG TERM CONTROL 270383-170783 600 m

CX63: LONG TERM CONTROL 270383-170783 700 m

CX64 - CX66

CONTROL 280383-060583

CX64: CONTROL 280383-060583100 m

CX65: CONTROL 280383-060583 400 m

CX66: CONTROL 280383-060583 700 m

CX67 - CX69

CONTROL 190583-020783

CX67: CONTROL 190583-020783 100 m

CX68: CONTROL 190583-020783 400 m

CX69: CONTROL 190583-020783 700 m

CX70 - CX72

SUBSTRATE DISTURBANCE 210383-060583

The substrate contained by the cages was manually stirred down to the anoxic layer every 2 days. The stirring (c. 30 sec) was such that the sediment was completely loosened. The disturbance was conducted at low tide and therefore no appreciable sediment loss occurred during the stirring action.

CX70: SUBSTRATE DISTURBANCE 210383-060583 100 m

CX71: SUBSTRATE DISTURBANCE 210383-060583 400 m

CX72: SUBSTRATE DISTURBANCE 210383-060583 700 m

CX73 - CX78

SUBSTRATE TRANSLOCATIONS 140283-210383

For the substrate translocations the cages were forced into the substrate in the usual manner. The sediment immediately surrounding each cage was then removed and a metal plate pushed through the anoxic layer beneath the bottom of the cage. This allowed the cage to be lifted from the substrate without disturbance to the contents. The cage (with its substrate) was then translocated to a different position on the beach. At the new site a hole was created in the substrate by removing the sediment (+biota) from a dummy cage. The translocated cage could then be inserted into the hole. The surrounding sediment settled against the cage within minutes to produce a tight fit.

CX73: SUBSTRATE TRANSLOCATIONS 140283-210383 100 m translocated to 400 m

CX74: SUBSTRATE TRANSLOCATIONS 140283-210383 100 m translocated to 700 m

CX75: SUBSTRATE TRANSLOCATIONS 140283-210383 400 m translocated to 100 m

CX76: SUBSTRATE TRANSLOCATIONS 140283-210383 400 m translocated to 700 m

CX77: SUBSTRATE TRANSLOCATIONS 140283-210383 700 m translocated to 100 m

CX78: SUBSTRATE TRANSLOCATIONS 140283-210383 700 m translocated to 400 m

CX79 - CX84

LONG TERM SUBSTRATE TRANSLOCATION 080483-170783

CX79: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 100 m translocated to 400 m

CX80: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 100 m translocated to 700 m

CX81: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 400 m translocated to 100 m

CX82: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 400 m translocated to 700 m

CX83: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 700 m translocated to 100 m

CX84: LONG TERM SUBSTRATE TRANSLOCATION 080483-170783 700 m translocated to 400 m

CX85 - CX87

ANAPELLA GROUP I ADDITION 190283-230383

50 Group I *Anapella* animals were added to each cage.

As with all the following addition experiments, the additions were made immediately following the cage insertion. In all cases the added animals were obtained by sorting through fresh substrate samples in the laboratory. The samples were collected in the region of the beach where the target animals were most abundant. The sorting process was similar to that applied to the quadrat and cage samples except that the sieving was conducted using recirculating 15 ^{0}C sea water.

The sorting was conducted on the same day as the substrate samples were collected. The removed animals were retained in fresh, aerated sea water at 10 ^{0}C overnight and the additions were made the following day. The animals were transported to the tidal-flat in aerated sea water contained in capped plastic vials. The transportation time (laboratory to cage) was typically less than 1.5 hrs.

The above treatment appeared to have no detrimental effect on the animals; they were able to survive for at least a week in the overnight storage conditions and tests showed that all species could survive at least 3 round trips to the beach.

CX85: *ANAPELLA* GROUP I ADDITION 190283-230383 100 m

CX86: *ANAPELLA* GROUP I ADDITION 190283-230383 300 m

CX87: *ANAPELLA* GROUP I ADDITION 190283-230383 700 m

CX88 - CX90

ANAPELLA GROUP V ADDITION 211282-280183

5 Group V *Anapella* animals were added to each cage.

CX88: *ANAPELLA* GROUP V ADDITION 211282-280183 200 m

CX89: *ANAPELLA* GROUP V ADDITION 211282-280183 500 m

CX90: *ANAPELLA* GROUP V ADDITION 211282-280183 700 m

CX91 - CX93

KATELYSIA GROUP I ADDITION 190283-230383

50 Group I *Katelysia* animals were added to each cage.

CX91: *KATELYSIA* GROUP I ADDITION 190283-230383 100 m

CX92: *KATELYSIA* GROUP I ADDITION 190283-230383 300 m

CX93: *KATELYSIA* GROUP I ADDITION 190283-230383 700 m

CX94 - CX96

KATELYSIA GROUP V ADDITION 211282-280183

5 Group V *Katelysia* animals were added to each cage.

CX94: *KATELYSIA* GROUP V ADDITION 211282-280183 100 m

CX95: *KATELYSIA* GROUP V ADDITION 211282-280183 400 m

CX96: *KATELYSIA* GROUP V ADDITION 211282-280183 600 m

CX97 - CX99

HYDROCOCCUS GROUP I ADDITION 190283-230383

50 Group I *Hydrococcus* animals were added to each cage.

CX97: *HYDROCOCCUS* GROUP I ADDITION 190283-230383 100 m

CX98: *HYDROCOCCUS* GROUP I ADDITION 190283-230383 300 m

CX99: *HYDROCOCCUS* GROUP I ADDITION 190283-230383 700 m

CX100 - CX102

HYDROCOCCUS GROUP IV ADDITION 190283-230383

20 Group IV *Hydrococcus* animals were added to each cage.

CX100: *HYDROCOCCUS* GROUP IV ADDITION 190283-230383 100 m

CX101: *HYDROCOCCUS* GROUP IV ADDITION 190283-230383 300 m

CX102: *HYDROCOCCUS* GROUP IV ADDITION 190283-230383 700 m

CX103 - CX105

ZEACUMANTUS GROUP II ADDITION 211282-270183

10 Group II *Zeacumantus* animals were added to each cage.

CX103: *ZEACUMANTUS* GROUP II ADDITION 211282-270183 300 m

CX104: *ZEACUMANTUS* GROUP II ADDITION 211282-270183 500 m

CX105: *ZEACUMANTUS* GROUP II ADDITION 211282-270183 700 m

CX106 - CX108

SALINATOR GROUP II ADDITION 190583-020783

5 *Salinator* 10+ mm animals were added to each cage.

CX106: *SALINATOR* GROUP II ADDITION 190583-02078 100 m

CX107: *SALINATOR* GROUP II ADDITION 190583-020783 400 m

CX108: *SALINATOR* GROUP II ADDITION 190583-020783 700 m

CX109 - CX111

NASSARIUS ADDITION 280383-060583

5 *Nassarius* 14-15+ mm animals were added to each cage.

CX109: *NASSARIUS* ADDITION 280383-060583 100 m

CX110: *NASSARIUS* ADDITION 280383-060583 400 m

CX111: *NASSARIUS* ADDITION 280383-060583 700 m

CX112 - CX115

BEMBICIUM ADDITION 211282-270183

5 *Bembicium* 8-10+ mm animals were added to each cage.

CX112: *BEMBICIUM* ADDITION 211282-270183 30 m

CX113: *BEMBICIUM* ADDITION 211282-270183 300 m

CX114: *BEMBICIUM* ADDITION 211282-270183 500 m

CX115: *BEMBICIUM* ADDITION 211282-270183 700 m

CX116 - CX118

AUSTROCOCHLEA ADDITION 190583-020783

5 *Austrocochlea* 12+ mm animals were added to each cage.

CX116: *AUSTROCOCHLEA* ADDITION 190583-020783 100 m

CX117: *AUSTROCOCHLEA* ADDITION 190583-020783 400 m

CX118: *AUSTROCOCHLEA* ADDITION 190583-020783 700 m

CX119 - CX128

ANAPELLA + *KATELYSIA* GROUP V ADDITION 260283-040483

In the combined species addition experiments either one species was added alone or both species were added together. If either *Anapella* or *Katelysia* was added alone, either 5 or 10 Group V animals were added; the 10 animal experiments are identified by (x2). If both species were added 5 Group V animals from each species were added.

CX119: *ANAPELLA* 300 m

CX120: *KATELYSIA* 300 m

CX121: *ANAPELLA* (x2) 300 m

CX122: *KATELYSIA* (x2) 300 m

CX123: *ANAPELLA* + *KATELYSIA* 300 m

CX124: *ANAPELLA* 500 m

CX125: *KATELYSIA* 500 m

CX126: *ANAPELLA* (x2) 500 m

CX127: *KATELYSIA* (x2) 500 m

CX128: *ANAPELLA* + *KATELYSIA* 500 m

CX129 - CX138

SALINATOR + *BEMBICIUM* ADDITION 260283-040483

If either *Salinator* or *Bembicium* was added alone either 10 or 20 animals (8-10+ mm) were added; the 20 animal experiments are identified by (x2). If both species were added 10 animals from each species were added.

CX129: *SALINATOR* 50 m

CX130: *BEMBICIUM* 50 m

CX131: *SALINATOR* (x2) 50 m

CX132: *BEMBICIUM* (x2) 50 m

CX133: *SALINATOR* + *BEMBICIUM* 50 m

CX134: *SALINATOR* 300 m

CX135: *BEMBICIUM* 300 m

CX136: *SALINATOR* (x2) 300 m

CX137: *BEMBICIUM* (x2) 300 m

CX138: *SALINATOR* + *BEMBICIUM* 300 m

7.3 Results

The results of the experiments are presented as t-test comparisons of the various treatments, using the sign and significance coding introduced in previous chapters. The raw data are held on magnetic tape in the University of Tasmania Archives.

7.3.1 Pitfall traps (Fig.7.1)

The following comparisons are between traps left for one tidal period and the background at the time of collection.

Juvenile and small *Anapalla* show lower numbers in the traps near the top of the beach, as do group III *Anapella* animals in the middle of the beach.

Small/medium *Hydrococcus* trap numbers are low at the bottom of the transect.

Small *Zeacumantus* animals have low trap numbers in the top half of the beach while all *Zeacumantus* groups show low trap numbers at the top station.

7.3.2 Control caging experiments (Figs. 7.2 - 7.8)

In the following, references to 'higher' and 'lower' abundances, or similar, are applied to comparisons between the control cages and the background samples at a given station.

7.3.2.1 Control 141282-280183 (Fig. 7.2)

Initial background versus control

Juvenile *Anapella* have higher numbers in the control at 700 m while small (group II) *Anapella* numbers are lower in the control at 100 m and 500 m.

Small *Katelysia* have a weak excess of numbers in the control at 700 m.

Hydrococcus is the species most strongly affected by the caging process. All *Hydrococcus* groups are higher in the control at 100 m (also 200 m for group I animals). The smallest *Hydrococcus* group numbers are low in the control near the bottom of the beach. At the 700 m station group III and group IV numbers are respectively lower and higher in the control.

Medium sized *Zeacumantus* show high numbers in the 100 m control.

Large *Salinator* numbers are low in the control at the top of the beach.

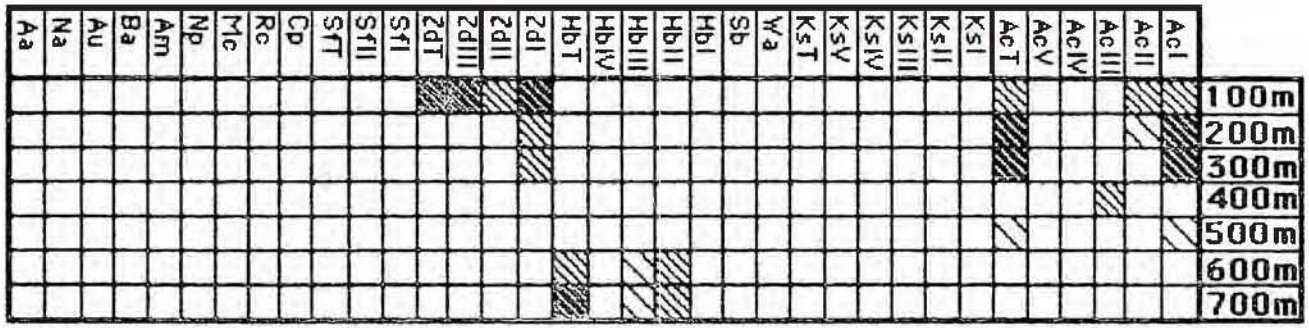
Near the middle of the beach *Cylichnina* numbers are higher in the control.

Control versus final background

Juvenile *Anapella* numbers are lower in the control at 500 m. Small *Anapella* show high control numbers near the bottom of the beach, as do large *Anapella* near the top of the beach.

Juvenile and large *Katelysia* numbers are lower in the controls at the bottom and middle of the beach respectively.

All *Hydrococcus* groups except group I have higher control numbers at the top of



PITFALL TRAPS 170482 - 180482 / BACKGROUND 180482

Fig. 7.1 Comparison of pitfall traps and initial background. Species abbreviations are as defined in Table 5.1. Shadings identify sign and significance of t-statistic according to definitions of Table 5.2. The first term of the legend is the first term of the t-statistic (in this case a negative t-value indicates that the background number is higher than the pitfall trap number, and *vice versa*). These conventions are followed throughout Fig. 7.

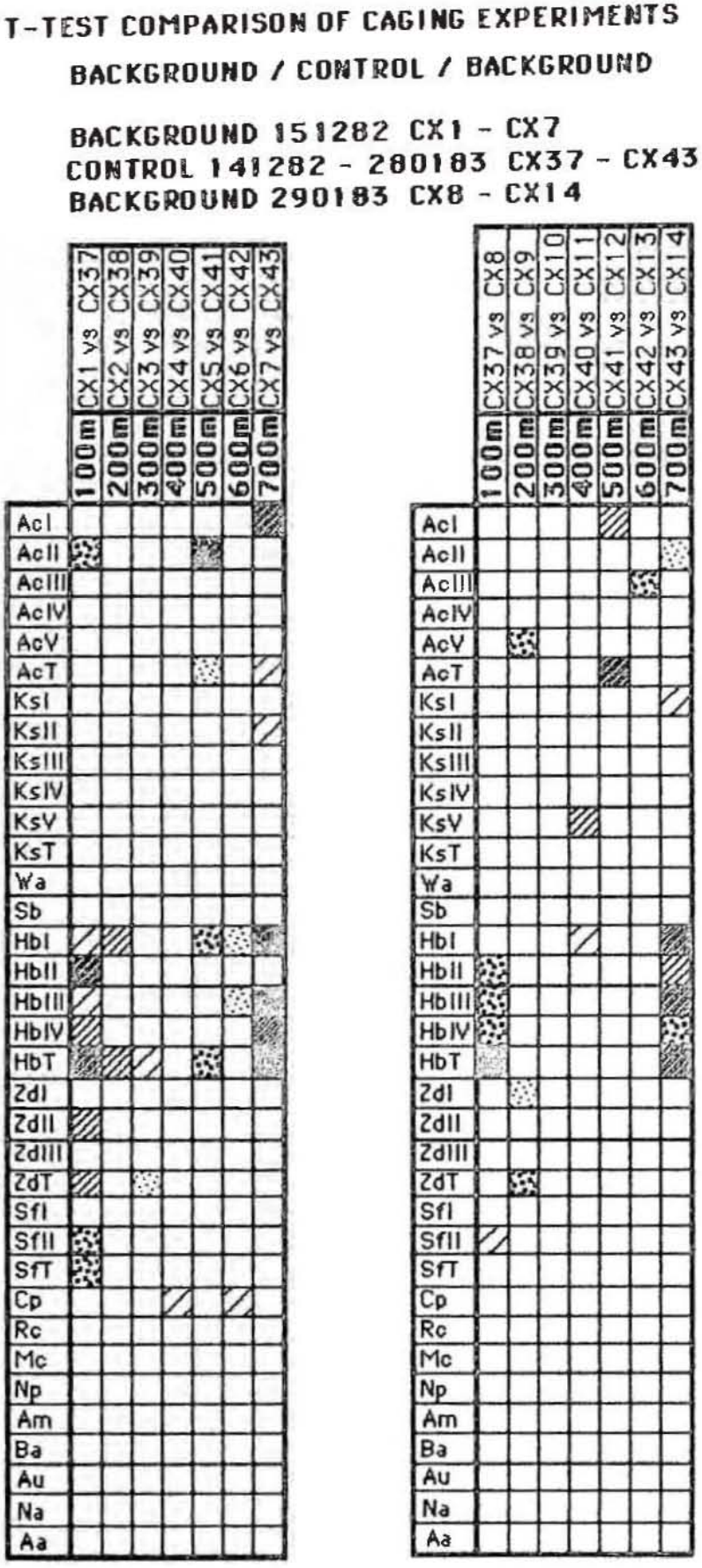


Fig. 7.2 Effect of caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

the beach and at the bottom of the beach all but group IV have low control numbers; group IV is more abundant in the latter controls.

At 200 m *Zeacumantus* group I animals are more abundant (slight) in the controls.

Large *Salinator* numbers are low in the 100 m controls.

7.3.2.2 Control 140283-210383 (Fig.7.3)

Initial background versus control

Small *Anapella* numbers are higher and lower in the 200 m and 400 m controls respectively. Group III *Anapella* show slightly lower numbers in the 100 m and 500 m controls while large *Anapella* is more abundant in the 200 m controls.

Juvenile *Katelysia* numbers are reduced in the middle-beach controls but are increased at the bottom controls.

Near the bottom of the beach, juvenile *Hydrococcus* numbers are lower in the controls while group II *Hydrococcus* numbers are greater in the 100 m control. Large *Hydrococcus* is more abundant in the top- and bottom-beach controls.

At 100 m juvenile *Zeacumantus* numbers are low in the controls.

Low control numbers also occur with *Cylichnina* in the middle sections of the beach. *Rissopsis* abundances are increased in the controls near the top of the beach.

Control versus final background

Juvenile *Anapella* numbers are lower in the 400 m controls, as are the numbers of small *Anapella* at 100 m and 300 m.

Numbers of juvenile *Katelysia* are lower and higher in the controls at the middle and bottom of the beach respectively.

In the 500 m controls *Wallucina* shows reduced numbers.

Juvenile *Hydrococcus* abundances are reduced in the controls in the middle sections of the beach.

At 100 m small *Salinator* numbers are low in the control cages.

Cylichnina numbers are low in the 300 m controls.

At 300 m *Anthopleura* abundances are higher in the controls.

7.3.2.3 Control 210383-060583 (Fig. 7.4)

(Cages restricted to 100 m, 400 m and 700 m.)

Initial background versus control

Juvenile *Anapella* numbers are low in the controls at the top and middle of the beach.

Group III *Anapella* shows similar deviations at 100 m.

In the middle of the beach juvenile *Katelysia* numbers are slightly higher in the controls.

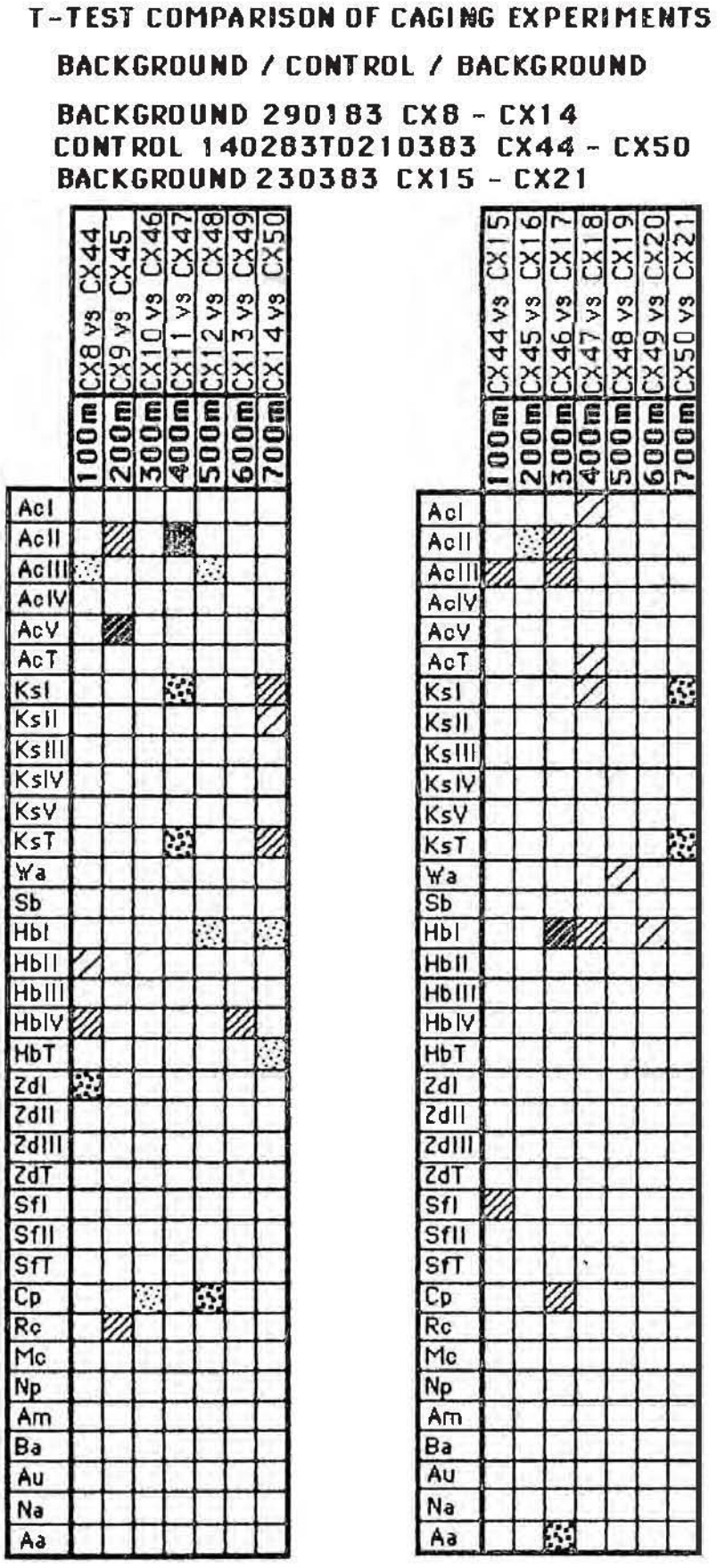


Fig. 7.3 Effect of caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

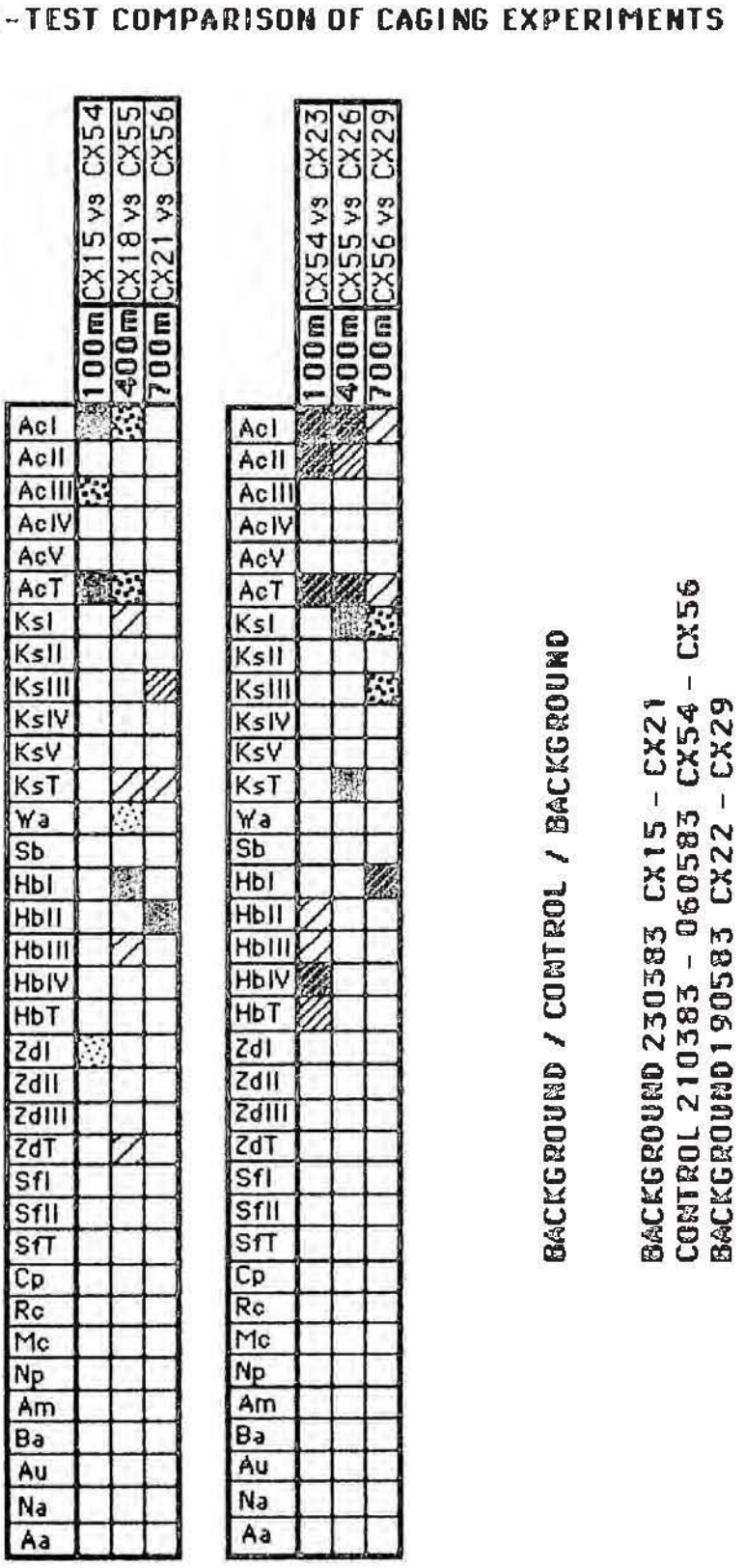


Fig. 7.4 Effect of caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

Control *Wallucina* numbers are low (slight) at 400 m.

Juvenile *Hydrococcus* abundances are low in the middle-beach controls, as are group II numbers at 700 m. Group III *Hydrococcus* shows slightly higher numbers in the mid-beach controls.

At the top of the beach juvenile *Zeacumantus* numbers are slightly reduced in the controls.

Control versus final background

Juvenile *Anapella* numbers are low in all controls (weakly so at 700 m). Small *Anapella* control numbers are also low, at the 100 m and 400 m stations.

Juvenile *Katelysia* abundances are higher in the controls at 400 m and 700 m, as are group II numbers at 700 m.

In the 700 m controls juvenile *Hydrococus* numbers are low. All other *Hydrococccus* groups show reduced numbers in the 100 m controls.

7.3.2.4 Control 280383-060583 (Fig.7.5)

(Cages restricted to 100 m, 400 m and 700 m.)

Initial background versus control

The numbers of juvenile *Anapella* are low in the 100 m and 400 m controls. Group III *Anapella* also shows low control numbers at the top of the beach.

Katelysia groups I, II and III have high abundances in the controls at the bottom station.

Juvenile *Hydrococcus* numbers are reduced in the 400 m and 700 m controls.

In the 100 m controls the numbers of small *Salinator* are low.

Control versus final background

In the mid-beach controls juvenile *Anapella* numbers are low. Small *Anapella* show low abundances in the 100 m and 400 m controls.

The numbers of juvenile *Katelysia* are low in the 400 m and 700 m controls while group III *Katelysia* has increased abundance in the 700 m controls.

At 700 m the number of juvenile *Hydrococcus* in the controls is low.

7.3.2.5 Control 190583-020783 (Fig.7.6)

(Cages restricted to 100 m, 400 m and 700 m.)

Initial background versus control

At 100 m and 400 m, juvenile *Anapella* numbers are low in the control cages, as are group II numbers at 100 m. Large *Anapella* control abundances are high at 700 m.

Group II and IV *Hydrococcus* abundances are reduced in the 700 m controls.

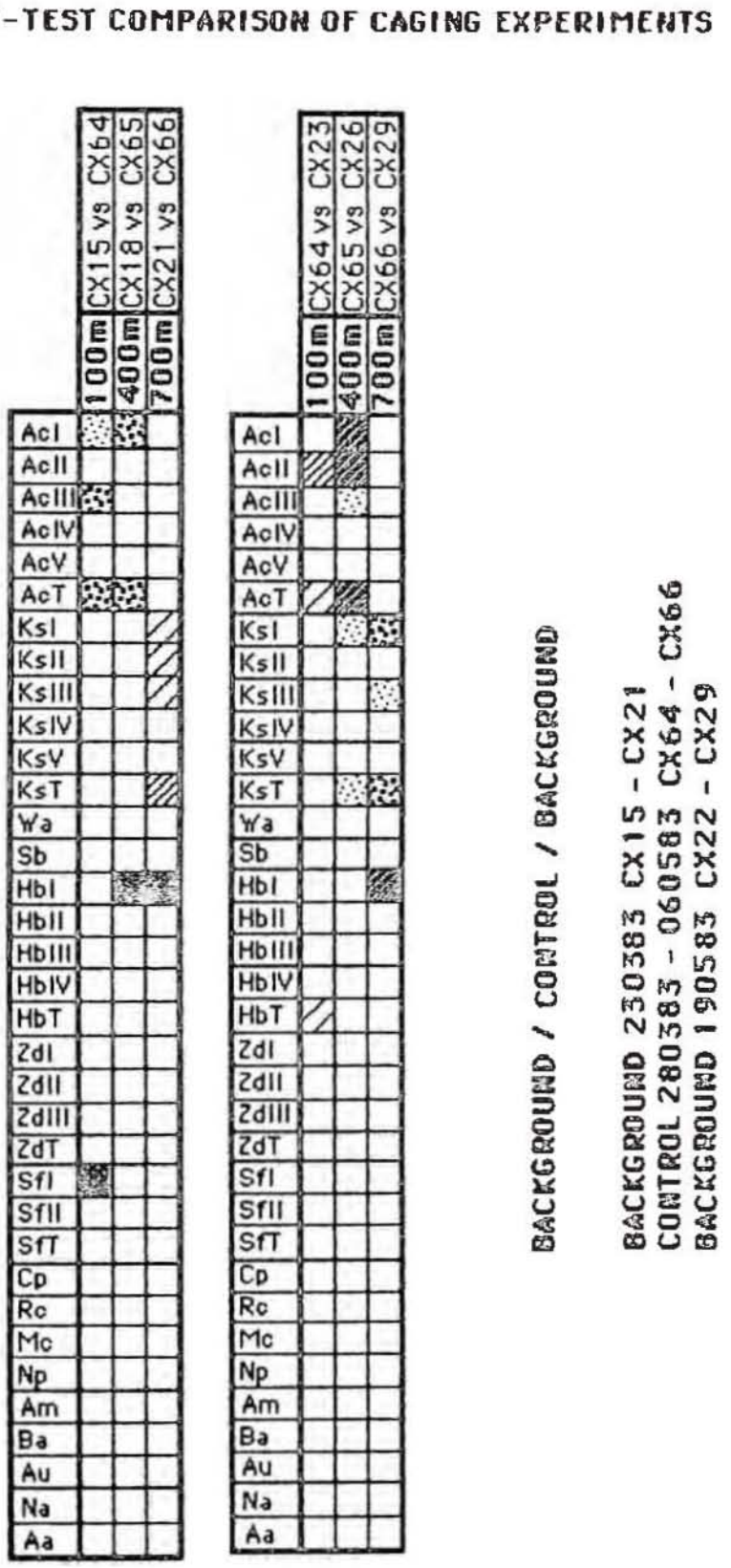


Fig. 7.5 Effect of caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

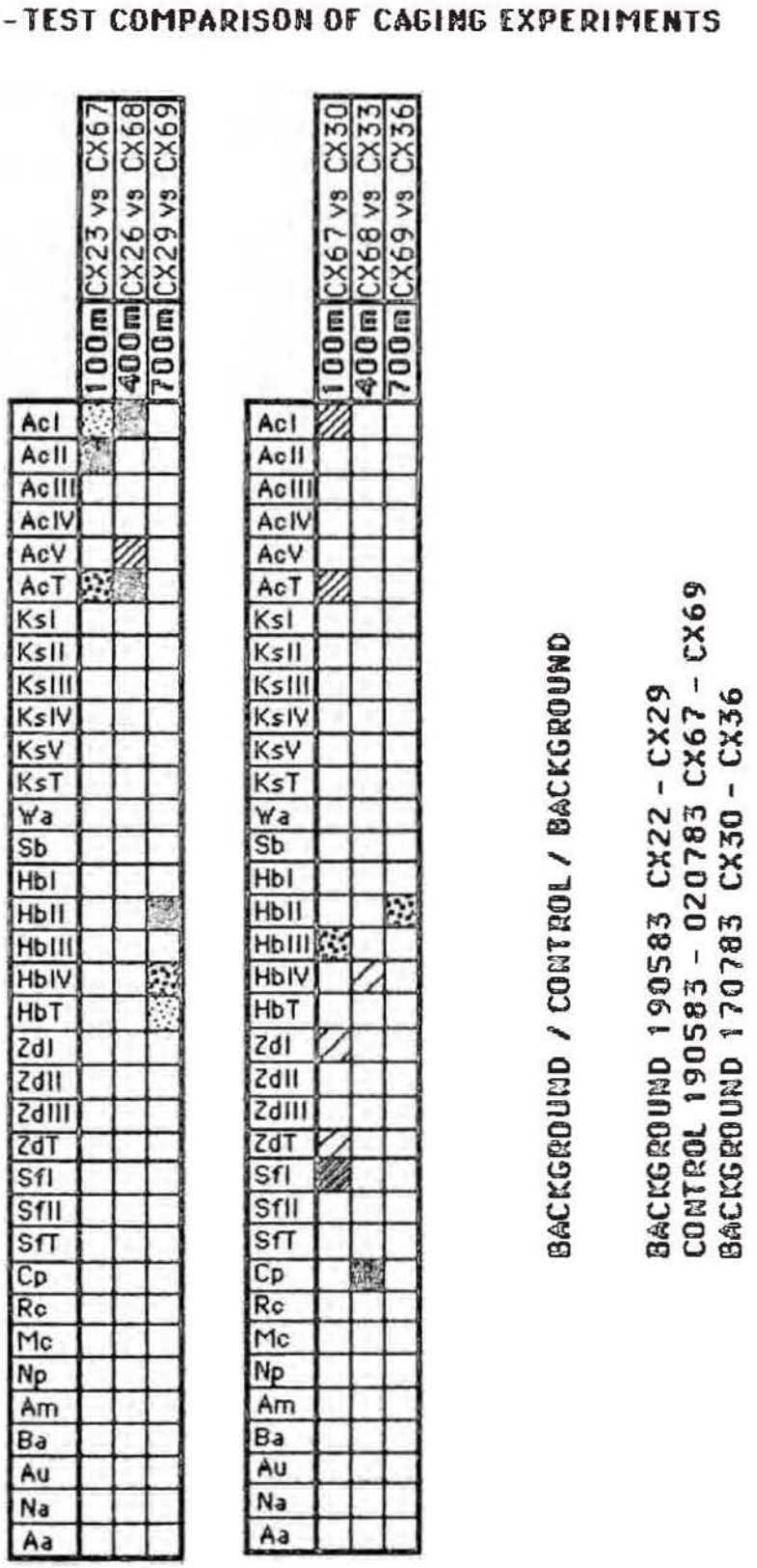


Fig. 7.6 Effect of caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

Control versus final background

In the 100 m controls juvenile *Anapella* are less abundant.

Group II and III *Hydrococcus* are more abundant at 700 m and 100 m respectively while at 400 m, the control numbers of large *Hydrococcus* are reduced.

At 100 m small *Zeacumantus* and also small *Salinator* abundances are less in the controls.

Cylichnina is more abundant in the 400 m control.

7.3.2.6 Long term control 270383-170783 (Fig. 7.7)

Initial background versus control

Small *Anapella* are in low numbers in the controls of the top half of the beach. Group III *Anapella* numbers are low in the 200 m and 300 m controls while group IV *Anapella* abundances are high at the 300 m control station.

At 600 m juvenile *Katelysia* are in low numbers in the control cages; group III *Katelysia* abundances increase in the 700 m controls.

In the middle of the beach the control numbers of *Wallucina* are low.

Group I *Hydrococcus* abundances are low in the mid- and low-beach controls. Group II and III *Hydrococcus* control numbers are high and low at 500 m and 600 m respectively.

At 100 m the number of juvenile *Zeacumantus* in the control cages is high.

Small and large *Salinator* are respectively low and high in the 100 m and 300 m cages.

In the 300 m control *Cylichnina* shows a reduced abundance.

Control versus final background

At 100 m and 500 m group I *Anapella* numbers are low in the control cages. Group III abundances are high and low in the 100 m and 500 m controls respectively. In the mid-beach controls, large *Anapella* have a high abundance.

Juvenile *Katelysia* numbers are low in the 600 m controls while group II and III *Katelysia* abundances are high in the middle and at the bottom of the beach respectively. In the 300 m control, group I *Hydrococcus* numbers are low; similar deviations occur with group II animals at 600 m. Larger *Hydrococcus* animals have a high abundance in the 700 m control.

At 100 m there are low numbers of juvenile *Zeacumantus* in the control cages.

Cylichnina abundances are high in the mid-beach controls.

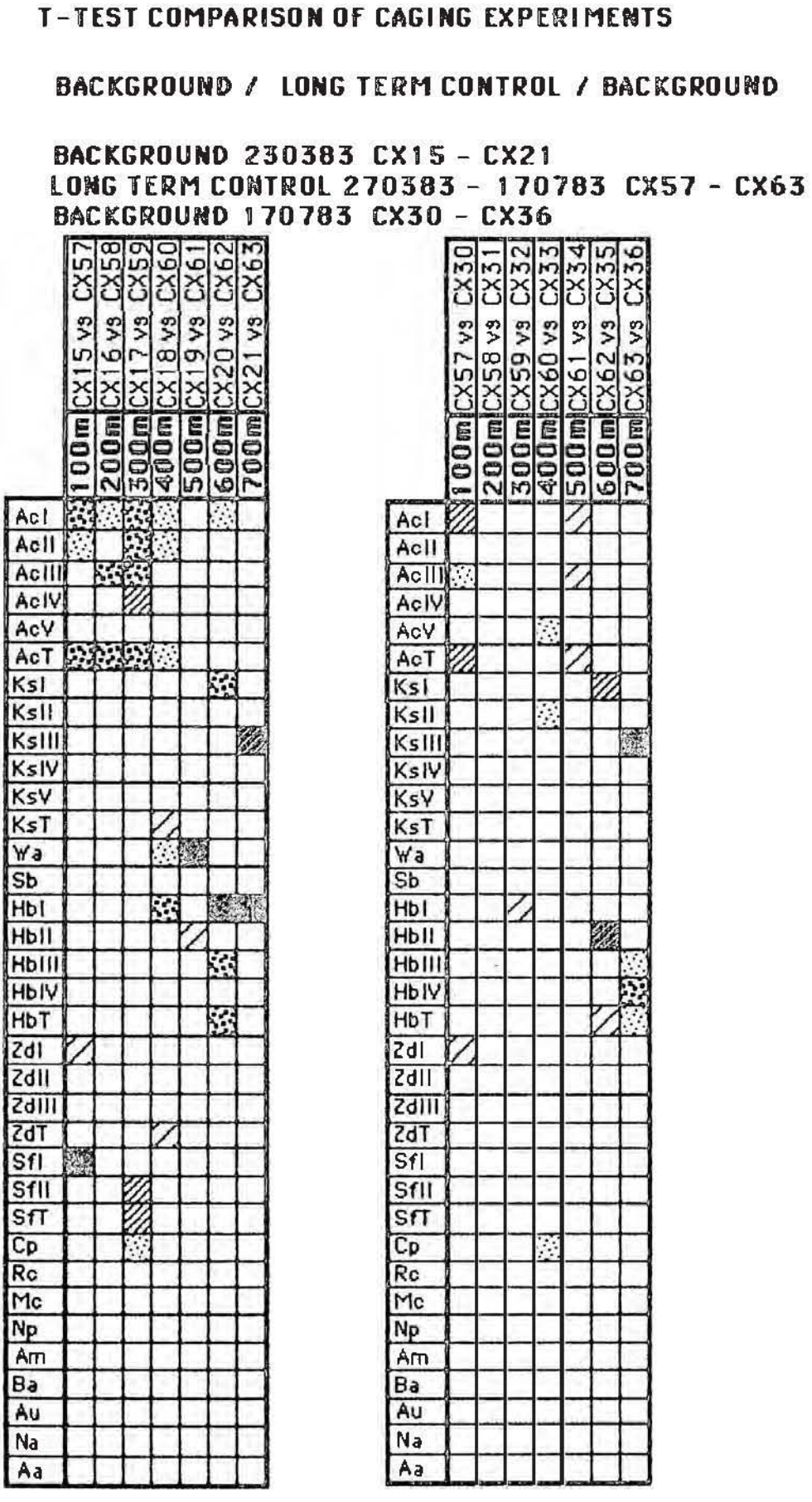


Fig. 7.7 Effect of long term caging on lagoon fauna. Comparisons are between cage contents and initial and final background.

7.3.2.7 **Control versus long term control** (Fig. 7.8)

At 400 m group II *Anapella* numbers are higher in the short term control while large *Anapella* are less abundant in the short term control.

Group II and III *Katelysia* short term control numbers are low at 400 m and 700 m respectively.

At 700 m juvenile and large *Hydrococcus* are respectively higher and lower in the short term controls.

7.3.3 **Substrate disturbance 210383-060583** (Fig. 7.9)

Substrate disturbance leads to an increase in the survival of group I and III *Anapella* at 100 m when compared to control cages.

All but the largest *Hydrococcus* group show diminished numbers in disturbed cages at 700 m.

7.3.4 **Substrate translocation** (Figs. 7.10-7.11)

In the following, references to 'higher' and 'lower' abundances, or similar, are applied to comparisons between the translocated cages and the control cages at the relevant station.

7.3.4.1 **Substrate translocation 140283-210383** (Fig. 7.10)

The survival of group I *Anapella* diminishes when the animals are moved from 400 m to 700 m. Group II *Anapella* numbers are greater and lower in the 100 m to 700 m and 700 m to 100 m translocations respectively. *Anapella* group III survival increases when the animals are moved from 400 m to 700 m.

Katelysia group I survival is enhanced when moved from 100 m and 400 m to 700 m but is diminished when moved from 700 m to 400 m and 100 m. Group II *Katelysia* shows similar responses except that there is negligible change in survival in the 100 m to 700 m move.

The survival of *Wallucina* is slightly enhanced in the 700 m to 100 m move.

Group I *Hydrococcus* survival decreases in the 400 m to 100 m, 700 m to 100 m and the 700 m to 400 m moves. In the 700 m to 100 m translocation the survival of group III *Hydrococcus* also decreases.

Total *Salinator* numbers are greater in the 100 m to 400 m translocations.

Cylichnina shows a weak decrease in survival following the 400 m to 700 m translocation.

7.3.4.2 **Long term substrate translocation 080483-170783** (Fig. 7.11)

The survival of large *Anapella* decreases following the 100 m to 700 m move.

Group I *Katelysia* survival is enhanced in the 100 m to 400 m and the 100 m to 700 m moves but decreases in the 400 m to 100 m translocation. Following the

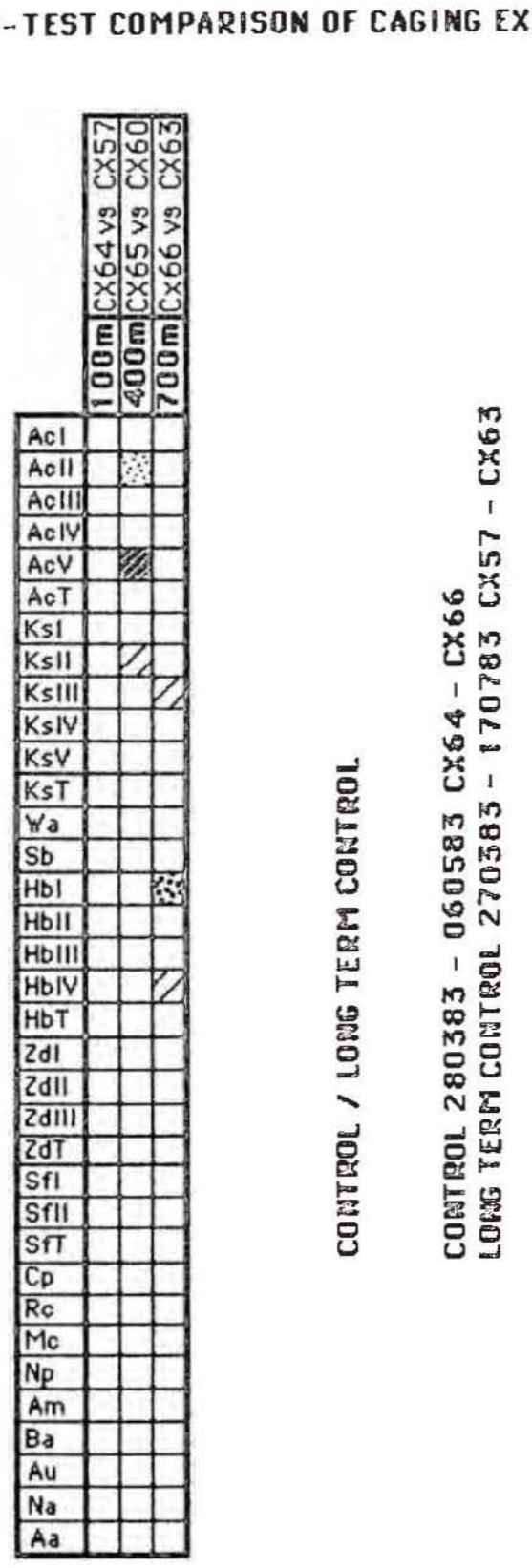


Fig. 7.8 Comparison of effect of caging and effect of long term caging on lagoon fauna.

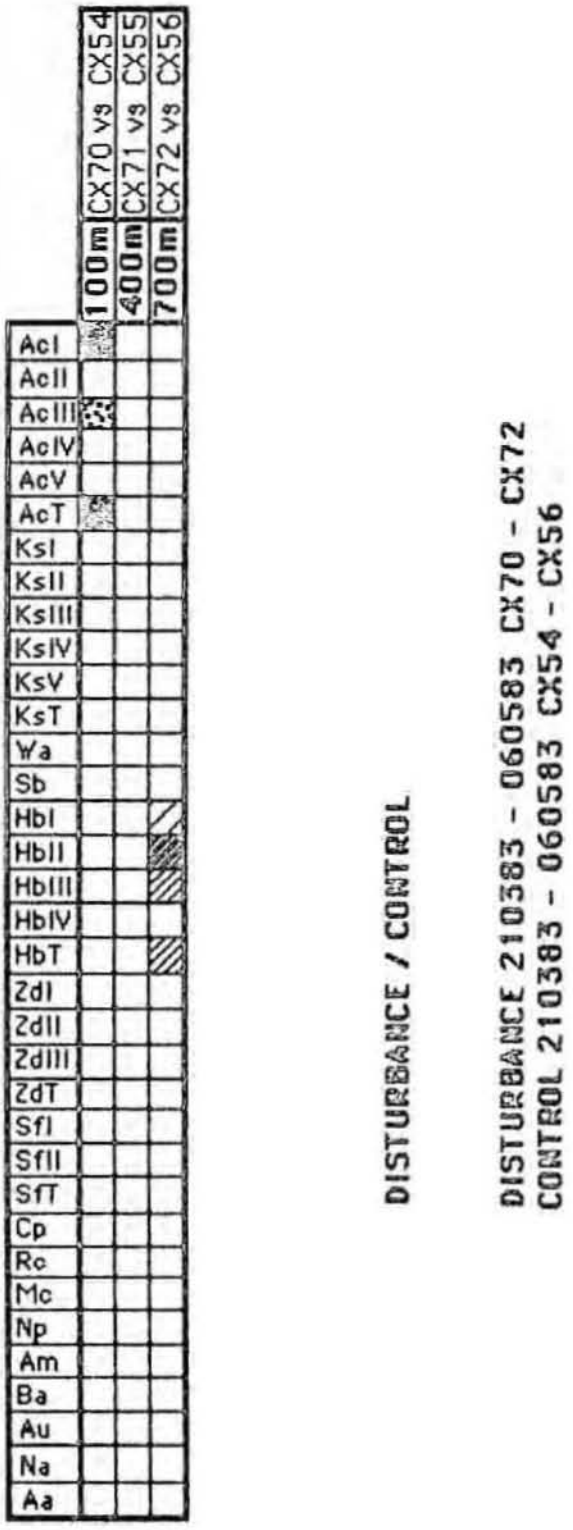


Fig. 7.9 Effect of regular disturbance on lagoon fauna.

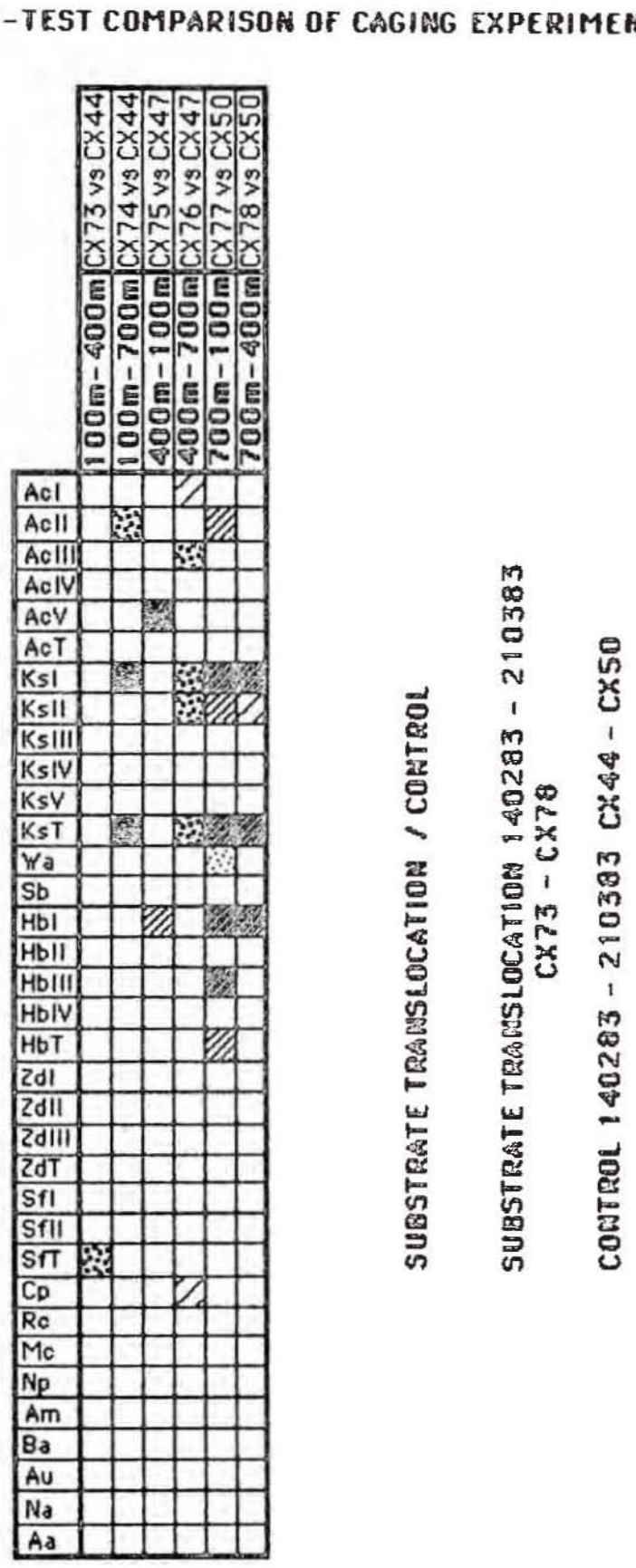


Fig. 7.10 Effect of translocation on lagoon fauna. Comparisons are between translocated cages and cages at origin.

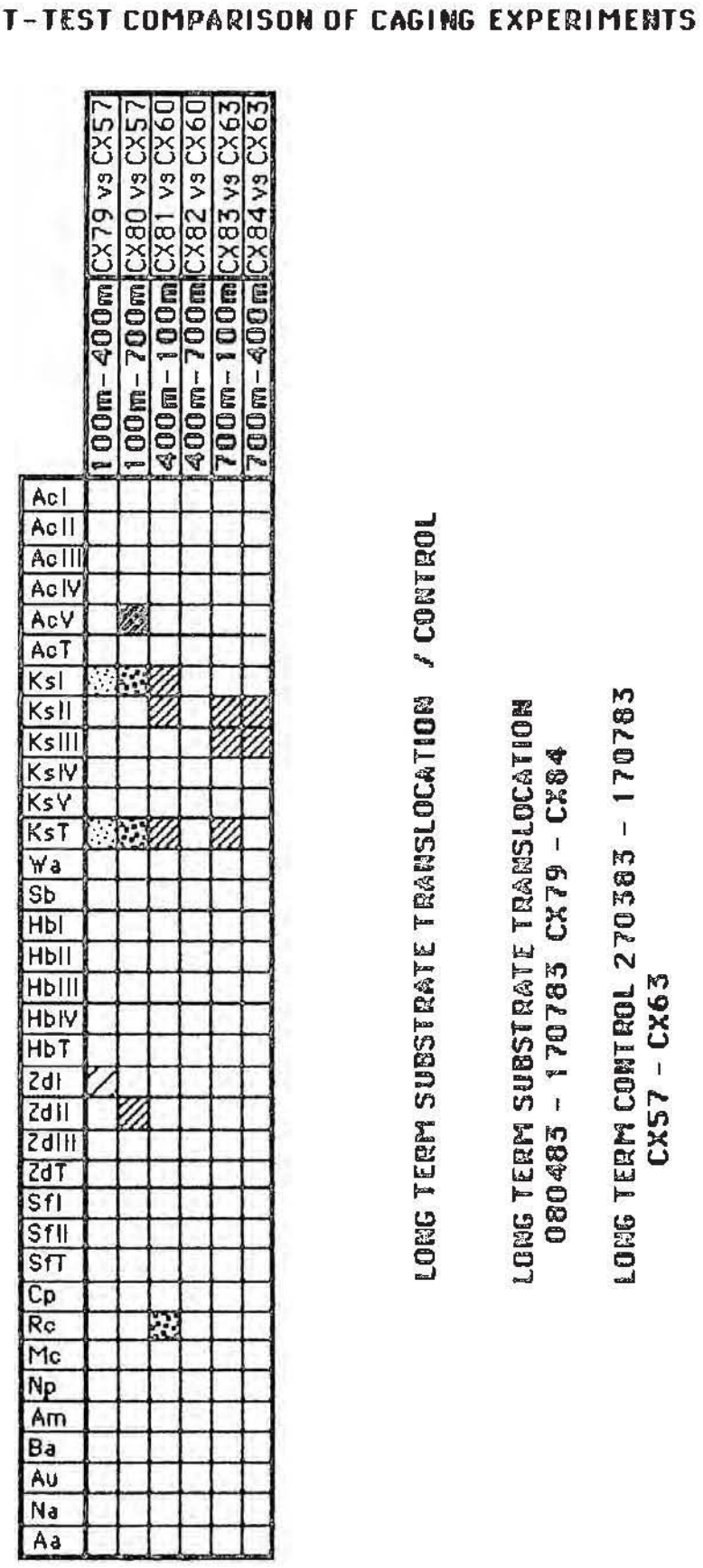


Fig. 7.11 Effect of long term translocation on lagoon fauna. Comparisons are between translocated cages and cages at origin.

400 m to 100 m, 700 m to 100 m and 700 m to 400 m translocations, group II *Katelysia* survival is reduced. Group III *Katelysia* numbers are low in the 700 m to 100 m and 700 m to 400 m translocations.

There is a weak decrease in survival among group I and II *Zeacumantus* following the 100 m to 400 m and 100 m to 700 m translocations respectively.

Rissopsis survival is enhanced in the 400 m to 100 m translocations.

7.3.5 Species additions (Figs. 7.12-7.25)

In the following, references to 'higher' and 'lower' abundances, or similar, are applied to comparisons between the addition cages and the control cages at the relevant station.

7.3.5.1 *Anapella* group I addition 190283-230383 (Fig. 7.12)

The addition of *Anapella* juveniles decreases the survival of similar animals at 700 m. The survival of group II animals is enhanced at 100 m. Large *Anapella* numbers are low at 100 m.

Katelysia group I numbers are greater at 700 m.

There is a strong decrease in group I and III *Hydrococcus* at 700 m and weak decreases in group II and IV *Hydrococcus* numbers at 100 m.

Group I *Salinator* numbers are greater at 100 m.

There is a weak increase in *Rissopsis* survival at 300 m.

7.3.5.2 *Anapella* group V addition 211282-280183 (Fig. 7.13)

Group I and II *Anapella* numbers are reduced at 700 m but at 500 m group II numbers are high.

All *Hydrococcus* groups show an enhanced survival at 500 m and 700 m (group I at 700 m only).

7.3.5.3 *Katelysia* group I addition 190283-230383 (Fig. 7.14)

Total *Anapella* numbers show a weak increase at 300 m.

Group I *Katelysia* numbers decreases at 100 m and 300 m but group II abundances are greater at the same distances.

There is a weak increase in the survival of juvenile *Hydrococcus* at 300 m.

At 700 m the numbers of group III *Hydrococcus* are slightly reduced.

Group I *Zeacumantus* survival is enhanced at 100 m and 300 m.

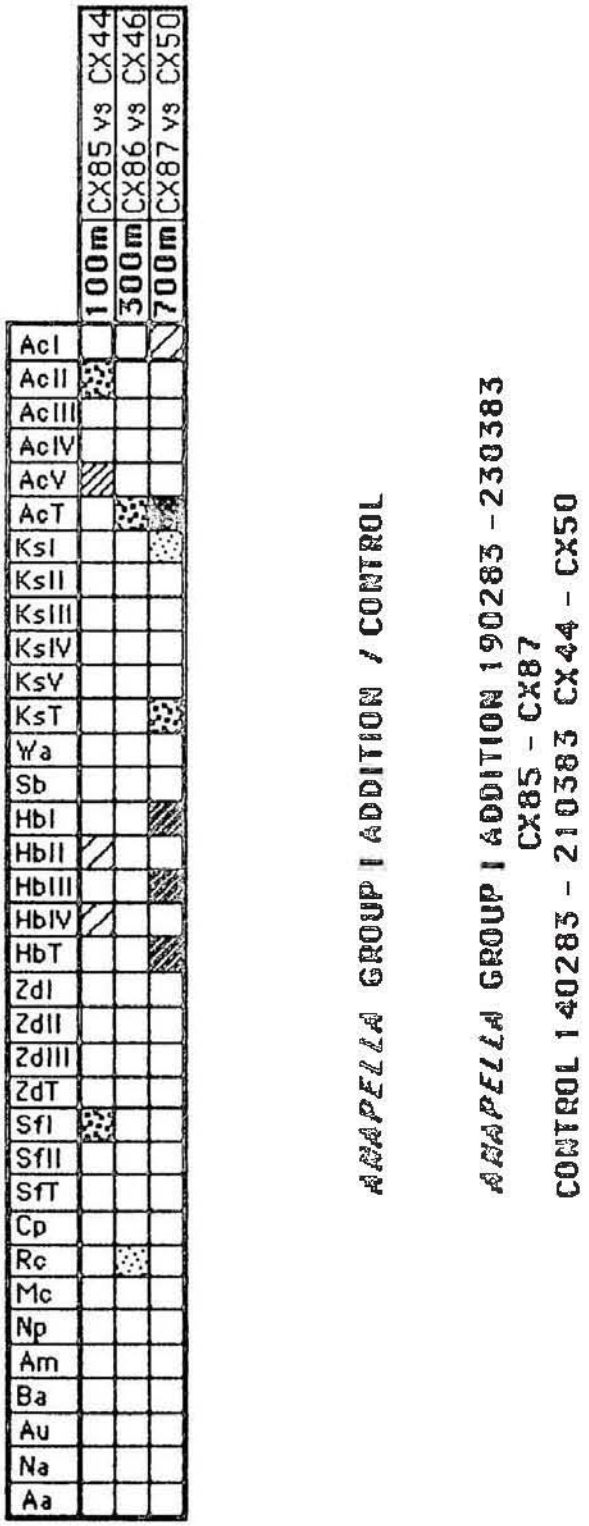
Both *Salinator* groups have greater abundances at 100 m.

The number of *Anthopleura* is low at 300 m.

7.3.5.4 *Katelysia* group V addition 211282-280183 (Fig. 7.15)

Group II *Anapella* survival is enhanced at 100 m and 600 m but group III shows a strong decrease at 600 m.

T-TEST COMPARISON OF CAGING EXPERIMENTS



ANAPELLA GROUP I ADDITION / CONTROL

ANAPELLA GROUP I ADDITION 190283 - 230383
CX85 - CX87
CONTROL 140283 - 210383 CX44 - CX50

Fig. 7.12 Effect of adding *Anapella* group I animals to cages. Added group numbers are adjusted prior to t-test; similar adjustments are made for all following addition experiments.

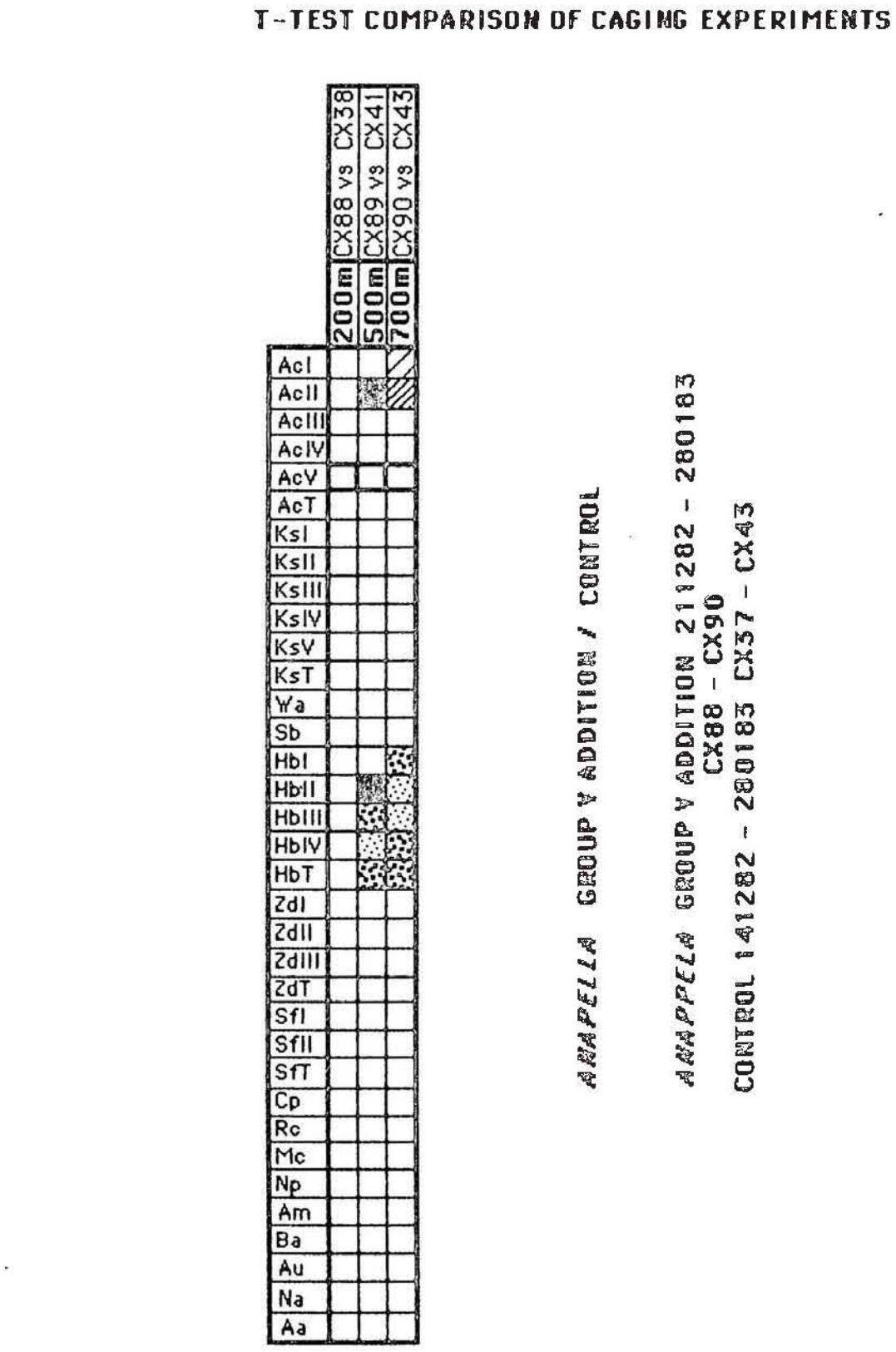


Fig. 7.13 Effect of adding *Anapella* group V animals to cages.

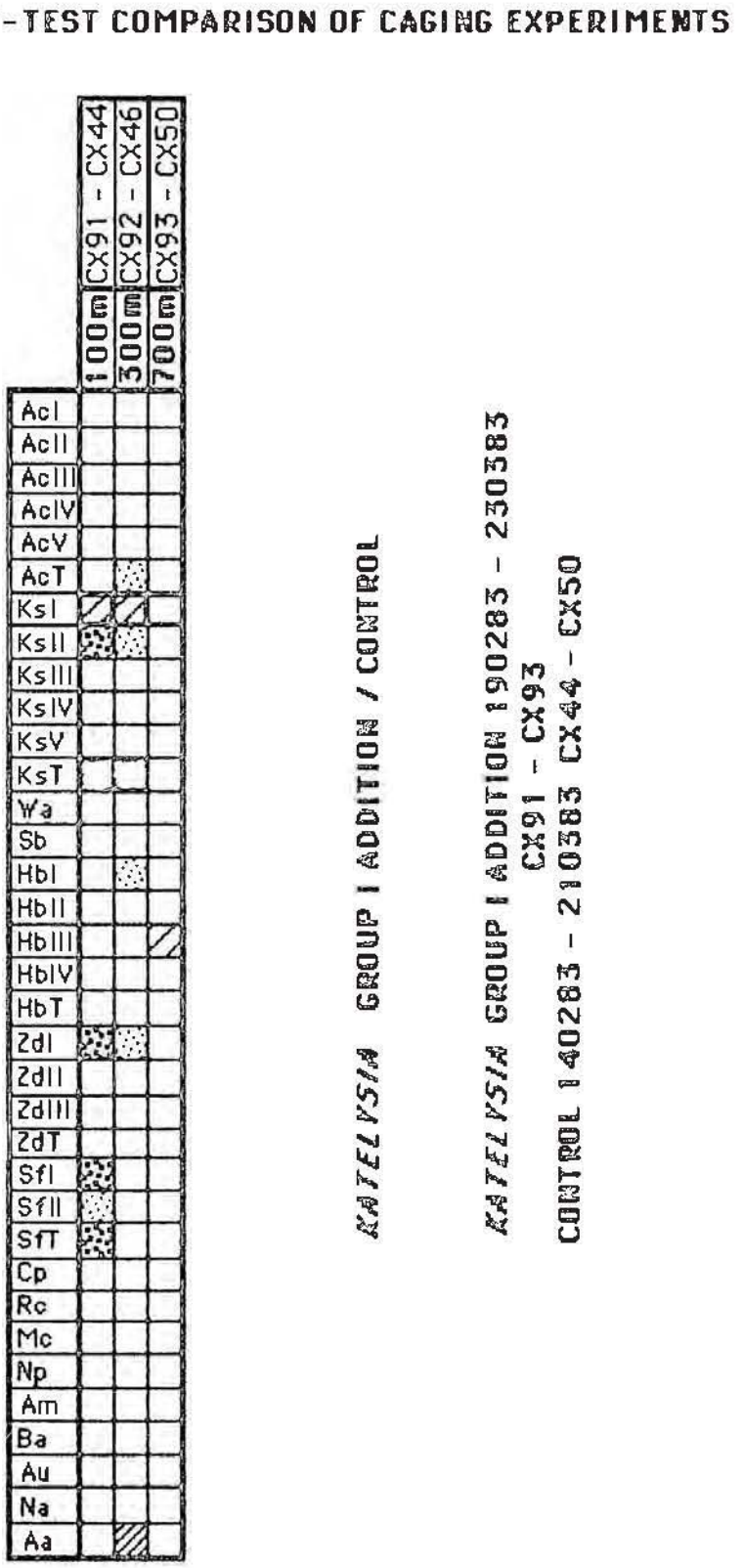


Fig. 7.14 Effect of adding *Katelysia* group I animals to cages.

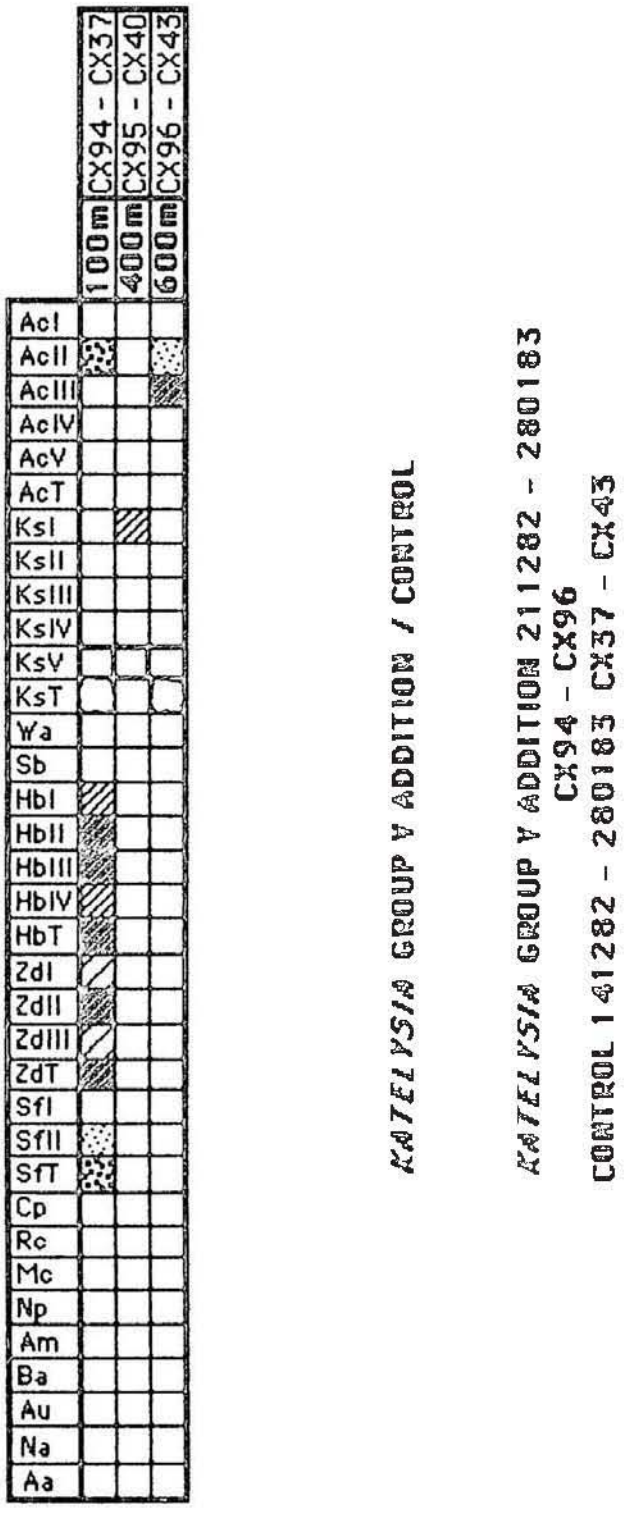


Fig. 7.15 Effect of adding *Katelysia* group V animals to cages.

Juvenile *Katelysia* numbers decreases at 600 m.

All *Hydrococcus* and *Zeacumantus* groups show decreased survival at 100 m.

There is a weak increase in the survival of large *Salinator* at 100 m.

7.3.5.5 *Anapella* group V + *Katelysia* group V addition

260283-040483 (Fig. 7.16)

The addition of 5 *Katelysia* enhances the survival of juvenile *Anapella* at 500 m.

Anapella group II numbers increase weakly at 500 m when 10 *Anapella* are added. The survival of group II *Anapella* at 500 m is slightly higher when 5 *Anapella* are added than when 5 *Katelysia* are added. Enhanced survival of group III *Anapella* is evident at 300 m following the addition of 5 or 10 *Katelysia* and at 500 m following the addition of 10 *Katelysia* ; group III survival is lower at 300 m when 5 *Anapella* are added than when 5 *Katelysia* are added. Adding 10 *Anapella* slightly decreases the survival of that group at 300 m and 500 m. Group V *Anapella* survival is strongly reduced at 300 m following the addition of 5 *Anapella* + 5 *Katelysia*. The survival of that *Anapella* group is slightly greater at 500 m when 10 *Katelysia* are added than when 5 *Anapella* + 5 *Katelysia* are added.

Juvenile *Katelysia* survival is slightly enhanced at 500 m when 10 *Anapella* are added but is decreased when 10 *Katelysia* are added. At 500 m the numbers of juvenile *Katelysia* are higher following the addition of 5 *Katelysia* than after 10 *Katelysia* are added. Adding 5 *Anapella* + 5 *Katelyia* at 500 m reduces the survival of group I *Katelysia* when compared to the effect of adding 10 *Anapella* and slightly enhances that survival when compared to the effect of adding 10 *Katelysia*.

Adding 10 *Katelysia* at 500 m decreases *Wallucina* abundances, and does so more than adding 5 *Anapella* + 5 *Katelysia* does. Adding 5 *Katelysia* at that distance produces a greater survival of *Wallucina* than adding 10 *Katelysia* does.

Juvenile *Hydrococcus* survival is greater after adding 10 *Anapella* at 300 m than after adding 5 *Anapella* + 5 *Katelysia*. At 500 m, adding 10 *Katelysia* increases the survival of group II *Hydrococcus*. Total *Hydrococcus* numbers are higher at 500 m after adding 5 *Anapella* than after adding 10 *Anapella*. Also at that distance, total *Hydrococcus* abundance is less after adding 10 *Anapella* than after adding 5 *Anapella* + 5 *Katelysia*.

Group II *Zeacumantus* numbers are low following the addition of 5 *Anapella*, as are group III numbers following the addition of 5 *Anapella* + 5 *Katelysia*, at 300 m.

Cylichnina numbers are low after 10 *Anapella* are added at 300 m. At 500 m *Cylichnina* survival is lower after adding 5 *Katelysia* than after adding 10

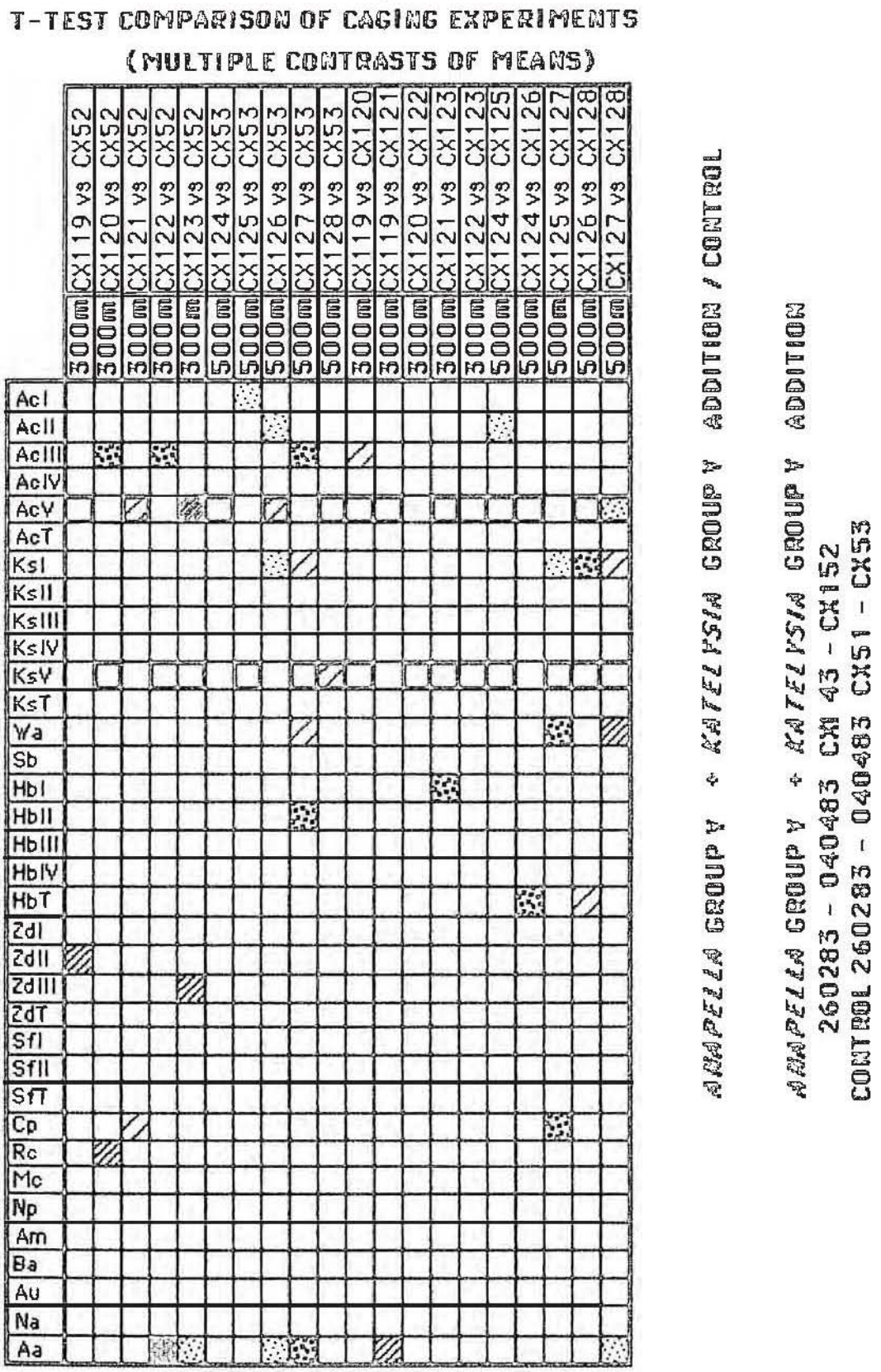


Fig. 7.16 Effect of adding combination of *Anapella* group V and *Katelysia* group V animals to cages.

Katelysia.

Rissopsis abundance is reduced at 300 m following the addition of 5 *Katelysia*.

7.3.5.6 *Anapella* group I addition versus *Katelysia* group I addition 190283-230383 (Fig. 7.17)

At 700 m group I *Anapella* numbers are lower after adding *Anapella* than after adding *Katelysia*.

Katelysia group I and II numbers are lower at 100 m and 300 m following the addition of *Anapella* than after adding *Katelysia*.

The survival of *Hydrococcus* group I animals is reduced at 300 m and 700 m after adding *Anapella*, when compared to the effect of adding *Katelysia*. Group III abundance is lower at 700 m following the addition of *Anapella* than following the adddition of *Katelysia*.

Adding *Anapella* leads to lower group I and III *Zeacumantus* numbers at 300 m and 100 m respectively, when compared to the effect of adding *Katelysia*.

Cylichnina and *Rissopsis* abundances are enhanced at 100 m after adding *Anapella*, relative to the effect of adding *Katelysia*.

7.3.5.7 *Hydrococcus* group I addition 190283-230383 (Fig. 7.18)

Group II *Anapella* survival is slightly enhanced by the addition of *Hydrococcus* at 100 m.

At 100 m (weak), 300 m and 700 m juvenile *Hydrococcus* numbers are reduced following the *Hydrococcus* addition. Large *Hydrococcus* are present in slightly increased numbers at 700 m when *Hydrococcus* is added.

Group I *Zeacumantus* and *Salinator* survival is enhanced at 100 m following the *Hydrococcus* addition.

Anthopleura shows a low abundance at 300 m.

7.3.5.8 *Hydrococcus* group IV addition 190283-230383 (Fig. 7.19)

Following the addition of *Hydrococcus*, juvenile *Hydrococcus* survival is reduced at 700 m, group III survival is enhanced at 300 m and group IV survival is reduced at 100 m, 300 m and 700 m.

There is a weak increase in large *Zeacumantus* survival at 100 m.

Total *Salinator* and *Cylichnina* numbers are greater at 300 m following the addition of *Hydrococcus*.

Anthopleura shows a low abundance at 300 m.

7.3.5.9 *Zeacumantus* group II addition 211282-280183 (Fig. 7.20)

Group I and II *Anapella* survival is reduced at 700 m following the addition of

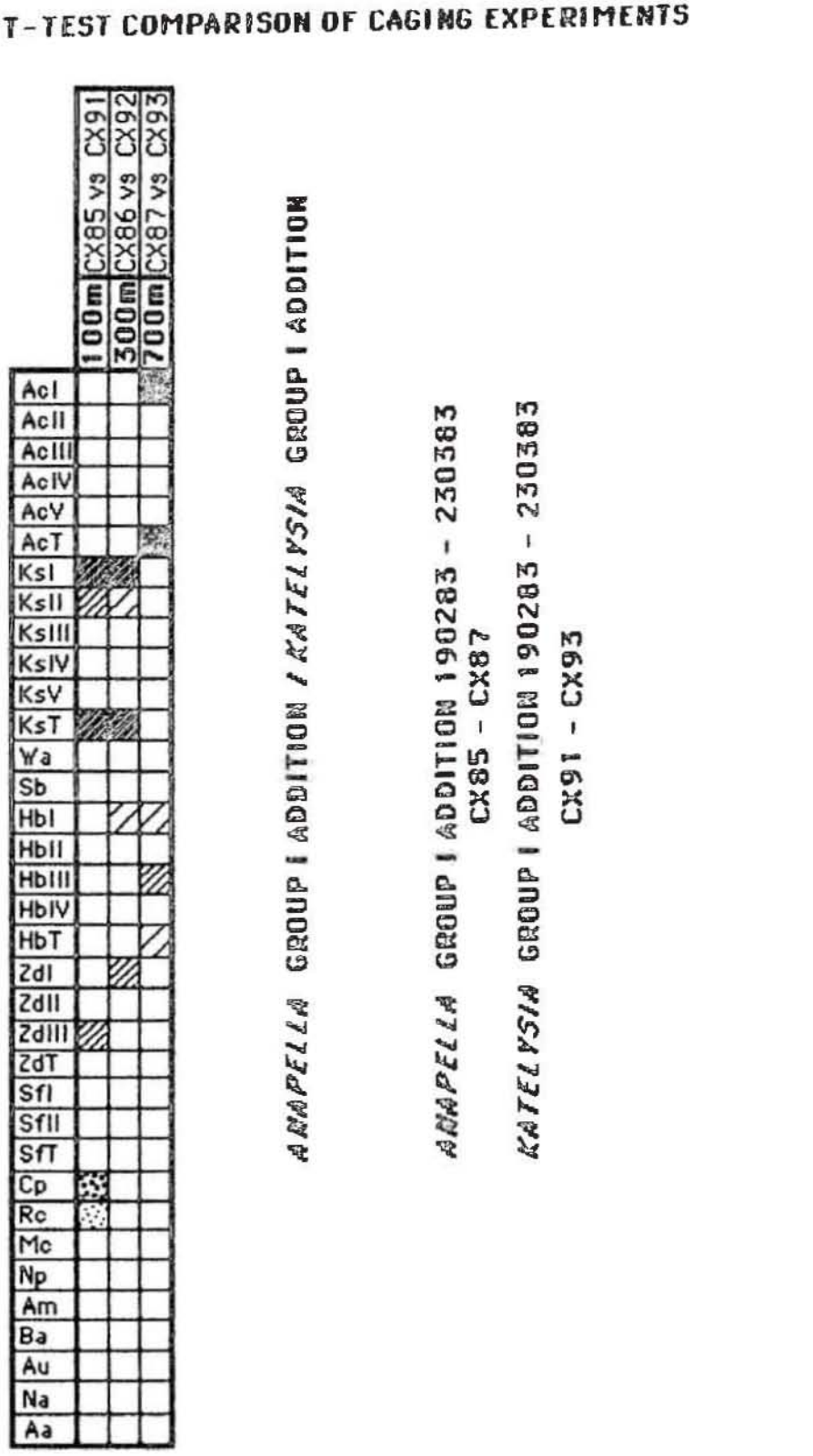


Fig. 7.17 Comparison of effects of adding *Anapella* group I animals and effects of adding *Katelysia* group I animals.

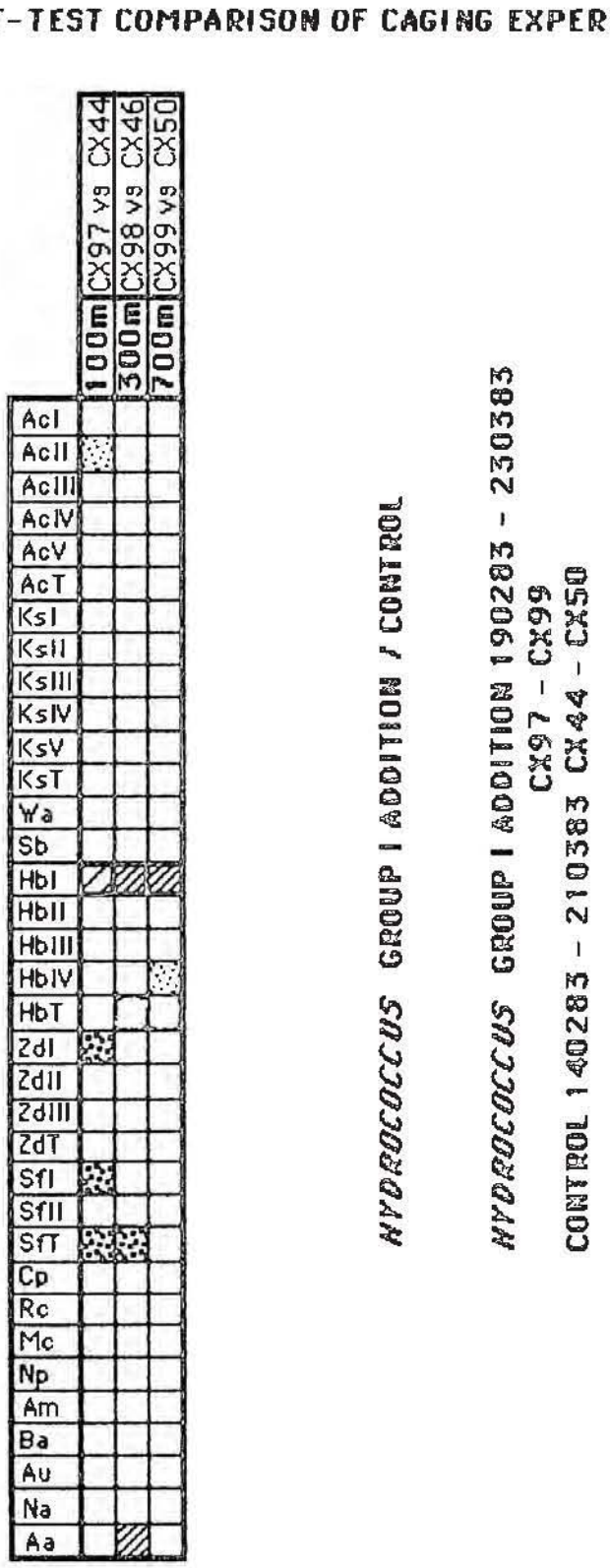


Fig. 7.18 Effect of adding *Hydrococcus* group I animals to cages.

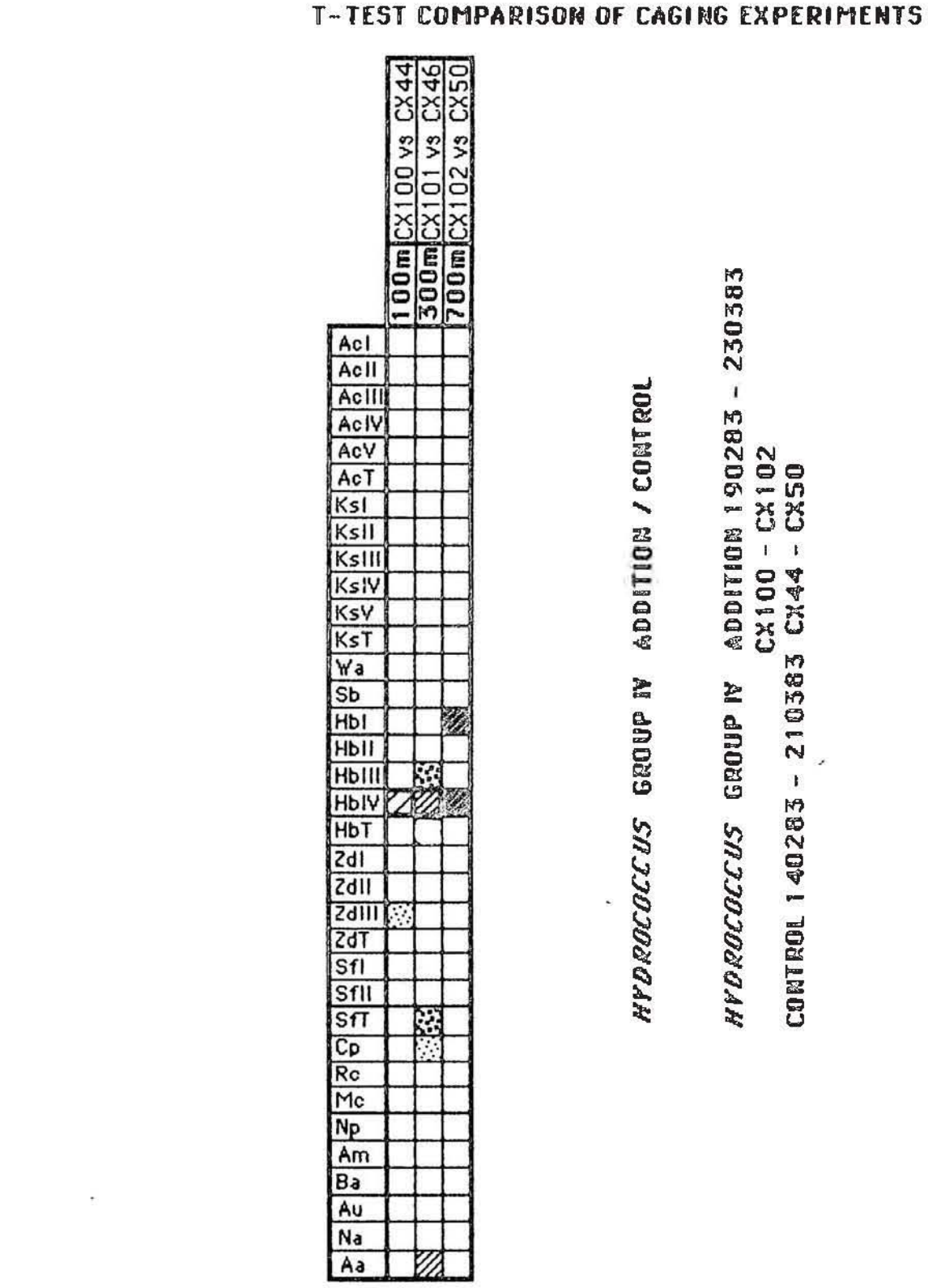


Fig. 7.19 Effect of adding *Hydrococcus* group IV animals to cages.

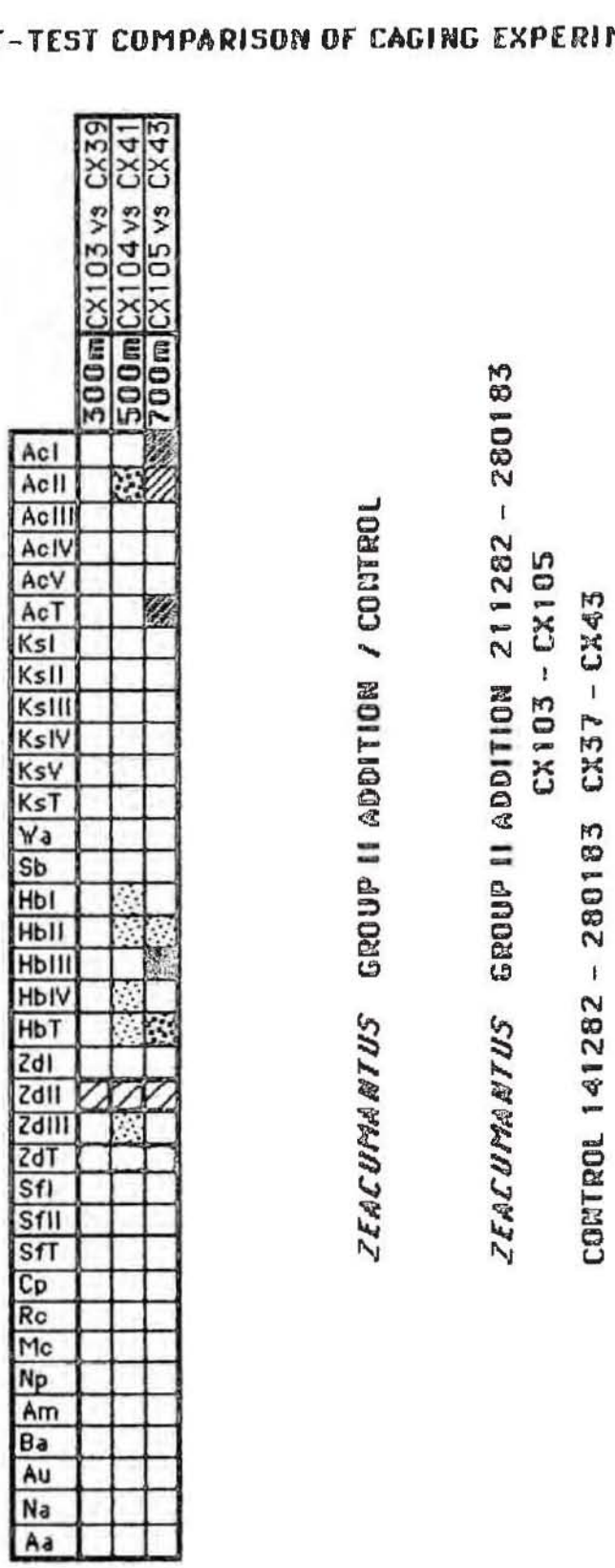


Fig. 7.20 Effect of adding *Zeacumantus* group II animals to cages.

Zeacumantus while group II survival is greater at 500 m.

All *Hydrococcus* groups except group III have a slightly enhanced survival at 500 m. Group II (weak) and group III (strong) *Hydrococcus* survival is enhanced at 700 m.

At all stations the addition of group II *Zeacumantus* leads to a reduced survival of those animals while at 500 m group III survival is slightly greater.

7.3.5.10 ***Salinator*** **group II addition 190583-020783** (Fig. 7.21)

Adding group II *Salinator* has no significant effect at any station.

7.3.5.11 ***Salinator*** **group II +** ***Bembicium*** **addition 260283-040483** (Fig. 7.22)

Anapella group I survival is reduced following the addition of 10 *Bembicium* at 50 m. Adding 10 *Bembicium* there leads to slightly lower *Anapella* juvenile survival than does the addition of 20 *Bembicium*. At 300 m the survival of group I *Anapella* is greater after adding 20 *Bembicium* than after adding 10 *Salinator* + 10 *Bembicium*. Group III *Anapella* survival is greatly enhanced by adding 10 or 20 *Salinator* at 300 m; at that distance group III *Anapella* survival is greater with 10 *Salinator* added than with 10 *Bembicium* added. Large *Anapella* show higher numbers at 300 m after 20 *Salinator* are added; adding 20 *Bembicium* leads to greater *Anapella* group V survival than adding 10 *Bembicium* does. Adding 20 *Salinator* leads to higher group V *Anapella* numbers at 300 m than adding 10 *Salinator* + 10 *Bembicium* does.

The addition of 20 *Salinator* at 300 m decreases the numbers of group I *Hydrococcus*. Adding 20 *Bembicium* at 50 m leads to a slight enhancement of group II *Hydrococcus* survival and this survival is greater than after adding 10 *Salinator* + 10 *Bembicium*. Group III *Hydrococcus* abundance at 50 m is less after adding 10 or 20 (weak) *Salinator*. Adding 10 *Salinator* leads to lower group IV *Hydrococcus* numbers than adding 10 *Bembicium*.

There is a slight enhancement of group I *Zeacumantus* survival following the addition of 10 *Salinator* at 50 m. Adding 20 *Bembicium* at 300 m reduces the number of group II *Zeacumantus*. At 50 m the addition of 10 *Bembicium* decreases group II *Zeacumantus* numbers more than adding 20 *Bembicium* does. Also at 50 m, adding 20 *Salinator* leads to greatly lower numbers of that *Zeacumantus* group than does the addition of 10 *Salinator* + 10 *Bembicium*.

The survival of group II *Salinator* is reduced at 50 m and 300 m following the addition of 10 *Salinator*, and at 50 m following the addition of 20 *Salinator*. The

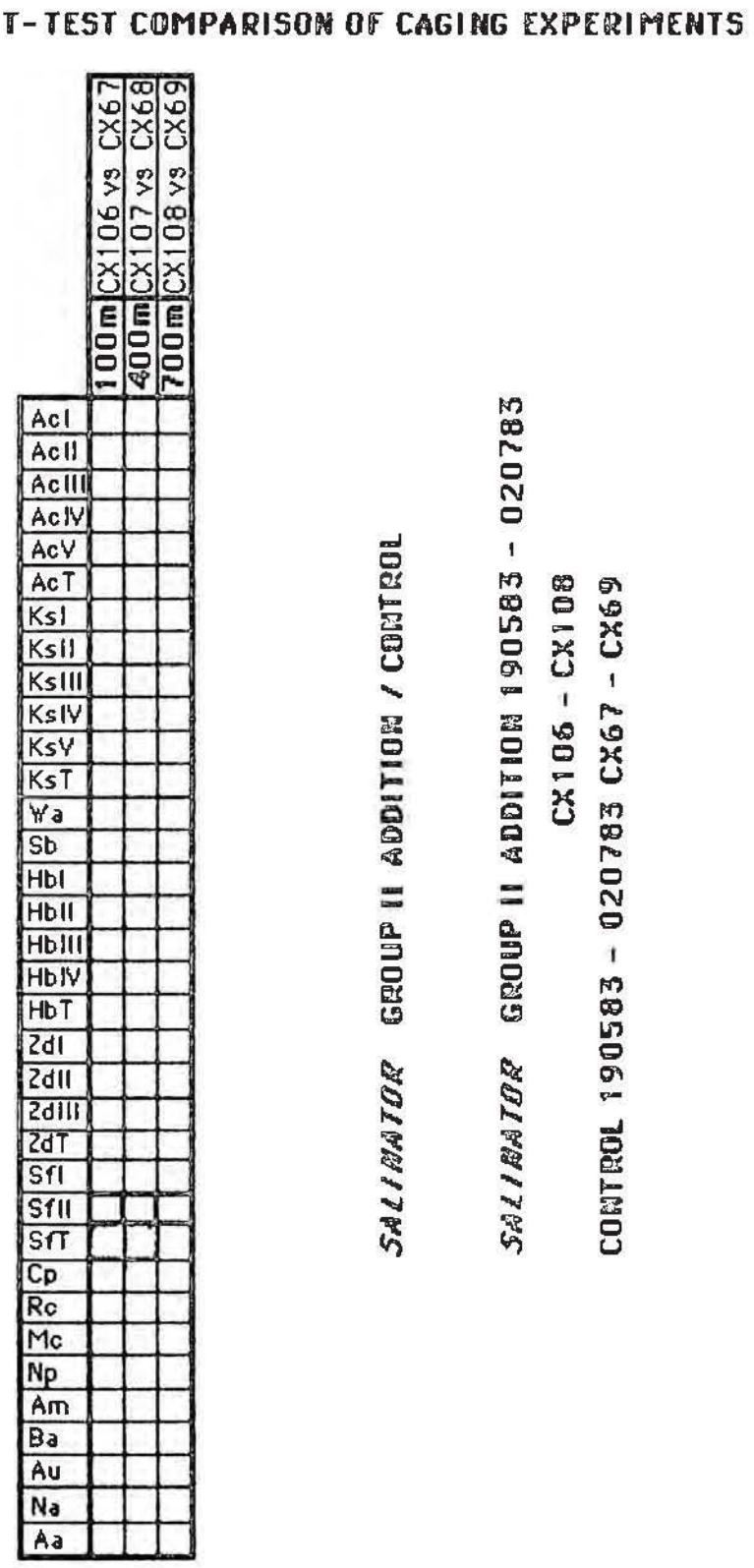


Fig. 7.21 Effect of adding *Salinator* group II animals to cages.

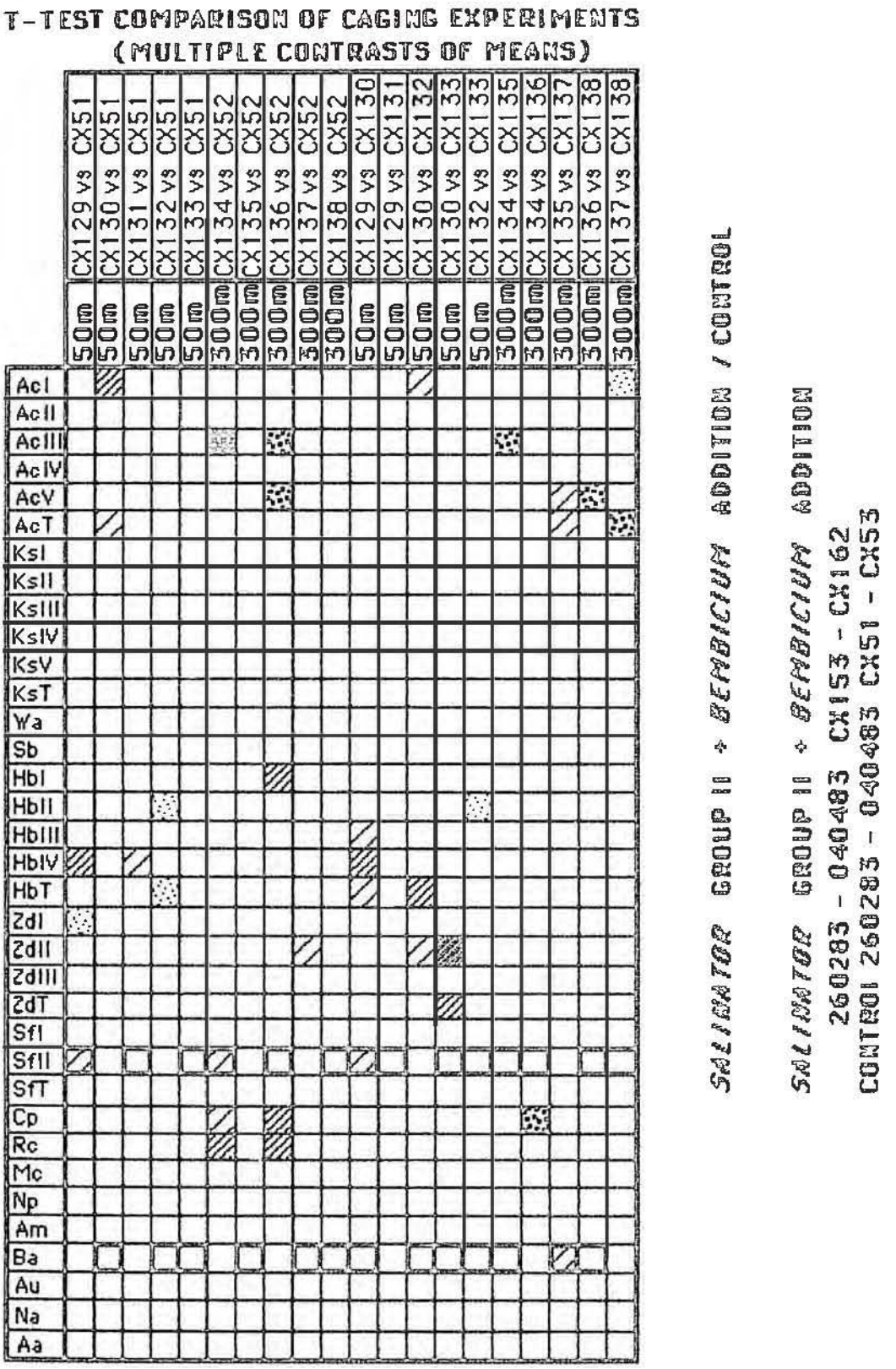


Fig. 7.22 Comparison of effects of adding *Salinator* group II animals and effects of adding *Bembicium*.

number of group II *Salinator* surviving after adding 10 *Bembicium* is greater than after adding 10 *Salinator*.

At 300 m, adding 10 (weak) or 20 *Salinator* reduces the survival of *Cylichnina*. The survival of *Cylichnina* following the addition of 10 *Salinator* is lower than after adding 10 *Bembicium* ; adding 20 Salinator decreases *Cylichnina* numbers more than adding 10 *Salinator*.

Rissopsis survival is reduced at 300 m by the addition of 10 or 20 *Salinator*.

The survival of *Bembicium* is slightly lower at 300 m following the addition of 10 *Bembicium* compared with that after the addition of 20 *Bembicium*.

7.3.5.12 *Nassarius* addition 280383-060583 (Fig. 7.23)

Large *Anapella* are slightly more abundant at 400 m following the addition of *Nassarius*.

At 700 m juvenile *Hydrococcus* survival is slightly reduced.

7.3.5.13 *Bembicium* addition 211282-270183 (Fig. 7.24)

Adding *Bembicium* increases and decreases the survival of group II *Anapella* at 300 m and 700 m respectively.

Group II *Hydrococcus* survival is enhanced at 500 m and 700 m, as is group II survival at 700 m.

At 300 m the numbers of group II *Zeacumantus* are higher after the addition of *Bembicium*.

7.3.5.14 *Austrocochlea* addition 190583-020783 (Fig 7.25)

Juvenile *Kalelysia* survival is slightly increased following the addition of *Austrocochlea* at 400 m.

Large *Hydrococcus* have a greater abundance at 700 m.

Large *Zeacumantus* are more numerous at 400 m after the *Austrocochlea* addition.

There is a weak reduction in the abundance of *Cylichnina* at 400 m.

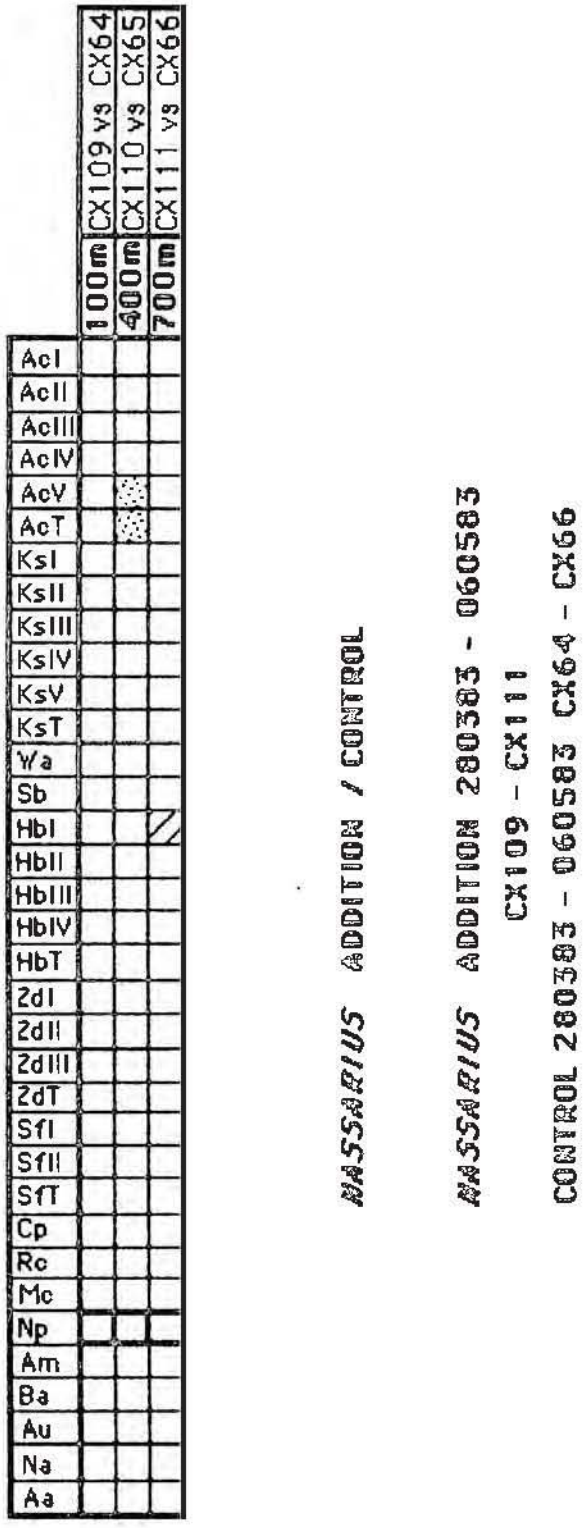


Fig. 7.23 Effect of adding *Nassarius* to cages.

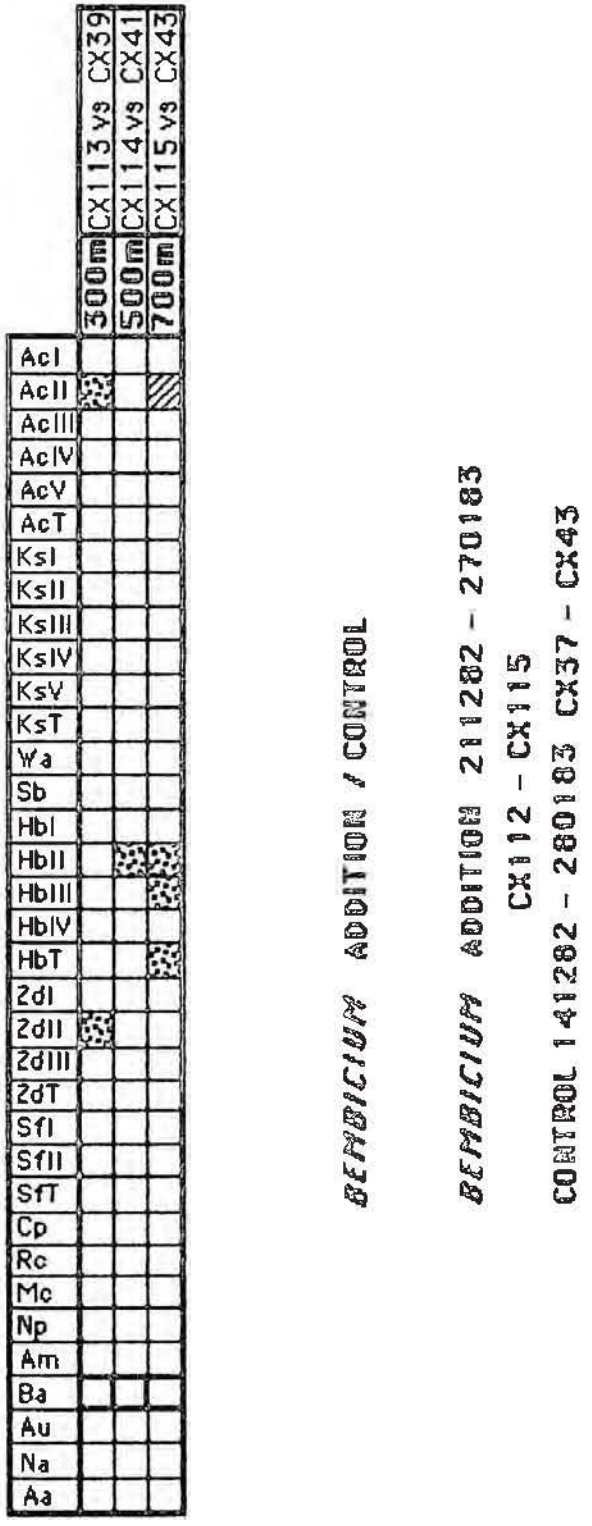


Fig. 7.24 Effect of adding *Bembicium* to cages.

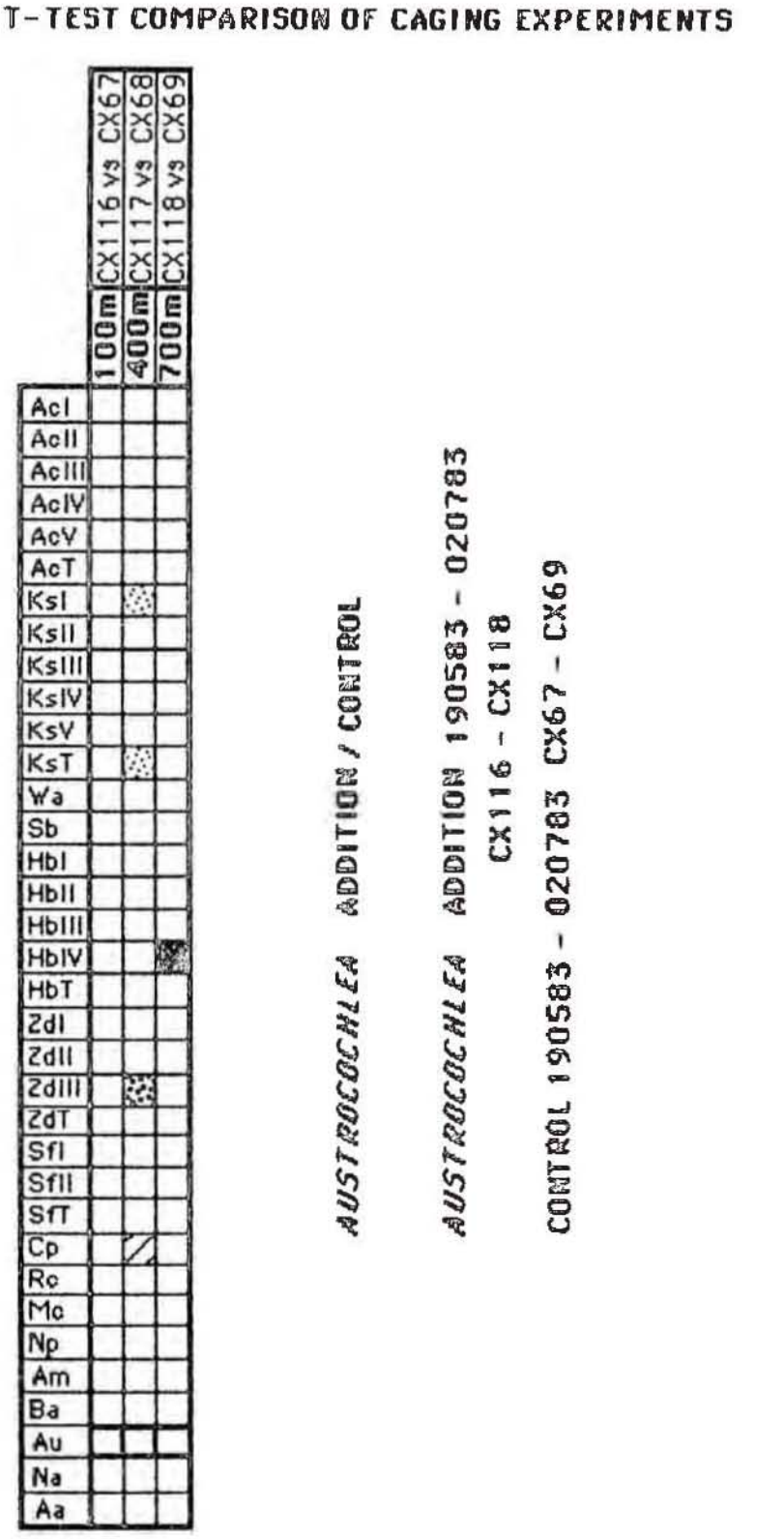


Fig. 7.25 Effect of adding *Austrocochlea* to cages.

7.4 Discussion

Wave induced pits in the natural substrate are common throughout the lagoon beach. These typically arise during southwesterly storms which blow up the beach. Small depressions disappear relatively quickly, within a matter of days. In some cases, however, the depressions may fill with algal mats which act as buffers and allow the depressions to remain patent for several weeks. This occurs most commonly in the upper half of the beach. If the depressions are not filled with the algal mats, water-borne sediments are washed in, with the interstitial fauna being returned passively to the depauperated area. The pitfall traps show that all but *Anapella*, *Hydrococcus* and *Zeacumnatus* are replaced within one tidal period. The pitfall traps were almost completely filled with substrate after the immersion and it is probable that the entire species complements would be returned within only a few tidal immersions.

The cage design proved to be well suited for use on the tidal flat and there was little build up of sediments within the cages or against the cage walls, as has been found in a number of studies (Virnstein 1978; Hulberg and Oliver 1980). Despite this it is apparent that the act of caging significantly affects the biota.

In the cooler months, caging results in a general reduction in the density of juvenile *Anapella* in the top sections of the beach. In summer and autumn, however, juvenile *Anapella* numbers increase inside the cages, relative to the starting densities. This appears to be at least partly due to a general increase in densities in those sections of the beach and newly settled *Anapella* (< 0.5 mm) could become trapped inside the cages. A concomitant effect could be the shading effect provided by the cages which would reduce the dessicatory stress in exposed areas during the warmer months. Juvenile *Katelysia* survival appears to be increased by caging in most seasons (in the lower half of the beach) and this probably reflects the lesser tolerance to exposure shown by that species. Long term caging, however, eventually reduces juvenile *Katelysia* numbers.

Larger *Anapella* show enhanced survival inside the cages at the top of the autumn beach and in the lower sections of the winter beach. Larger *Katelysia*, however, do not show major caging effects although the survival of medium *Katelysia* appears to be slightly greater inside the cages. Again, this could be due to the shading effect of the cages. *Anthopleura* survival also increases inside the cages during autumn, probably in association with the greater survival of large *Anapella*.

In summer and autumn, small (particularly) and large *Hydrococcus* show enhanced survival inside the cages at the top of the beach. Again, this could be due to the shading effect of the cages. In all seasons, however, juvenile *Hydrococcus* numbers decline in

the middle or at the bottom of the beach when caged. The winter reductions may be partly attributed to general reductions in densities in those areas of the tidal-flat.

Caging appears to enhance the survival of *Cylichnina* in the middle sections of the beach - only in autumn do numbers decrease. *Cylichnina* is probably a rapacious predator of *Hydrococcus*, actively searching for its prey. Caging should lead to an increase in predator numbers at the expense of its prey and this appears to be the case with *Cylichnina* and *Hydrococcus*. There is some suggestion that the autumn survival of large *Hydrococcus* is aided by caging. A corresponding reduction in *Cylichnina* numbers during that season support the suggestion of a functional predator-prey relationship.

In all seasons but summer, caging decreases the survival of small *Zeacumantus* at the top of the beach. Caging also decreases the densities of *Salinator* at the top of the beach. Both these species appear to be highly tolerant of aerial exposure, and are found naturally high on the beach. While caging may reduce the dessicatory stress on other species, *Salinator* and *Zeacumantus* are not advantaged by it. *Rissopsis* survival, however, is enhanced at the top of the beach.

There is relatively little effect caused by the regular disturbance of the substrate inside the cages. The significant effects are opposite to those expected under the trophic amensalism hypothesis. Thus, the survival of small *Anapella* appears to be aided by the disturbance at the top of the beach while *Hydrococcus* survival is reduced at the bottom of the beach. It is possible that the manual disturbance of the sediments inside the cages was too infrequent to produce any of the effects associated with trophic amensalism. Under natural conditions, the substrate disturbance produced by deposit feeders would be a continual process, in contrast to the bidaily disturbance inside the cages.

The decline in *Hydrococcus* numbers at the bottom of the beach may be related to the relatively shallow anoxic layer there. Each manual disturbance returned more anoxic sediments to the surface at 700 m than it did higher up on the beach and this could reduce the survival of *Hydrococcus*.

The translocation of entire substrate cores from one region of the beach to another provides a rigorous test of the importance of exposure to the biota. The cage mesh would provide a barrier to minimise any effects due to biotic interactions and the translocations effectively represent a switching of exposure regimes.

Juvenile *Anapella* survival decreases when animals are moved further down the beach but medium *Anapella* survival increases. With longer translocations, large *Anapella* survival decreases when moved from the top to the bottom of the beach. This

suggests that the natural absence of *Anapella* from the lower sections of the beach is due to an intolerance to extended periods of immersion. *Wallucina* shows similar effects. In contrast, juvenile and small *Katelysia* survival increases when they are moved further down the beach and *vice versa*. Thus, the natural low beach zonation shown be *Katelysia* appears to be largely due to an intolerance to aerial exposure.

Juvenile and medium *Hydrococcus* survival decreases when they are moved up the beach. The natural densities of juvenile *Hydrococcus* are greatest near the bottom of the beach and this is probably due to an intolerance to exposure. The survival of larger *Hydrococcus* appears to be independent of the position on the tidal gradient.

Although *Salinator* is commonly found at or above the high water mark, its survival is greater when the animals are moved from the top to the middle of the beach. The increase in survival is only apparent in total *Salinator* numbers, however, and it is possible that the smaller animals account for most of the increase.

Cylichnina survival decreases after the animals are moved from the middle to the bottom of the beach. Given that small *Hydrococcus* probably form the major component of the diet of *Cylichnina*, it is apparent that the position on the tidal gradient takes precedence over the availability of food in determining the distribution of *Cylichnina*.

In longer translocations, small *Zeacumantus* decreases when moved from the top to the middle and bottom of the beach. Also, *Rissopsis* survival is enhanced when moved from the middle to the top of the beach. It appears that the natural high-beach zonation of these species is at least partly due to an intolerance to extended periods of immersion.

The addition of animals to the experimental cages provides a test of many of the conclusions drawn from the correlation analyses of the spatial distributions of the species on the tidal flat.

Spatial correlations among small *Anapella* are generally positive and at the top of the beach the addition of juvenile *Anapella* does appear to enhance the survival of like animals. At the bottom of the beach, however, the same actions decrease the densities of small *Anapella*. Similarly, the addition of juvenile *Katelysia* reduces the survival of that group in the top sections of the beach. The addition of large *Anapella* at the bottom of the beach causes a reduction in the survival of small *Anapella*, although their survival is enhanced on the 500 m beach ridge. *Katelysia* does not appear to be affected by the addition of large *Anapella*. Large *Katelysia*, however, appear to facilitate a weak increase in juvenile *Anapella* survival at each end of the beach but the survival of medium *Anapella* is strongly decreased at 600 m. Juvenile *Katelysia* survival is also reduced near the bottom of the beach when large animals of that species are added.

In each case it appears that the species are resource limited in regions away from their preferred zones. Tolerance to immersion or emmersion, therefore, is not the only determinant of the distribution of the bivalves. In fact, exposure and resource limitation may act synergistically.

The addition of one bivalve leads to a slight enhancement in the survival of similarly sized animals of the other species in the latter species preferred zone. It is difficult to suggest any functional relationship that could account for this. The comparison of the effects of adding juveniles of each species indicates that *Anapella* is the most strongly interacting of the two. The apparent mutual enhancement of juvenile survival shown by *Anapella* and *Katelysia* at the ends of the beach contrasts with the spatial correlations which suggested that those species tended to segregate in those areas. The enhancement is supported by the results of adding combinations of large *Anapella* and *Katelysia*. Those experiments also support the suggestion that *Anapella* is the dominant bivalve with respect to interactions - the effects of adding the two species are strongest when high numbers of *Anapella* are present.

The spatial correlations indicated a segregation between small *Anapella* and large *Hydrococcus* in the middle sections of the beach, while positive correlations occurred near the ends of the beach. The caging experiments show that negative interactions can be induced between those species at each end of the beach. In contrast, the addition of large *Anapella* enhances the survival of *Hydrococcus* at the bottom of the beach, although the effect reverses when higher numbers of *Anapella* are added. Although the addition of small *Katelysia* has little effect on *Hydrococcus*, large *Katelysia* strongly reduce the survival of *Hydrococcus* at the top of the beach. These interactions are hilighted by the relative effects of adding combinations of large *Anapella* and *Katelysia*.

The trophic group amensalism hypothesis is generally regarded as being the negative effect exerted by deposit feeders on suspension feeders. The caging experiments, however, suggest that there may also be a relationship acting in the opposite direction. Large bivalves could reduce *Hydrococcus* numbers simply by reducing the availability of space within the cages. It is unlikely, however, that space reductions would arise when juvenile bivalves are added. The bivalves may reduce the availability of food for the deposit feeders by removing it from the water column before it can settle onto the substrate. This presupposes that the bivalves and gastropods share a common food resource. It is more likely that the bivalves reduce the availability of nutrients that would normally enrich the food supply of the deposit feeders.

Katelysia and *Zeacumantus* interact strongly when *Katelysia* is added to cages in

the top sections of the beach. Although juvenile *Katelysia* appear to enhance the survival of small *Zeacumantus*, large *Katelysia* reduce the survival of that gastropod. Similar, indirect relationships could exist between *Katelysia* and *Zeacumantus* as were suggested for *Anapella* and *Katelysia*. *Katelysia* and *Zeacumantus* have mutually exclusive distributions on the tidal flat and the spatial correlations between these two species are negative. The caging experiments suggest that this could be due to a functional relationship between the two species. At the bottom of the beach, the addition of *Zeacumantus* or *Bembicium* reduces the survival of small *Anapella* indicating that similar relationships may extend to *Anapella* when that species is in a stressed zone.

Large *Katelysia* also appear to reduce the survival of *Rissopsis* and *Cylichnina* near the middle of the beach but the effect is not proportional to the number of animals added. *Katelysia* and *Rissopsis* did not show segregation in the correlation analyses but it appears that segregation could be induced, possibly due to similar causes as were suggested for the segregation betweeen *Katelysia* and *Zeacumantus*. The apparent relationship between large *Katelysia* and *Cylichnina* is difficult to interpret.

The addition of juvenile *Hydrococcus* leads to a reduction in the numbers of small *Hydrococcus* in all sections of the beach. Similarly, large *Hydrococus* tend to reduce the survival of other *Hydrococcus* at each end of the beach when added to the cages. Both cases probably reflect resource limitation. Particle size selection among *Hydrococcus* would tend to restrict food resource overlap to similarly sized animals. Thus, small animals would compete for similarly sized particles while larger animals would utilise larger particles. This could account for the relatively weak effects on juvenile *Hydrococcus* following the addition of large animals.

Salinator and *Cylichnina* appear to be advanteged by the addition of *Hydrococcus* in the top regions of the beach. Although *Salinator* shares food resources with *Hydrococcus*, there does not appear to be competitive exclusion between the two species following the caging manipulation experiments. The occasional segregation between the two species shown in the spatial correlation analyses is probably a localised occurence, with the general positive association prevailing. The enhancement of *Cylichnina* survival following the adddition of *Hydrococcus* can be attributed to factors similar to those described for the control experiments.

Anthopleura numbers appear to reduce, and *Zeacumantus* increase, following the addition of *Hydrococcus*, but it is difficult to attribute these effects to a functional relationship. Because *Hydrococcus* forms part of the diet of *Anthopleura*, the opposite effect would be expected. Indeed, the two species were shown to segregate on the tidal flat;

other factors may play a dominant role in the caging experiments. The apparent benefit to *Zeacumantus* could be due to the substrate disturbance produced during *Hydrococcus* feeding. This may allow an increase in the production of the microalgae which *Zeacumantus* feeds on. The caging observations are supported by the strong positive relationships between *Hydrococcus* and *Zeacumantus* shown in the spatial correlation analyses. *Zeacumantus*, *Bembicium* and *Austrocochlea* enhance the survival of *Hydrococcus* when added near the bottom of the beach, suggesting there may be a mutual relationship between *Hydrococcus* and the algivorous gastropods.

When *Zeacumantus* is added to the cages, the existing *Zeacumantus* densities are reduced, suggesting resource limitation. Towards the middle of the beach it appears that *Zeacumantus* survival is increased by the addition of *Bembicium* or *Austrocochlea*, indicating a mutual relationship among these algivorous gastropods. The correlation analyses also suggested such relationships.

The combined addition of *Salinator* and *Bembicium* show that *Bembicium* tends to reduce the survival of juvenile *Anapella* and increase the survival of *Hydrococcus* at the top of the beach. These observations support the conclusions derived from other addition experiments. *Salinator* addition decreases the survival of *Hydrococcus* (and other *Salinator*) and *Zeacumantus* at the top of the beach while increasing the survival of non-juvenile *Anapella* in the middle reaches of the beach. The former relationship is probably due to resource limitation between the two deposit feeders, but the latter is unexpected. The interaction between *Salinator* and *Zeacumantus* could be mediated by factors similar to those acting between *Hydrococcus* and the algivorous gastropods. *Bembicium* addition leads to a reduction in the survival of *Zeacumantus* at the top and near the middle of the beach; existing *Bembicium* densities are also reduced. The distributions of *Bembicium* and *Zeacumantus* suggested that a possible segregation and the correlation experiments indicated that this probably occurs in winter, when food could be limiting. It appears that microalgae are a limiting resource near the top of the beach.

The combined addition experiments reveal that *Cylichnina* and *Rissopsis* survival is reduced by the addition of high numbers of *Salinator*. These observations are opposite to those produced following the addition of *Hydrococcus* and are also opposite to those suggested by the correlation analyses. The *Salinator* addition experiments did not produce any significant effects and it appears that the role of *Salinator* varies with the season. The combined experiments were conducted in summer/autumn while the *Salinator* addition experiments were conducted in winter. A possible explaination of the

negative effect of caged *Salinator* in summer is one of physical disturbance. *Salinator* is a particularly active animal and normally wanders over large distances. Confining a large number of *Salinator* in a small area would lead to considerable disturbance of the substrate and this may be detrimental to *Cylichnina* and *Rissopsis* survival. This could be exagerrated with increased activity in the warmer months. The fact that the bivalves remain unaffected following the addition of *Salinator* suggests that the disturbance would be more of a physical nature, rather than a resuspension of the sediments.

Although it was expected that *Nassarius* would produce a significant decline in the numbers of surviving *Anapella* and *Katelysia*, this did not occur. The experiments may not have been continued for a sufficient length of time; individual *Nassarius* may not need to feed frequently.

CHAPTER 8

GENERAL DISCUSSION

Turbulence remains one of the last great problems of classical physics (Judson 1980) and I suggest that it provides a useful analogy for problems in community ecology. While the turbulence of fluids is commonplace, and can be seen in the passage of any fluid past an obstacle, it is not yet possible to accurately predict its nature. This is despite the fact that the properties of fluids in motion are well understood and can be modelled by relatively simple equations. The problems of predicting turbulence arise because of the immense complexity that develops when many cores of moving fluids combine and interact: the combination of many predictable flows leads to a single unpredictable flow. Judson (1980) notes that man's earliest attempts to make sense of hydrodynamics came from artists who composed visual essays on liquid motion. He points out that:

> "Science now is only beginning to reach beyond such precise observations toward an explanation of turbulent flow" (Judson 1980, p. 14).

The present study is in many ways analogous to a pictorial description of biological 'turbulence'. Within the tidal flat mollusc community at Pipe Clay Lagoon, the hierarchical interaction of entities (individuals, populations, species) successively increases the complexity of the system as a whole. While the complexity of the community has been observed and sketched in this work, it has not been explained. As is readily apparent from Chapters 5 and 6, the sketches of the community patterns are themselves complex and difficult to interpret. Hopefully, future pencils and brushes of quantitative ecology will develop to a point where they are capable of producing clear and unambiguous descriptions of patterns; only then will we be able to search for explanations of those patterns.

This study has raised innumerable questions while failing to unambiguously answer any. With the luxury of hindsight, it is clear that the aims were too ambitious. Too much effort needed to be devoted to simply establishing the makeup of the community to allow for any refinement of the analytical products. This problem could be redressed in a similar study of a well known community.

Despite the difficulties associated with interpreting many of the results of the analyses, this study has produced an outline of how the community appears to behave. One of the most striking features of the habitat is its stability. The beach profile showed little

change throughout the sampling and there were no obvious sediment sorting gradients over the transects. Natural disturbances to sediment stability have frequently been implicated as the mediating agent in the development and maintenance of soft-substrate communities (Thistle 1981; Gallagher *et al* 1983; Probert 1984) but disturbance does not appear to be important in Pipe Clay Lagoon, at least on a large scale. The habitat stability was reflected in the relative stability of the populations making up the community. No species exhibited marked changes in distribution and abundance from season to season, apart from those associated with recruitment. Constancy of community composition may be a characteristic feature of coastal lagoons. Peterson (1977) also found little change in commmunity makeup of similar lagoons over a three year period. Similar long term studies of Pipe Clay Lagoon are obviously warranted but these would require considerable effort if the minimum size (0.5 mm animals) used in this study was to be maintained.

The tidal flat habitat of Pipe Clay Lagoon is very homogeneous at a macrofaunal level, although undoubtedly significant variations occur at the micro- and meiofaunal level. The tidal gradient can be regarded as the overriding environmental parameter and it appears to exert its strongest influence on the species during their recruitment. Reproductive patterns vary both between and within species according to the position on the beach. In most species, recruitment appears to be ~~virtua~~ consistent ~~y continuous~~ although considerable temporal variations occur. Generally, bivalve recruitment is greatest over the cooler months of the year and reproductive success, as measured by settled juveniles, tends to increase in high beach areas during the cooler months. The gastropods appear to be less sensitive to desiccatory stress and the principal period of recruitment is spring/summer; this could be related to the availability of food.

The spatial and temporal variations in the structure of the community allowed a working hypothesis to be proposed in Chapter 4. This was essentially a synthesis of hypotheses developed from other studies of similar communities, applied to the observations of the survey work. One of the most interesting findings from this study is that it is possible to link the trophic amensalism hypothesis of Rhoads and Young (1970) with Huston's (1979) dynamic equilibrium hypothesis for the maintainance of species diversity. It appears that trophic amensalism, acting on juvenile animals, may be the controlling factor for maintaining the observed trends in diversity along the transects.

The second half of this work was an attempt to test the working hypothesis in three stages, each having successively greater fidelity. Unfortunately the difficulties of reducing the information content of the community to manegeable and unambiguous proportions has prevented a solid hypothesis from being suggested. The working

hypothesis can be reconsidered, however, with modifications suggested by the spatial correlation and caging experiment analyses.

The distributions of most abundant bivalve (*Anapella*) and the most abundant gastropod (*Hydrococcus*) appear to be relatively independent of beach height, and this independence is likely to be largely responsible for the numerical dominance of those species. Two species show evidence of strong vertical zonation: *Katelysia* in the lower sections of the beach and *Bembicium* in the extreme upper section of the beach. In the former species the restricted zonation is probably associated with competitive exclusion, exerted by *Anapella*. Exclusion may also occur between *Zeacumantus* and *Bembicium* but the very restricted zone of *Bembicium* could have prevented this from being detected. The remaining species do not show strong vertical zonation, although most have preferred zones. Tidal height appears to be the principal environmental factor in determining the distribution patterns of species although most species show preference for a particular sediment size fraction . Since that fraction is so dominant (c. 80%), however, it is may be a casual, rather than a causal, relationship. Despite the importance of aerial exposure, there are no indications of a demarcation of faunal types according to beach height, as has been suggested by Seapy and Kitting (1978).

In general, the serial and planar correlation analyses revealed similar relationships among the biota and these relationships were largely supported by the caging experiments. Large *Anapella* and *Katelysia* exclude juveniles of the opposite species and this, together with the lower tolerance to desiccation shown by *Katelysia*, may partly account for the restricted zonation shown by *Katelysia*. The remaining suspension feeding bivalve, *Wallucina*, appears to be excluded from areas of high densities of *Anapella* or *Katelysia*, probably through resource limitation.

Adult-larval interactions are very important in soft-substrate habitats and they are often thought to be mediated by cannibalistic predation by suspension feeders (Woodin 1976; Peterson 1979; Williams 1980). Negative interactions do occur between juveniles and adults of *Anapella* and *Katelysia*, and *vice versa*, but not within the same species. Unless the bivalves are able to recognise conspecific larvae (perhaps on a size basis), this suggests that the ingestion of larvae by adult suspension feeders does not play a major role in Pipe Clay Lagoon.

Peterson (1982) also found little evidence for recruitment being affected by the adult densities of two suspension feeding bivalves although very high densities of the dominant species were associated with decreased recruitment of the other. In general, he showed that intraspecific effects were very much stronger than interspecific effects, and found

indications of an ecological separation between the two species, with food being the limiting resource. A separation also occurs in Pipe Clay Lagoon and is reflected in the distribution of *Anapella* and *Katelysia* on the beach. The correlation analyses showed that the separation between similarly sized animals along the tidal gradient is not actively maintained, although juveniles of one species and adults of the other do segregate.

The distributions of the suspension feeding bivalves are also influenced by the densities of the deposit feeding species, particularly *Hydrococcus* and *Salinator*. The caging experiments suggest that the trophic amensalism may be mutual.

Surprisingly, there are also indications that the mutually exclusive zones of *Katelysia* and *Zeacumantus* have a functional basis; *Zeacumantus* and *Anapella* also show evidence of segregation. In addition to *Zeacumantus*, two other algivorous gastropods, *Rissopsis* and *Austrocochlea*, appear to segregate with the major bivalves. It is difficult to suggest the mechanism for such exclusions, however. Suspension feeders and algivorous gastropods are unlikely to share food resources and the exclusions are probably not associated with exploitation competition. A possible explanation may be a form of interference competition, related to the trophic group amensalism hypothesis. Just as sediment reworking by deposit feeders can be disadvantageous to suspension feeders, so mobile algivores may disturb the sediments sufficiently to cause clogging of suspension feeding structures. Interference competition of another form may also be acting between the deposit feeders and the algivorous gastropods, which also show evidence of segregation.

Predation has been shown to play a significant role in the control of community structure on both hard and soft substrates (Menge and Sutherland 1976; Peterson 1979). In Pipe Clay Lagoon, however, predation appears to be of relatively minor importance. Predation does occur and it does affect the distribution of species to a small degree, but its role is minor in comparison to those played by exposure and trophic amensalism. The largest carnivore, *Nassarius*, has a relatively uniform distribution over the middle sections of the beach and feeds mainly on large *Anapella* and *Katelysia* while *Cylichnina*, with a more restricted distribution, probably feeds on juvenile bivalves and juvenile deposit feeders. Although both predators show significant relationships with their prey in the correlation analyses, no major effects are evident in the overall community structure. No firm conclusions can be drawn about the relationships of the presumed ectoparasite, *Agatha*, with other members of the community. Although the correlation analyses suggest that *Zeacumantus* is a likely host, *Agatha* does not appear to be capable of significantly influencing the community structure.

The anemone, *Anthopleura*, however, may play an indirect role in influencing the community structure. Field observations, together with the correlation analyses show that *Anthopleura* is capable of reducing the densities of the major deposit feeder, *Hydrococcus*. The low numbers of *Anthopleura* at either end of the beach may have allowed the comparatively high densities of *Hydrococcus* to develop there, and hence have mediated the effects of trophic amensalism in those regions.

In the light of the above, the working hypothesis can be restated as follows:

Hypothesis for the maintenance of the community struture

The deposit feeding gastropods, *Hydrococcus* and *Salinator*, can tolerate a wide range of conditions, are distributed over most of the beach and compete for trophic resources. The two species show evidence of competitive exclusion in areas of high densities. Their feeding activities rework the substrate, making the sediment-water interface unstable.

Anapella and *Katelysia* larvae settle indiscriminantly on the substrate but are unable to survive in areas of highly reworked sediment. In those areas where there are relatively low densities of deposit feeders, the bivalves are able to survive to maturity. Competition for resources (space and/or food) between adults of one bivalve and juveniles of the other leads to a segregation of the two species along the tidal gradient. *Katelysia*, being less tolerant of desiccation, becomes confined to the lower sections of the beach.

Wallucina is able to take advantage of low numbers of *Anapella* and *Katelysia* near the 500 m beach ridge and reaches its highest densities there.

Anthopleura uses large bivalves as a substrate and is most abundant in the middle sections of the beach. Passive predation by *Anthopleura* acts to keep the numbers of deposit feeding gastropods low, thus minimising the effects of trophic amensalism in those regions. In the absence of *Anthopleura* at either end of the transect, relatively high numbers of deposit feeding gastropods lead to an exclusion of suspension feeding bivalves and hence to a reduction in community diversity.

The upper half of the beach appears to be most suitable for gastropods feeding on microalgae. Although the distributions of the algivorous gastropods suggest a degree of local competitive exclusion, this cannot be detected statistically.

Interference competition between the algivorous gastropods and both the suspension feeding bivalves and the deposit feeding gastropods may be sufficient to influence the local distributions of those species.

Nassarius obtains its main food supply by scavenging dead, and preying on living *Anapella* and *Katelysia* and is therefore most abundant in the middle sections of the beach. *Cylichnina* probably feeds on juvenile bivalves and also on juvenile *Hydrococcus* (and to a lesser extent juvenile *Salinator*) and its distribution reflects those of its prey. Typically, the distribution of the predators is determined by the distribution of the prey and not *vice versa*. Apart from *Anthopleura*, therefore, predation appears to play a minor role in the maintenance of the community structure.

The above remains largely hypothetical and intensive experimental work would be required to prove or disprove the various components of the hypothesis. Also, the possibility that species outside the defined mollusc community might influence the molluscs cannot be dismissed. As discussed in Chapter 2, the roles of species such as crabs, fish and wading birds are probably not important in the Pipe Clay Lagoon tidal flat, but they undoubtedly exert some degree of influence. Their neglect in this study has been one of pragmatism only, as was the neglect of the third spatial dimension during the survey and experimental work. Molluscs, particularly bivalves, may show segregation according to depth in the substrate (Peterson 1982) and this study indicates that *Anapella* and *Katelysia* are likely candidates for such a relationship.

The difficulties in interpreting the results of the analyses highlight a paradox that is unavoidable in community studies. To understand the structural dynamics of an entire community, intensive sampling is required. Ideally, the community should be sampled more frequently, with respect to both time and space, than was possible in this study. This, however, would lead to even greater difficulties in interpretation. The paradox is that greater understanding of an entire community can only come from a more intimate knowledge of that community, but greater knowledge makes that understanding more

difficult to achieve. This paradox only applies to the primary analysis. Secondary analysis (that is, analysis of the analysis), could reduce the difficulties. The second level of analysis, however, can only proceed on the basis of hypotheses generated by the first level.

This work is clearly divisible into two sections. The first four chapters led to the formulation of the hypothesis for the maintenance of the community structure. The hypothesis was an amalgamation of the observations of the survey work and established community hypotheses derived from the literature. As is obvious from the later chapters, there was virtually no opportunity to place the spatial analyses into a perspective provided by previously published work. This raises a problem that plagues the study of complex communities. For general concepts, such as diversity or trophic group amensalism, it is possible to construct a framework of relevant literature, within which new observations can be placed; the working hypothesis was based on such a framework. The testing of such constructions, however, deals with concepts that are unique to the particular community being studied. The fact that *Anapella* and *Hydrococcus* have a certain serial correlation at a certain lag, for example, has no counterpart in the literature, other than the indirect links through the general concepts; the second half of this work is relevant only to the first half. This was a major source of frustation in that the very complex products of the correlation analyses could not be placed into an independent framework that was based on other work. The only opportunity to establish such a framework would come through a comparison with the products of similar analytical methods (rather than similar communities), the link being the tool rather than the object being manipulated.

For this reason, a standardisation of the analytical methods is highly desirable. I suggest that the approach adopted in this study could prove particularly useful. A methodical survey of species distributions along an environmental gradient, followed by serial and planar correlation analyses similar to those used here could identify the most important interrelationships among species and between species and environmental variables. These could then be tested by appropriate experimental work. As is obvious from this study, compromises may need to be made in the ratio of experimental to survey work, depending on the intensity of the survey and the manpower resources. For communities that are already well known, experimental work could predominate while the serial and planar analyses could be used to reveal a hierarchy of testable interactions within the community.

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APPENDIX A

COMPUTER PROGRAM LISTINGS

This appendix lists source codes of the FORTRAN IV programs used for the serial and planar spatial analysis of species dispersion patterns, described in Chapters 5 and 6. The programs were developed on a Burroughs B6800 computer and may require slight modifications for use on other computers. The programs are stored on a magnetic tape deposited in the University of Tasmania Library with this thesis.

CEREAL/CROSS jobs

The job templates for autocorrelation and crosscorrelation using CEREAL/CROSS have the same basic format. In general, the jobs require the following cards (comments in *italics*):

1. title
2. READ (*data input parameter card*)
3. no. observations, interval between observations, no. of species,
   no. of classes for each species listed from first to last species
4. FIT (*smoothing parameter card*)
5. smoothing code for each species total (0=no smoothing, 1=smoothing)
6. smoothing code for each class of each species
7. power of fit polynomial, range of moving average
8. CRSS or SEAL (*auto- or cross-correlation parameter card*)
9. maximum lag
10. correlation code for each species (autocorrelation only)
    (0=no correlations calculated, 1=correlations calculated)

Example of job for autocorrelation analysis

```
?BEGIN JOB CEREAL/TRANSRAW/200381; job title
QUEUE=33; priority queue
RUN OBJECT/CEREAL/CROSS;
FILE FILE5=TRANSRAW/200381; data file
FILE 4(KIND=READER); job file type
DATA job data cards follow
CROSS/200381 title
READ
36,1,16,24,5,13,31,11,11,6,3,3,7,4,16,13,9,1,11
FIT
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
1,1,1,1,1,
1,1,1,1,1,1,1,1,1,1,1,1,1,1,
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
```

```
1,1,1,1,1,1,
1,1,1,
1,1,1,
1,1,1,1,1,1,1,
1,1,1,1,
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
1,1,1,1,1,1,1,1,1,1,1,1,1,
1,1,1,1,1,1,1,1,1,
1,
1,1,1,1,1,1,1,1,1,1,1
2,5
SEAL
9
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
? end of job data cards
?END JOB
```

Example of job for cross-correlation analysis

```
?BEGIN JOB CROSS/200381; job title
QUEUE=33; priority queue
RUN OBJECT/CEREAL/CROSS;
FILE FILE5=TRANS/GROUP/200381; data file
FILE 4(KIND=READER); job file type
DATA job data cards follow
CEREAL/GROUP/200381 title
READ
36,20,16,5,4,3,5,2,1,1,1,1,1,1,1,1,1,1,1
FIT
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,
```

```
LIST CEREAL/CROSS


100 $RESET FREE
200 $CHARS=4
300 C     PROGRAM CEREAL:PACKAGE FOR SERIES ANALYSIS,SPECIFICALLY FOR
400 C     A SMALL NUMBER (<50) OF OBSERVATIONS.TREND LINES ARE FITTED
500 C     AS DESCRIBED BY KENDALL & STUART (1966).MOVING AVERAGES BETWEEN
600 C     5 AND 11 POINTS ARE AVAILABLE FOR POLYNOMIALS OF POWER 2 TO 5.
700 C     AUTOCORRELATIONS ARE CALCULATED USING THE EXACT FORMULA RATHER
800 C     THAN THE USUAL APPROXIMATION TO AVOID ERRORS ASSOCIATED WITH
900 C     SMALL N.
1000 C     OBS<=36
1100 C     SP<=16
1200 C     CLASS<=31
1300 C     (POWER,RANGE) COMBINATIONS: (2,5),(2,7),(2,9),(2,11)
1400 C                                 (3,5),(3,7),(3,9),(3,11)
1500 C                                 (4,7),(4,9),(4,11)
1600 C                                 (5,7),(5,9),(5,11)
1700 C     LAG<=12
1800 FILE  4(KIND=READER,TITLE='COMMANDS')
1900 FILE  5(KIND=DISK,FILETYPE=8)
2000 FILE  6(KIND=PRINTER)
2100       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
2200      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
2300      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
2400       DATA WEIGHT/35,31,9,-3,-5,3,0,0,0,0,0,0,
2500      -35,9,13,12,6,-5,0,0,0,0,0,0,
2600      -35,-3,12,17,12,-3,0,0,0,0,0,0,
2700      -35,-5,6,12,13,9,0,0,0,0,0,0,
2800      -35,3,-5,-3,9,31,0,0,0,0,0,0,
2900      -0,0,0,0,0,0,0,0,0,0,0,0,
3000      -0,0,0,0,0,0,0,0,0,0,0,0,
3100      -0,0,0,0,0,0,0,0,0,0,0,0,
3200      -0,0,0,0,0,0,0,0,0,0,0,0,
3300      -0,0,0,0,0,0,0,0,0,0,0,0,
3400      -0,0,0,0,0,0,0,0,0,0,0,0,
3500      -42,32,15,3,-4,-6,-3,5,0,0,0,0,
3600      -14,5,4,3,2,1,0,-1,0,0,0,0,
3700      -14,1,3,4,4,3,1,-2,0,0,0,0,
3800      -21,-2,3,6,7,6,3,2,0,0,0,0,
3900      -14,-2,1,3,4,4,3,1,0,0,0,0,
4000      -14,-1,0,1,2,3,4,5,0,0,0,0,
4100      -42,5,-3,-6,-4,3,15,32,0,0,0,0,
4200      -0,0,0,0,0,0,0,0,0,0,0,0,
4300      -0,0,0,0,0,0,0,0,0,0,0,0,
4400      -0,0,0,0,0,0,0,0,0,0,0,0,
4500      -0,0,0,0,0,0,0,0,0,0,0,0,
4600      -165,109,63,27,1,-15,-21,-17,-3,21,0,0,
4700      -330,126,92,63,39,20,6,-3,-7,-6,0,0,
4800      -2310,378,441,464,447,390,293,156,-21,-238,0,0,
4900      -2310,14,273,447,536,540,459,293,42,-294,0,0,
5000      -231,-21,14,39,54,59,54,39,14,-21,0,0,
5100      -2310,-294,42,293,459,540,536,447,273,14,0,0,
5200      -2310,-238,-21,156,293,390,447,464,441,378,0,0,
5300      -330,-6,-7,-3,6,20,39,63,92,126,0,0,
5400      -165,21,-3,-17,-21,-15,1,27,63,109,0,0,
5500      -0,0,0,0,0,0,0,0,0,0,0,0,
5600      -0,0,0,0,0,0,0,0,0,0,0,0,
5700      -143,83,54,30,11,-3,-12,-16,-15,-9,2,18,
5800      -715,270,199,138,87,46,15,-6,-17,-18,-9,10,
```

```
5900      -2145,450,414,373,327,276,220,159,93,22,-54,-135,
6000      -715,55,87,109,121,123,115,97,69,31,-17,-75,
6100      -715,-15,46,92,123,139,140,126,97,53,-6,-80,
6200      -429,-36,9,44,69,84,89,84,69,44,9,-36,
6300      -715,-80,-6,53,97,126,140,139,123,92,46,-15,
6400      -715,-75,-17,31,69,97,115,123,121,109,87,55,
6500      -2145,-135,-54,22,93,159,220,276,327,373,414,450,
6600      -715,10,-9,-18,-17,-6,15,46,87,138,199,270,
6700      -143,18,2,-9,-15,-16,-12,-3,11,30,54,83,
6800      -70,69,4,-6,4,-1,0,0,0,0,0,0,
6900      -35,2,27,12,-8,2,0,0,0,0,0,0,
7000      -35,-3,12,17,12,-3,0,0,0,0,0,0,
7100      -35,2,-8,12,27,2,0,0,0,0,0,0,
7200      -70,-1,4,-6,4,69,0,0,0,0,0,0,
7300      -0,0,0,0,0,0,0,0,0,0,0,0,
7400      -0,0,0,0,0,0,0,0,0,0,0,0,
7500      -0,0,0,0,0,0,0,0,0,0,0,0,
7600      -0,0,0,0,0,0,0,0,0,0,0,0,
7700      -0,0,0,0,0,0,0,0,0,0,0,0,
7800      -0,0,0,0,0,0,0,0,0,0,0,0,
7900      -42,39,8,-4,-4,1,4,-2,0,0,0,0,
8000      -42,8,19,16,6,-4,-7,4,0,0,0,0,
8100      -42,-4,16,19,12,2,-4,1,0,0,0,0,
8200      -21,-2,3,6,7,6,3,-2,0,0,0,0,
8300      -42,1,-4,2,12,19,16,-4,0,0,0,0,
8400      -42,4,-7,-4,6,16,19,8,0,0,0,0,
8500      -42,-2,4,1,-4,-4,8,39,0,0,0,0,
8600      -0,0,0,0,0,0,0,0,0,0,0,0,
8700      -0,0,0,0,0,0,0,0,0,0,0,0,
8800      -0,0,0,0,0,0,0,0,0,0,0,0,
8900      -0,0,0,0,0,0,0,0,0,0,0,0,
9000      -99,85,28,-2,-12,-9,0,8,8,-7,0,0,
9100      -198,56,65,56,36,12,-9,-20,-14,16,0,0,
9200      -1386,-28,392,515,432,234,12,-143,-140,112,0,0,
9300      -462,-56,84,144,145,108,54,4,-21,0,0,0,
9400      -231,-21,14,39,54,59,54,39,14,-21,0,0,
9500      -462,0,-21,4,54,108,145,144,84,-56,0,0,
9600      -1386,112,-140,-143,12,234,432,515,392,-28,0,0,
9700      -198,16,-14,-20,-9,12,36,56,65,56,0,0,
9800      -99,-7,8,8,0,-9,-12,-2,28,85,0,0,
9900      -0,0,0,0,0,0,0,0,0,0,0,0,
10000      -0,0,0,0,0,0,0,0,0,0,0,0,
10100      -143,113,48,8,-12,-17,-12,-2,8,13,8,-12,
10200      -143,48,41,32,22,12,3,-4,-8,-8,-3,8,
10300      -429,24,96,123,116,86,44,1,-32,-44,-24,39,
10400      -858,-72,132,232,251,212,138,52,-23,-64,-48,48,
10500      -429,-51,36,86,106,103,84,56,26,1,-12,-6,
10600      -429,-36,9,44,69,84,89,84,69,44,9,-36,
10700      -429,-6,-12,1,26,56,84,103,106,86,36,-51,
10800      -858,48,-48,-64,-23,52,138,212,251,232,132,-72,
10900      -429,39,-24,-44,-32,1,44,86,116,123,96,24,
11000      -143,8,-3,-8,-8,-4,3,12,22,32,41,48,
11100      -143,-12,8,13,8,-2,-12,-17,-12,8,48,113,
11200      -0,0,0,0,0,0,0,0,0,0,0,0,
11300      -0,0,0,0,0,0,0,0,0,0,0,0,
11400      -0,0,0,0,0,0,0,0,0,0,0,0,
11500      -0,0,0,0,0,0,0,0,0,0,0,0,
11600      -0,0,0,0,0,0,0,0,0,0,0,0,
11700      -0,0,0,0,0,0,0,0,0,0,0,0,
11800      -0,0,0,0,0,0,0,0,0,0,0,0,
11900      -0,0,0,0,0,0,0,0,0,0,0,0,
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12000      -0,0,0,0,0,0,0,0,0,0,0,0,
12100      -0,0,0,0,0,0,0,0,0,0,0,0,
12200      -0,0,0,0,0,0,0,0,0,0,0,0,
12300      -462,456,25,-35,10,20,-19,5,0,0,0,0,
12400      -462,25,356,155,-60,-65,70,-19,0,0,0,0,
12500      -462,-35,155,212,150,25,-65,20,0,0,0,0,
12600      -231,5,-30,75,131,75,-30,5,0,0,0,0,
12700      -462,20,-65,25,150,212,155,-35,0,0,0,0,
12800      -462,-19,70,-65,-60,155,356,25,0,0,0,0,
12900      -462,5,-19,20,10,-35,25,456,0,0,0,0,
13000      -0,0,0,0,0,0,0,0,0,0,0,0,
13100      -0,0,0,0,0,0,0,0,0,0,0,0,
13200      -0,0,0,0,0,0,0,0,0,0,0,0,
13300      -0,0,0,0,0,0,0,0,0,0,0,0,
13400      -1287,1231,175,-125,-75,45,81,5,-85,35,0,0,
13500      -2574,350,1412,1025,225,-330,-360,37,385,-170,0,0,
13600      -2574,-250,1025,1112,675,180,-105,-110,37,10,0,0,
13700      -858,-50,75,225,304,270,135,-35,-120,54,0,0,
13800      -429,15,-55,30,135,179,135,30,-55,15,0,0,
13900      -858,54,-120,-35,135,270,304,225,75,-50,0,0,
14000      -2574,10,37,-110,-105,180,675,1112,1025,-250,0,0,
14100      -2574,-170,385,37,-360,-330,225,1025,1412,350,0,0,
14200      -1287,35,-85,5,81,45,-75,-125,175,1231,0,0,
14300      -0,0,0,0,0,0,0,0,0,0,0,0,
14400      -0,0,0,0,0,0,0,0,0,0,0,0,
14500      -143,131,30,-10,-15,-5,6,10,5,-5,-10,6,
14600      -143,30,59,50,25,0,-15,-16,-5,10,15,-10,
14700      -429,-30,150,177,125,50,-10,-35,-23,10,30,-15,
14800      -429,-45,75,125,127,100,60,20,-10,-23,-15,15,
14900      -429,-15,0,50,100,127,120,80,20,-35,-48,30,
15000      -429,18,-45,-10,60,120,148,120,60,-10,-45,18,
15100      -429,30,-48,-35,20,80,120,127,100,50,0,-15,
15200      -429,15,-15,-23,-10,20,60,100,127,125,75,-45,
15300      -429,-15,30,10,-23,-35,-10,50,125,177,150,-30,
15400      -143,-10,15,10,-5,-16,-15,0,25,50,59,30,
15500      -143,6,-10,-5,5,10,6,-5,-15,-10,30,131,
15600      -0,0,0,0,0,0,0,0,0,0,0,0,
15700      -0,0,0,0,0,0,0,0,0,0,0,0,
15800      -0,0,0,0,0,0,0,0,0,0,0,0,
15900      -0,0,0,0,0,0,0,0,0,0,0,0,
16000      -0,0,0,0,0,0,0,0,0,0,0,0,
16100      -0,0,0,0,0,0,0,0,0,0,0,0,
16200      -0,0,0,0,0,0,0,0,0,0,0,0,
16300      -0,0,0,0,0,0,0,0,0,0,0,0,
16400      -0,0,0,0,0,0,0,0,0,0,0,0,
16500      -0,0,0,0,0,0,0,0,0,0,0,0,
16600      -0,0,0,0,0,0,0,0,0,0,0,0,
16700      -924,923,6,-15,20,-15,6,-1,0,0,0,0,
16800      -154,1,148,15,-20,15,-6,1,0,0,0,0,
16900      -308,-5,30,233,100,-75,30,-5,0,0,0,0,
17000      -231,5,-30,75,131,75,-30,5,0,0,0,0,
17100      -308,-5,30,-75,100,233,30,-5,0,0,0,0,
17200      -154,1,-6,15,-20,15,148,1,0,0,0,0,
17300      -924,-1,6,-15,20,-15,6,923,0,0,0,0,
17400      -0,0,0,0,0,0,0,0,0,0,0,0,
17500      -0,0,0,0,0,0,0,0,0,0,0,0,
17600      -0,0,0,0,0,0,0,0,0,0,0,0,
17700      -0,0,0,0,0,0,0,0,0,0,0,0,
17800      -429,425,18,-27,8,15,-6,-13,12,-3,0,0,
17900      -1716,72,1385,522,-213,-220,123,186,-187,48,0,0,
18000      -858,-54,261,400,291,60,-101,-66,93,-26,0,0,
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18100       -1716,32,-213,582,905,540,-27,-202,123,-24,0,0,
18200       -429,15,-55,30,135,179,135,30,-55,15,0,0,
18300       -1716,-24,123,-202,-27,540,905,582,-213,32,0,0,
18400       -858,-26,93,-66,-101,60,291,400,261,-54,0,0,
18500       -1716,48,-187,186,123,-220,-213,522,1385,72,0,0,
18600       -429,-3,12,-13,-6,15,8,-27,18,425,0,0,
18700       -0,0,0,0,0,0,0,0,0,0,0,0,
18800       -0,0,0,0,0,0,0,0,0,0,0,0,
18900       -572,557,54,-51,-16,24,24,-4,-24,-9,26,-9,
19000       -286,27,184,111,6,-44,-30,12,34,9,-36,13,
19100       -1716,-153,666,719,456,156,-40,-96,-48,29,54,-27,
19200       -143,-4,3,38,57,48,20,-8,-18,-4,17,-6,
19300       -143,6,-22,13,48,57,40,12,-8,-8,6,-1,
19400       -429,18,-45,-10,60,120,143,120,60,-10,-45,18,
19500       -143,-1,6,-8,-8,12,40,57,48,13,-22,6,
19600       -143,-6,17,-4,-18,-8,20,48,57,38,3,-4,
19700       -1716,-27,54,29,-48,-96,-40,156,456,719,666,-153,
19800       -286,13,-36,9,34,12,-30,-44,6,111,184,27,
19900       -572,-9,26,-9,-24,-4,24,24,-16,-51,54,557/
20000        DIMENSION PROC(10),TITLE(80)
20100        READ(4,50)TITLE
20200        WRITE(6,60)TITLE
20300     50 FORMAT(80A1)
20400     60 FORMAT(1X,80A1)
20500     10 FORMAT(A4)
20600     20 STEP=STEP+1
20700        READ(4,10,END=30) PROC(STEP)
20800        IF(PROC(STEP).EQ.'STOP') GOTO 30
20900        GOTO 40
21000     40 IF(PROC(STEP).EQ.'READ') CALL READIN
21100        IF(PROC(STEP).EQ.'FIT') CALL FIT
21200        IF(PROC(STEP).EQ.'PRT1') CALL PRINT1
21300        IF(PROC(STEP).EQ.'SEAL')CALL SEAL
21350        IF(PROC(STEP).EQ.'CRSS')CALL CROSS
21400        GOTO 20
21500     30 CLOSE(6,DISP=CRUNCH)
21600        END
21700        SUBROUTINE READIN
21800        COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
21900       &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
22000       &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
22100        READ(4,)OBS,INTRVL,SP,(CLASS(J),J=1,SP)
22200        IF(SP.EQ.-1.0)READ(5,)(DATA(OBSN,1,1),OBSN=1,OBS)
22300        IF(SP.EQ.-1.0)GOTO 2
22400        DO 1 OBSN=1,OBS
22500        DO 1 SPN=1,SP
22600        READ(5,) (DATA(OBSN,SPN,J),J=1,CLASS(SPN))
22700      1 CONTINUE
22800      2 CALL TOTAL
22900        RETURN
23000        END
23100        SUBROUTINE FIT
23200        COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
23300       &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
23400       &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
23500        DIMENSION FITSP(20),FITCLS(20,32)
23600        READ(4,)(FITSP(I),I=1,SP)
23700        READ(4,)((FITCLS(I,J),J=1,CLASS(I)),I=1,SP)
23800        READ(4,)POWER,RANGE
23900        WRITE(6,3) POWER,RANGE
24000      3 FORMAT(3X,'POWER=',I1,';',' RANGE=',I2//)
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24100        POWER=POWER-1
24200        DO 1 SPN=1,SP
24300        IF(SPSUM(SPN).EQ.0.0)GOTO 1
24400        IF(FITSP(SPN).EQ.0.0)GOTO 1
24500        FITCLS(SPN,CLASS(SPN)+1)=1.0
24600        DO 2  CLASSN=1,CLASS(SPN)+1
24700        IF(FITCLS(SPN,CLASSN).EQ.0.0) GOTO 2
24800        CALL SMOOTH
24900        IF(CSUM(SPN,CLASSN).EQ.0.0) GOTO 2
25000        CALL RESIDL
25100      2 CONTINUE
25200      1 CONTINUE
25300        RETURN
25400        END
25500        SUBROUTINE SMOOTH
25600        COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
25700       &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
25800       &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
25900        DO 1 OBSN=1,OBS
26000        CSUM(SPN,CLASSN)=CSUM(SPN,CLASSN)+DATA(OBSN,SPN,CLASSN)
26100        SERIES(OBSN)=DATA(OBSN,SPN,CLASSN)
26200      1 CONTINUE
26300        IF(CSUM(SPN,CLASSN).EQ.0.0)RETURN
26400 C      FIND MOVING AVERAGE OF FIRST & LAST (RANGE-1)/2 POINTS
26500 C      FIRST END POINTS:
26600        DO 2 OBSN=1,(RANGE-1)/2
26700        DO 3 POINT=1,RANGE
26800        SUM=SUM+SERIES(POINT)*WEIGHT(POINT,OBSN,(RANGE-5)/2+1,POWER)
26900      3 CONTINUE
27000        TREND(OBSN,SPN,CLASSN)=SUM/WEIGHT(0,OBSN,(RANGE-5)/2+1,POWER)
27100        SUM=0.0
27200      2 CONTINUE
27300 C      TREND FITTED FOR FIRST END POINTS
27400 C      NOW LAST END POINTS:
27500        DO 4 OBSN=1,(RANGE-1)/2
27600        OBSNN=(RANGE-1)/2-OBSN+1
27700        DO 5 POINT=1,RANGE
27800        POYNT=RANGE-POINT+1
27900        SUM=SUM+SERIES(OBS-RANGE+POINT)*WEIGHT(POYNT,OBSNN,(RANGE-
28000       &5)/2+1,POWER)
28100      5 CONTINUE
28200        TREND(OBS-OBSNN+1,SPN,CLASSN)=SUM/WEIGHT(0,OBSNN,
28300       &(RANGE-5)/2+1,POWER)
28400        SUM=0.0
28500      4 CONTINUE
28600 C      TREND FITTED FOR LAST END POINTS
28700 C      NOW INTERMEDIATE POINTS:
28800        DO 6 OBSN=(RANGE-1)/2+1,OBS-(RANGE-1)/2
28900        DO 7 POINT=1,RANGE
29000        SUM=SUM+SERIES(OBSN-(RANGE-1)/2-1+POINT)*WEIGHT(POINT,(RANGE-1)/2
29100       &+1,(RANGE-5)/2+1,POWER)
29200      7 CONTINUE
29300        TREND(OBSN,SPN,CLASSN)=SUM/WEIGHT(0,(RANGE-1)/2+1,(RANGE-5)/2+1,
29400       &POWER)
29500        SUM=0.0
29600      6 CONTINUE
29700 C      TREND NOW FITTED TO ALL POINTS
29800        RETURN
29900        END
30000        SUBROUTINE RESIDL
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30100       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
30200      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
30300      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
30400       DO 1 OBSN=1,OBS
30500     1 RSDL(OBSN,SPN,CLASSN)=DATA(OBSN,SPN,CLASSN)-TREND(OBSN,SPN,CLASSN)
30600       RETURN
30700       END
30800       SUBROUTINE TOTAL
30900       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
31000      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
31100      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
31200       DIMENSION TOTL(50,20)
31300       DO 1 OBSN=1,OBS
31400       DO 1 SPN=1,SP
31500       DO 1 CLASSN=1,CLASS(SPN)
31600     1 TOTL(OBSN,SPN)=TOTL(OBSN,SPN)+DATA(OBSN,SPN,CLASSN)
31700       DO 2 OBSN=1,OBS
31800       DO 2 SPN=1,SP
31900     2 DATA(OBSN,SPN,CLASS(SPN)+1)=TOTL(OBSN,SPN)
32000 C     TOTALS STORED IN LAST+1 CLASS OF EACH SPECIES
32100       DO 3 SPN=1,SP
32200       DO 3 OBSN=1,OBS
32300     3 SPSUM(SPN)=SPSUM(SPN)+TOTL(OBSN,SPN)
32400       RETURN
32500       END
32600       SUBROUTINE PRINT1
32700       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
32800      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
32900      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
33000       DIMENSION PRTSP(20),PRTCLS(20,32)
33100       READ(4,/) (PRTSP(SPN),SPN=1,SP)
33200       READ(4,/) ((PRTCLS(I,J),J=1,CLASS(I)),I=1,SP)
33300       WRITE(6,1)
33400     1 FORMAT(33X,'LISTING OF OBSERVED,FITTED AND RESIDUAL VALUES'/33X,
33500      -46('*')/)
33600       DO 2 SPN=1,SP
33700       IF(SPSUM(SPN).EQ.0.0) GOTO 2
33800       IF(PRTSP(SPN).EQ.0.0) GOTO 2
33900       PRTCLS(SPN,CLASS(SPN)+1)=1.0
34000       WRITE(6,4) SPN
34100     4 FORMAT(1X,'SPECIES',1X,I3)
34200       DO 3 CLASSN=1,CLASS(SPN)+1
34300       IF(CSUM(SPN,CLASSN).EQ.0.0) GOTO 3
34400       IF(PRTCLS(SPN,CLASSN).EQ.0.0) GOTO 3
34500       IF(CLASSN.LT.CLASS(SPN)+1) GOTO 10
34600       WRITE(6,12)
34700    12 FORMAT(12X,'TOTAL')
34800       GOTO 11
34900    10 WRITE(6,5) CLASSN
35000     5 FORMAT(12X,'CLASS',1X,I3)
35100    11 WRITE(6,6) (OBSN*INTRVL,OBSN=1,OBS)
35200     6 FORMAT(21X,'POINT',1X,15I7/27X,15I7/27X,15I7/,5I7/)
35300       WRITE(6,7)(DATA(OBSN,SPN,CLASSN),OBSN=1,OBS)
35400     7 FORMAT(21X,'OBS',3X,15F7.2/27X,15F7.2/27X,15F7.2/27X,5F7.2/)
35500       WRITE(6,8) (TREND(OBSN,SPN,CLASSN),OBSN=1,OBS)
35600     8 FORMAT(21X,'FIT',3X,15F7.2/27X,15F7.2/27X,15F7.2/27X,5F7.2/)
35700       WRITE(6,9) (RSDL(OBSN,SPN,CLASSN),OBSN=1,OBS)
35800     9 FORMAT(21X,'RESID',1X,15F7.2/27X,15F7.2/27X,15F7.2/27X,5F7.2/)
35900     3 CONTINUE
36000     2 CONTINUE
36100       RETURN
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36200       END
36300       SUBROUTINE SEAL
36400       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
36500      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
36600      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
36700       READ(4,/)LAG
36800       READ(4,/)(CORL(SPN),SPN=1,SP)
36900       CALL SERCOR
37000       CALL PRINT2
37100       RETURN
37200       END
37300       SUBROUTINE SERCOR
37400       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
37500      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
37600      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
37700       DO 1 SPN=1,SP
37800       IF(SPSUM(SPN).EQ.0.0) GOTO 1
37900       DO 2 CLASSN=1,CLASS(SPN)+1
38000       IF(CSUM(SPN,CLASSN).EQ.0.0) GOTO 2
38100       DO 4 LAGN=1,LAG
38200       DO 5 OBSN=1,OBS-LAGN
38300       TERM1=TERM1+RSDL(OBSN,SPN,CLASSN)
38400     5 TERM2=TERM2+RSDL(OBSN+LAGN,SPN,CLASSN)
38500       DO 6 OBSN=1,OBS-LAGN
38600       TOP=TOP+(RSDL(OBSN,SPN,CLASSN)-TERM1/(OBS-LAGN))*
38700      &(RSDL(OBSN+LAGN,SPN,CLASSN)-TERM2/(OBS-LAGN))
38800     6 TOP=TOP/(OBS-LAGN)
38900       DO 7 OBSN=1,OBS-LAGN
39000       BOT1=BOT1+(RSDL(OBSN,SPN,CLASSN)-TERM1/(OBS-LAGN))**2
39100     7 BOT2=BOT2+(RSDL(OBSN+LAGN,SPN,CLASSN)-TERM2/(OBS-LAGN))**2
39200       BOT=BOT1*BOT2/(OBS-1.0)/(OBS-LAGN)
39300       BOT=SQRT(BOT)
39400       IF(BOT.EQ.0.0) R(SPN,CLASSN,LAGN)=999
39500       IF(BOT.EQ.0.0) GOTO 9
39600       R(SPN,CLASSN,LAGN)=TOP/BOT
39700     9 TERM1=0.0;TERM2=0.0;TOP=0.0
39800       BOT1=0.0;BOT2=0.0;BOT=0.0
39900     4 CONTINUE
40000     2 CONTINUE
40100     1 CONTINUE
40200       RETURN
40300       END
40400       SUBROUTINE PRINT2
40500       COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
40600      &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
40700      &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
40800       WRITE(6,1)
40900     1 FORMAT(//50X,'SERIAL CORRELATION COEFFICIENTS'/50X,31('*')//)
41000       WRITE(6,8)(I,I=1,LAG)
41100     8 FORMAT(14X,'LAG',7X,12(1X,I7))
41200       DO 2 SPN=1,SP
41300       IF(SPSUM(SPN).EQ.0.0) GOTO 2
41400       WRITE(6,3)SPN
41500     3 FORMAT(//10X,'SPECIES',1X,I2/)
41600       IF(CORL(SPN).EQ.0.0)GOTO 4
41700       DO 5 CLASSN=1,CLASS(SPN)
41800       IF(CSUM(SPN,CLASSN).EQ.0.0) GOTO 5
41900       WRITE(6,6)CLASSN,(R(SPN,CLASSN,LAGN),LAGN=1,LAG)
42000     6 FORMAT(12X,'CLASS',1X,I2,4X,12(1X,F7.4))
42100     5 CONTINUE
42200     4 WRITE(6,7)(R(SPN,CLASS(SPN)+1,LAGN),LAGN=1,LAG)
```

```
42300      7 FORMAT(15X,'TOTAL',4X,12(1X,F7.4))
42400      2 CONTINUE
             RETURN
42500
42600
             END
42700
             SUBROUTINE CROSS
42710
             COMMON WEIGHT(0:11,11,4,4),DATA(36,16,32),TREND(36,16,32),
42720       &RSDL(36,16,32),SERIES(50),CLASS(20),CSUM(16,32),SPSUM(16),
42730       &RANGE,POWER,SP,OBS,INTRVL,SPN,CLASSN,LAG,CORL(20),R(16,32,12)
42750
             DIMENSION CCV(16,6,16,6,0:6),CCL(16,6,16,6,0:6)
42775
             READ(4,/)LAG
42800
             DO 1 K=0,LAG
42900
             DO 1 SPN=1,SP
43000
             DO 1 CLASSN=1,CLASS(SPN)+1
43100 C      CALCULATE MEAN FOR LEADING SERIES
43200
             DO 2 H=1,OBS-K
43300      2 MEAN1=MEAN1+RSDL(H+K,SPN,CLASSN)
43400
             MEAN1=MEAN1/(OBS-K)
43500
             DO 3 SPNN=1,SP
43600
             DO 3 KLASSN=1,CLASS(SPNN)+1
43700
             IF(SPNN.EQ.SPN.AND.CLASSN.EQ.KLASSN) GOTO 3
43800 C      CALCULATE MEAN FOR TRAILING SERIES
43900
             DO 4 H=1,OBS-K
44000      4 MEAN2=MEAN2+RSDL(H,SPNN,KLASSN)
44100
             MEAN2=MEAN2/(OBS-K)
44200 C       CALCULATE CROSS-COVARRIANCE BETWEEN THE TWO SERIES
44300
             DO 5 H=1,OBS-K
44400
             CCV(SPN,CLASSN,SPNN,KLASSN,K)=CCV(SPN,CLASSN,SPNN,KLASSN,K)+
44500       $(RSDL(H+K,SPN,CLASSN)-MEAN1)*(RSDL(H,SPNN,KLASSN)-MEAN2)
44600      5 CONTINUE
44700
             CCV(SPN,CLASSN,SPNN,KLASSN,K)=CCV(SPN,CLASSN,SPNN,KLASSN,K)
44900 C       CALCULATE DENOMINATOR TERMS FOR CROSS-CORRELATION
45000
             DO 6 H=1,OBS-K
45100
             TERM1=TERM1+(RSDL(H+K,SPN,CLASSN)-MEAN1)**2
45200      6 TERM2=TERM2+(RSDL(H,SPNN,KLASSN)-MEAN2)**2
45250
             IF(TERM1.EQ.0.0.OR.TERM2.EQ.0.0) GOTO 18
45300
             DENOM=SQRT(TERM1*TERM2)
45400 C       HENCE CROSS-CORRELATION CCL
45500
             CCL(SPN,CLASSN,SPNN,KLASSN,K)=CCV(SPN,CLASSN,SPNN,KLASSN,K)/DENOM
45600 C       SET VARIABLES TO ZERO
45650     18 CONTINUE
45700
             MEAN2=0.0;TERM1=0.0;TERM2=0.0
45800      3 CONTINUE
45900
             MEAN1=0.0
46000      1 CONTINUE
46100 C       LEFT WITH CCL FOR SP,CLASS VS SP,CLASS AT LAG WHERE TOTALS
46200 C      $ARE IN LAST+1 CLASS OF EACH SPECIES
46300 C       PRINT RESULTS
46400
             DO 7 SPN=1,SP
46500
             DO 7 CLASSN=1,CLASS(SPN)+1
46600
             IF(CLASSN.EQ.CLASS(SPN)+1) GOTO 9
46700
             WRITE(6,8)SPN,CLASSN
46800      8 FORMAT(1X,'LEADING SERIES:',1X,'SPECIES',1X,I3,1X,'CLASS',1X,I3)
46900
             GOTO 10
47000      9 WRITE(6,11)SPN
47100     11 FORMAT(1X,'LEADING SERIES:',1X,'SPECIES',1X,I3,1X,'TOTAL')
47200     10 CONTINUE
47300
             WRITE(6,13)
47400     13 FORMAT(1X,'TRAILING SERIES:  SPECIES  CLASS')
47500
             DO 14 SPNN=1,SP
47600
             DO 14 KLASSN=1,CLASS(SPNN)+1
47650
             IF(KLASSN.EQ.CLASS(SPNN)+1)GOTO 30
```

```
48500       WRITE(6,20)SPNN,KLASSN,(CCL(SPN,CLASSN,SPNN,KLASSN,K),K=0,LAG)
48600    20 FORMAT(19X,I3,5X,I3,8X,6(F7.4,1X))
48650       GOTO 31
48675    30 WRITE(6,21)SPNN,(CCL(SPN,CLASSN,SPNN,KLASSN,K),K=0,LAG)
48680    31 CONTINUE
48690    21 FORMAT(19X,I3,3X,'TOTAL',8X,6(F7.4,1X))
48700    14 CONTINUE
48800     7 CONTINUE
48900       RETURN
49000       END
```

ACORN jobs

ACORN is the most complicated, and also the most flexible, of the analysis programs. A full description of its capabilities and the methods for setting up a job have been included as ACORN/HELP, a file stored on the magnetic tape lodged with this thesis in the University of Tasmania Library. Basically, the job deck requires the following cards (comments in *italics*):

1. GRID (*read data parameter card*)
2. no. grid rows, no. grid columns, no. species, no. classes in each species listed from first to last
3. LINK (*weighting matrix parameter card*)
4. code no. for weighting matrix (1=rook, 2=bishop, 3=queen), distance between neighbours
5. MORC (*Moran statistic parameter card*)
6. analysis code for each species listed from first to last (0= analysis for species total only, 1= analysis for total and classes, 2= no analysis for that species)
7. ACCU (*accumulation parameter card*)
8. accumulation analysis code for each species listed from first to last (0= no accumulation analysis, 1= analysis calculated for successive accumulation of classes from smallest to largest)
9. CORM (*correlogram parameter card*)
10. correlogram code for each species listed from first to last (0= no correlogram calculated, 1= correlogram calculated for total only, 2= correlogram calculated for total and classes)
11. STOP

Example of job for planar autocorrelation analysis

```
?BEGIN JOB JACORN/200381/100M; job title
QUEUE=33; priority queue
RUN OBJECT/ACORN;
FILE FILE4=GRID/200381/100M; data file
FILE 5(KIND=READER); job file type
DATA job data cards follow
GRID
```

```
8,8,16,24,5,13,31,11,11,6,3,3,7,4,16,13,9,1,11
LINK
3,1
MORC
1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
ACCU
0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
CORM
2,2,2,2,2,2,2,2,2,2,2,2,2,2,2,2
STOP
? end job data cards
?END JOB
```

```
LIST ACORN


100 $RESET FREE
200 $CHARS=4
300 C       ************************************************
400 C       ************************************************
500 C       PROGRAM ACORN: PACKAGE FOR CALCULATING MORAN
600 C       STATISTICS FOR ABUNDANCE DATA STORED IN A GRID
700 C       MORAN STATISTICS CAN BE CALCULATED FOR EACH CLASS
800 C       AND/OR TOTAL FOR EACH SPECIES.ACCUMULATION OF CLASSES
900 C       FOR EACH SPECIES WITH MORAN STATISTIC CALCULATED
1000 C       AT EACH STEP IS OPTIONAL.
1100 C       ************************************************
1200 C       ************************************************
1300 FILE  4(KIND=DISK,FILETYPE=8)
1400 FILE  5(KIND=READER,TITLE='COMMANDS')
1500 FILE  6(KIND=DISK)
1600       DIMENSION PROC(10)
1700    .  COMMON CS2(40),SUM2(40),SUM4(40),CHOME2(40),ZERO(20,40),
1800       $CHOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
1900       $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
2000       $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
2100       $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
2200       $TZO(20),CODE,SD(20,40),THEAN(20),TSD(20),CMEAN(20,40),SUM1(20,40)
2300 C
2400 C
2500     10  FORMAT(A4)
2600     20  STEP=STEP+1
2700         READ(5,10,END=30)PROC(STEP)
2800         IF(PROC(STEP).EQ.'STOP') GO TO 30
2900         GO TO 40
3000     40  IF(PROC(STEP).EQ.'GRID') CALL GRID
3100         IF(PROC(STEP).EQ.'MORC') CALL MORCAL
3200 C        PROCEDURE LINK FITS IN HERE IN DRIVER
3300         IF(PROC(STEP).EQ.'ACCU') CALL ACCUME
3400         IF(PROC(STEP).EQ.'CORR') CALL CORAN
3500         GO TO 20
3600     30  CLOSE(6,DISP=CRUNCH)
3700         END
3800 C        ************************************************
3900        SUBROUTINE FILE
4000 C        ************************************************
4100        COMMON CS2(40),SUM2(40),SUM4(40),CHOME2(40),ZERO(20,40),
4200       $CHOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
4300       $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
4400       $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
4500       $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
4600       $TZO(20),CODE,SD(20,40),THEAN(20),TSD(20),CMEAN(20,40),SUM1(20,40)
4700 C        SUBROUTINE FILE CALCULATES WORKING VARIABLES
4800 C        FOR EACH CLASS AND ALSO TOTAL OF EACH SPECIES.
4900         CALL LINK
5000         DO 216 SP=1,SPN
5100 C        READ DATA FOR SPECIES
5200 C
5300         READ(4,103)(SNAME(SP,I),I=1,80)
5400    103  FORMAT(80A1)
5500         DO 201 SSALC=1,CLASS(SP)
5600         DO 201 WOR=1,ROW
5700         READ(4,/)(DATA(SSALC,WOR,LOC),LOC=1,COL)
5800    201  CONTINUE
```

```
5900 C        CONVERT GRID INTO VECTOR
6000 C
6100          DO 202 SSALC=1,CLASS(SP)
6200          DO 202 WOR=1,ROW
6300          DO 202 LOC=1,COL
6400          VECT(SSALC,(WOR-1)*COL+LOC)=DATA(SSALC,WOR,LOC)
6500    202   CONTINUE
6600 C        CALCULATE MEAN AND MOMENTS OF EACH CLASS
6700 C
6800          DO 203 SSALC=1,CLASS(SP)
6900          DO 203 CELL=1,CELLN
7000          CS2(SSALC)=CS2(SSALC)+VECT(SSALC,CELL)**2
7100          SUM(SP,SSALC)=SUM(SP,SSALC)+VECT(SSALC,CELL)
7200    203   CONTINUE
7300          DO 204 SSALC=1,CLASS(SP)
7400          IF(SUM(SP,SSALC).EQ.0.0) ZERO(SP,SSALC)=1.0
7500          CMEAN(SP,SSALC)=SUM(SP,SSALC)/CELLN
7600          SD(SP,SSALC)=SQRT((CS2(SSALC)-(SUM(SP,SSALC)**2)/
7700              $CELLN)/(CELLN-1.0))
7800          DO 205 CELL=1,CELLN
7900          SUM2(SSALC)=SUM2(SSALC)+(VECT(SSALC,CELL)-CMEAN(SP,SSALC))**2
8000          SUM4(SSALC)=SUM4(SSALC)+(VECT(SSALC,CELL)-CMEAN(SP,SSALC))**4
8100    205   CONTINUE
8200          CMOME2(SSALC)=SUM2(SSALC)/CELLN
8300          CMOME4(SSALC)=SUM4(SSALC)/CELLN
8400    204   CONTINUE
8500 C        CALCULATE B SQUARES
8600 C
8700          DO 206 SSALC=1,CLASS(SP)
8800          IF(ZERO(SP,SSALC).EQ.1.0) GOTO 206
8900          BTWO(SP,SSALC)=CMOME4(SSALC)/CMOME2(SSALC)**2
9000    206   CONTINUE
9100 C        CALCULATE Z VALUES
9200 C
9300          DO 207 SSALC=1,CLASS(SP)
9400          DO 207 CELL=1,CELLN
9500          Z(SSALC,CELL)=VECT(SSALC,CELL)-CMEAN(SP,SSALC)
9600    207   CONTINUE
9700 C        CALCULATE SUM OF Z-PRODUCT
9800 C
9900          DO 217 SSALC=1,CLASS(SP)
10000         DO 217 CELL1=1,CELLN
10100         DO 217 CELL2=1,CELLN
10200         ROT=Z(SSALC,CELL1)*Z(SSALC,CELL2)*WEIGHT(CELL1,CELL2)
10300         SUMZP(SP,SSALC)=SUMZP(SP,SSALC)+ROT
10400   217   CONTINUE
10500 C        CALCULATE SUM OF Z SQUARES
10600 C
10700         DO 208 SSALC=1,CLASS(SP)
10800         DO 208 CELL=1,CELLN
10900         SUMZ2(SP,SSALC)=SUMZ2(SP,SSALC)+Z(SSALC,CELL)**2
11000   208   CONTINUE
11100 C        CALCULATE TOTAL OF CLASSES
11200 C
11300         DO 209 CELL=1,CELLN
11400         DO 209 SSALC=1,CLASS(SP)
11500         TOTAL(CELL)=TOTAL(CELL)+VECT(SSALC,CELL)
11600   209   CONTINUE
11700 C        CALCULATE MEAN OF TOTAL
11800 C
11900         DO 210 CELL=1,CELLN
```

```
12000          TMEAN(SP)=TMEAN(SP)+TOTAL(CELL)
12100          TS2=TS2+TOTAL(CELL)**2
12200    210   CONTINUE
12300          IF(TMEAN(SP).EQ.0.0) TZ0(SP)=1.0
12400          TSD(SP)=SQRT((TS2-(TMEAN(SP)**2)/CELLN)/(CELLN-1.0))
12500          TMEAN(SP)=TMEAN(SP)/CELLN
12600 C         CALCULATE 2ND AND 4TH MOMENTS OF TOTAL
12700 C
12800          DO 211 CELL=1,CELLN
12900          TSUM2=TSUM2+(TOTAL(CELL)-TMEAN(SP))**2
13000          TSUM4=TSUM4+(TOTAL(CELL)-TMEAN(SP))**4
13100    211   CONTINUE
13200          TMOME2=TSUM2/CELLN
13300          TMOME4=TSUM4/CELLN
13400 C         CALCULATE B SQUARED FOR TOTAL
13500 C
13600          IF(TZ0(SP).EQ.1.0) GOTO213
13700          TBTWO(SP)=TMOME4/TMOME2**2
13800 C         CALCULATE Z VALUES FOR TOTAL
13900 C
14000          DO 212 CELL=1,CELLN
14100          TZ(CELL)=TOTAL(CELL)-TMEAN(SP)
14200    212   CONTINUE
14300 C         CALCULATE SUM OF Z-PRODUCT
14400 C
14500          DO 218 CELL1=1,CELLN
14600          DO 218 CELL2=1,CELLN
14700          TSUMZP(SP)=TSUMZP(SP)+TZ(CELL1)*TZ(CELL2)*WEIGHT(CELL1,CELL2)
14800    218   CONTINUE
14900 C         CALCULATE SUM OF Z SQUARES
15000 C
15100          DO 213 CELL=1,CELLN
15200          TSUMZ2(SP)=TSUMZ2(SP)+TZ(CELL)**2
15300    213   CONTINUE
15400 C         SET VARIABLES TO ZERO
15500 C
15600          DO 214 SSALC=1,CLASS(SP)
15700          SUM1(SP,SSALC)=0.0
15800          SUM2(SSALC)=0.0
15900          SUM4(SSALC)=0.0
16000          CS2(SSALC)=0.0
16100    214   CONTINUE
16200          DO 215 CELL=1,CELLN
16300          TOTAL(CELL)=0.0
16400    215   CONTINUE
16500          TS2=0.0;TSUM2=0.0;TSUM4=0.0
16600 C         RETURN AND REPEAT FOR NEXT SPECIES
16700 C
16800    216   CONTINUE
16900 C         LEAVE SUBROUTINE FILE PASSING BTWO(SP,CLASS),SUMZ2(SP,CLASS),
17000 C        TBTWO(SP),TSUMZ2(SP),TSUMZP(SP) AND SUMZP(SP,CLASS)
17100 C
17200          RETURN
17300          END
17400 C         ***************************************************
17500          SUBROUTINE MORCAL
17600 C         ***************************************************
17700          COMMON CS2(40),SUM2(40),SUM4(40),CMOME2(40),ZERO(20,40),
17800         $CMOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
17900         $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
18000         $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
```

```
      $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
      $TZO(20),CODE,SO(20,40),TMEAN(20),TSO(20),CMEAN(20,40),SUM(20,40)
C       'MORCAL' READS IN THE REQUIRMENTS FOR TOTALS AND/OR
C       CLASS FOR CALCULATION OF THE MORAN STATISTIC ,AND DRIVES THE '
C       'MORAN' SUBROUTINE.
C
C        READ REQUIREMENTS,0-TOTALS ONLY
C                          1-CLASSES AND TOTALS ANALYSED.
C                          2-NO ANALYSIS FOR THAT SPECIES
      READ(5,301)(WANT(I),I=1,SPN)
  301 FORMAT(20F1.0)
      CALL FILE
      IF(CODE.EQ.3.0) WRITE(6,11)V
       IF(CODE.EQ.1.0) WRITE(6,12)V
      IF(CODE.EQ.2.0)WRITE(6,13)V
   11 FORMAT(1X,'QUEEN WEIGHTING MATRIX WITH DISTANCE',1X,I3//)
   12 FORMAT(1X,'ROOK WEIGHTING MATRIX WITH DISTANCE',1X,I3//)
   13 FORMAT(1X,'BISHOP WEIGHTING MATRIX WITH DISTANCE',1X,I3//)
      WRITE(6,302)
  302 FORMAT(//55X,'MORAN STATISTICS'/55X,16('*')//)
      WRITE(6,305)
  305 FORMAT(4X,'SPECIES',1X,'CLASS',3X,'MEAN',5X,'SD',4X,
     $'E(I)',8X,'I',5X,
     $'SD(I)(NORM)',3X,'SD(I)(RAND)',3X,'ST.NORM.DEV.(NORM)',
     $3X,'ST.NORM.DEV.(RAND)')
      WRITE(6,303)
  303 FORMAT(122('-'))
      DO 401 SP=1,SPN
      IF(TZO(SP).EQ.1.0) GOTO 401
      IF(WANT(SP).EQ.2.0) GOTO 401
      WRITE(6,306)(SNAME(SP,I),I=1,80)
  306 FORMAT(5X,80A1)
      IF(WANT(SP).EQ.0.0) GO TO 403
      DO 402 SSALC=1,CLASS(SP)
      IF(ZERO(SP,SSALC).EQ.1.0) GOTO 402
      B2=BTWO(SP,SSALC)
      ZP=SUMZP(SP,SSALC)
      Z2=SUMZ2(SP,SSALC)
      CALL MORAN
      WRITE(6,307)SSALC,CMEAN(SP,SSALC),SD(SP,SSALC),EXPI,AIS,
     $SQRT(ENI2),SQRT(ERI2),DEVN,DEVR
  307 FORMAT(13X,I3,2X,F7.2,1X,F7.2,1X,F7.4,3X,F7.4,3X,F9.4,5X,F9.4,
     $8X,F9.4,11X,F9.4)
  402 CONTINUE
  403 B2=TBTWO(SP)
      ZP=TSUMZP(SP)
      Z2=TSUMZ2(SP)
      CALL MORAN
      WRITE(6,308)TMEAN(SP),TSD(SP),EXPI,AIS,SQRT(ENI2),
     $SQRT(ERI2),DEVN,DEVR
  308 FORMAT(11X,'TOTAL',2X,F7.2,1X,F7.2,1X,F7.4,3X,F7.4,3X,F9.4,
     $5X,F9.4,8X,F9.4,11X,F9.4)
      WRITE(6,303)
  401 CONTINUE
      RETURN
      END
C      ****************************************************
      SUBROUTINE ROOK
C      ****************************************************
      DIMENSION SLINK(100)
      COMMON CS2(40),SUM2(40),SUM4(40),CMOME2(40),ZERO(20,40),
```

```
24200        $CNOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
24300        $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
24400        $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
24500        $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
24600        $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
24700         REAL ANUME,CELLN
24800 C       SET WEIGHT MATRIX TO ZERO
24900         DO 770 I=1,CELLN
25000         DO 770 J=1,CELLN
25100    770  WEIGHT(I,J)=0.0
25200 C
25300         COL1=1.0
25400         DO 700 CELL=1,CELLN
25500         IF(CELL.GT.V*COL) WEIGHT(CELL,CELL-V*COL)=1.0
25600         IF(CELL.LT.CELLN-V*COL+1.0) WEIGHT(CELL,CELL+V*COL)=1.0
25700         IF(COL1+V-1.0.LT.CELL) WEIGHT(CELL,CELL-V)=1.0
25800         IF(CELL.LT.COL1+COL-V) WEIGHT(CELL,CELL+V)=1.0
25900         IF(AMOD(CELL,COL).EQ.0.0) COL1=COL1+COL
26000    700  CONTINUE
26100 C        CALCULATE LINKAGES
26200 C
26300         DO 710 I=1,CELLN
26400         DO 710 J=1,CELLN
26500         SLINK(I)=SLINK(I)+WEIGHT(I,J)
26600    710  CONTINUE
26700 C        CALCULATE A
26800 C
26900         DO 720 I=1,CELLN
27000         SL=SL+SLINK(I)
27100    720  CONTINUE
27200         A=0.5*SL
27300         SL=0.
27400 C        CALCULATE D
27500 C
27600         DO 730 I=1,CELLN
27700         SL=SL+SLINK(I)*(SLINK(I)-1.0)
27800    730  CONTINUE
27900         D=0.5*SL
28000         SL=0.
28100 C        CALCULATE W,S1,S2
28200 C       SET SLINK TO ZERO
28300         DO 760 I=1,CELLN
28400    760  SLINK(I)=0.0
28500         W=2.*A
28600         S1=4.*A
28700         S2=8.*(A+D)
28800    750  RETURN
28900         END
29000 C        ***************************************************
29100         SUBROUTINE MORAN
29200 C        ***************************************************
29300         COMMON CS2(40),SUM2(40),SUM4(40),CMOME2(40),ZERO(20,40),
29400        $CMOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
29500        $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
29600        $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
29700        $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
29800        $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
29900         ANUME=CELLN*ZP
30000         AIS=ANUME/(W*Z2)
30100         EXPI=1/(-(CELLN-1.0))
30200 C        CALCULATE EXPECTED I SQUARED FOR RANDOMISATION
```

```
30300 C
30400
30500         TRM11=CELLN*((CELLN**2-3.*CELLN+3.)*S1-CELLN*S2+3.*W*W)
30600         TRM12=B2*((CELLN**2-CELLN)*S1-2.*CELLN*S2+6.*W*W)
30700         DENOM=(CELLN-1.)*(CELLN-2.)*(CELLN-3.)*W*W
30800         ERI2=(TRM11-TRM12)/DENOM
30900 C        CALCULATE EXPECTED I SQUARED FOR NORMALITY
31000 C
31100         ANUME=CELLN*CELLN*S1-CELLN*S2+3.*W*W
31200         DENOM=W*W*(CELLN*CELLN-1.)
31300         ENI2=ANUME/DENOM
31400 C        CALCULATE STANDARD DEVIATE FOR NORMAL AND RANDOM MODELS
31500 C
31600         DEVR=(AIS-EXPI)/SQRT(ERI2)
31700         DEVN=(AIS-EXPI)/SQRT(ENI2)
31800         RETURN
31900         END
32000 C        ************************************************
32100         SUBROUTINE ACCUME
32200 C        ************************************************
32300         DIMENSION ACC(20),VZ(100)
32400         COMMON CS2(40),SUM2(40),SUM4(40),CNUME2(40),ZERO(20,40),
32500        $CNUME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
32600        $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
32700        $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
32800        $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
32900        $TZ0(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
33000 C         'ACCUME' STARTS WITH THE SMALLEST CLASS AND COMBINES
33100 C         WITH NEXT, THAT COMBINATION BEING LATER COMBINED WITH
33200 C         THE NEXT AND SO ON. THE MORAN STATISTIC IS CALCULATED
33300 C         AT EACH STEP.
33400         WRITE(6,513)
33500   513   FORMAT(//43X,'CLASS ACCUMULATION MORAN STATISTICS')
33600         WRITE(6,514)
33700   514   FORMAT(43X,35('*')//)
33800         WRITE(6,510)
33900   510   FORMAT(8X,'CLASSES GROUPED UP TO CLASS',2X,'E(I)',
34000        $8X,'I',5X,'SD(I)(NORM)',3X,'SD(I)(RAND)',3X,
34100        $'ST.NORM.DEV.(NORM)',3X,'ST.NORM.DEV.(RAND)')
34200   511   FORMAT(122('-'))
34300 C         REWIND DATA FILE
34400 C
34500         READ(5,512)(ACC(I),I=1,20)
34600   512   FORMAT(20F1.0)
34700         CALL LINK
34800         REWIND 4
34900   602   SP=SP+1;TRACK=0
35000         WRITE(6,511)
35100 C         READ NAME OF SPECIES
35200 C
35300         READ(4,501,END=614)(SNAME(SP,I),I=1,80)
35400   501   FORMAT(80A1)
35500 C         IF ACCUME NOT NEEDED DUMMY READ DATA
35600 C
35700         IF(ACC(SP).EQ.1.0) GO TO 603
35800         DO 601 SSALC=1,CLASS(SP)
35900         DO 601 WOR=1,ROW
36000         READ(4,/)(DATA(1,WOR,LOC),LOC=1,COL)
36100   601   CONTINUE
36200         GO TO 602
36300 C         IF ACCUME NEEDED START ACCUMULATING
```

```
36400   603  WRITE(6,502)(SNAME(SP,I),I=1,80)
36500   502  FORMAT(5X,'SPECIES',1X,80A1/)
36600        DO 604 WOR=1,ROW
36700        READ(4,/)(DATA(1,WOR,LOC),LOC=1,COL)
36800   604  CONTINUE
36900 C       CONVERT TO VECTOR
37000 C
37100        DO 605 WOR=1,ROW
37200        DO 605 LOC=1,COL
37300        VECT(1,(WOR-1)*COL+LOC)=DATA(1,WOR,LOC)
37400   605  CONTINUE
37500 C       CALCULATE PARAMETERS FOR SUBROUTINE MORAN
37600 C       START WITH MEAN OF THE VECTOR
37700 C
37800   613  SID=0.0
37900        DO 606 CELL=1,CELLN
38000        SID=SID+VECT(1,CELL)
38100   606  CONTINUE
38200        VMEAN=SID/CELLN
38300        IF(VMEAN.EQ.0.0) GOTO 50
38400 C       CALCULATE MOMENTS
38500 C
38600        VSUM2=0.0;VSUM4=0.0
38700        DO 607 CELL=1,CELLN
38800        VSUM2=VSUM2+(VECT(1,CELL)-VMEAN)**2
38900        VSUM4=VSUM4+(VECT(1,CELL)-VMEAN)**4
39000   607  CONTINUE
39100        VMOME2=VSUM2/CELLN
39200        VMOME4=VSUM4/CELLN
39300 C       CALCULATE B SQUARE
39400 C
39500        VBTWO=VMOME4/VMOME2**2
39600 C       CALCULATE Z VALUE
39700 C
39800        DO 608 CELL=1,CELLN
39900        VZ(CELL)=VECT(1,CELL)-VMEAN
40000     608 CONTINUE
40000   608  CONTINUE
40100 C       CALCULATE SUM OF Z-PRODUCT
40200        VSUMZP=0.0
40300        DO 615 CELL1=1,CELLN
40400        DO 615 CELL2=1,CELLN
40500        VSUMZP=VSUMZP+VZ(CELL1)*VZ(CELL2)*WEIGHT(CELL1,CELL2)
40600   615  CONTINUE
40700 C       CALCULATE SUM OF Z SQUARES
40800 C
40900        VSUMZ2=0.0
41000        DO 609 CELL=1,CELLN
41100        VSUMZ2=VSUMZ2+VZ(CELL)**2
41200   609  CONTINUE
41300        ZP=VSUMZP
41400        B2=VBTWO
41500        Z2=VSUMZ2
41600        CALL MORAN
41700        WRITE(6,503)TRACK+1,EXPI,AIS,SQRT(ENI2),SQRT(ERI2),DEVN,DEVR
41800  503   FORMAT(31X,I3,2X,F7.4,3X,F7.4,3X,F9.4,5X,F9.4,8X,F9.4,11X,F9.4)
41900 C       KEEP TRACK OF NUMBER OF CLASSES
42000 C
42100    50  TRACK=TRACK+1
42200 C       IF NUMBER OF CLASSES REACHES END GOTO NEXT SPECIES.
42300 C
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42400          IF(TRACK.EQ.CLASS(SP)) GO TO 602
42500 C         IF NOT ADD ON NEXT CLASS
42600 C
42700          DO 610 WOR=1,ROW
42800          READ(4,/)(DATA(1,WOR,LOC),LOC=1,COL)
42900    610   CONTINUE
43000 C         CONVERT TO VECTOR
43100 C
43200          DO 611 WOR=1,ROW
43300          DO 611 LOC=1,COL
43400          VECT(2,(WOR-1)*COL+LOC)=DATA(1,WOR,LOC)
43500    611   CONTINUE
43600 C         ADD TO EXISTING VECTOR
43700 C
43800          DO 612 CELL=1,CELLN
43900          VECT(1,CELL)=VECT(1,CELL)+VECT(2,CELL)
44000    612   CONTINUE
44100 C         CALCULATE MORAN STATISTIC
44200          GO TO 613
44300    614   RETURN
44400          END
44500 C         ***************************************************
44600          SUBROUTINE BISHOP
44700 C         ***************************************************
44800          DIMENSION SLINK(100)
44900          COMMON CS2(40),SUM2(40),SUM4(40),CHOME2(40),ZERO(20,40),
45000         $CHOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
45100         $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
45200         $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
45300         $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
45400         $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
45500          REAL ANAME,CELLN
45600 C
45700 C         SET WEIGHT MATRIX TO ZERO
45800          DO 770 I=1,CELLN
45900          DO 770 J=1,CELLN
46000    770   WEIGHT(I,J)=0.0
46100 C         DETERMINE WEIGHTING COEFFICIENTS
46200          COL1=COL
46300          DO 1 CELL=1,CELLN
46400          IF(CELL.LE.COL1-V.AND.CELL+V*COL+V.LE.CELLN)
46500         $WEIGHT(CELL,CELL+V*COL+V)=1.0
46600          IF(CELL.LE.COL1-V.AND.CELL-V*COL+V.GE.1.0)
46700         $WEIGHT(CELL,CELL-V*COL+V)=1.0
46800          IF(CELL.GE.COL1-COL+V+1.0.AND.CELL+V*COL-V.LE.CELLN)
46900         $WEIGHT(CELL,CELL+V*COL-V)=1.0
47000          IF(CELL.GE.COL1-COL+V+1.0.AND.CELL-V*COL-V.GE.1.0)
47100         $WEIGHT(CELL,CELL-V*COL-V)=1.0
47200          IF(AMOD(CELL,COL).EQ.0.0) COL1=COL1+COL
47300        1 CONTINUE
47400 C         CALCULATE LINKAGES
47500 C
47600          DO 710 I=1,CELLN
47700          DO 710 J=1,CELLN
47800          SLINK(I)=SLINK(I)+WEIGHT(I,J)
47900    710   CONTINUE
48000 C         CALCULATE A
48100 C
48200          DO 720 I=1,CELLN
48300          SL=SL+SLINK(I)
48400    720   CONTINUE
```

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48500          A=0.5*SL
48600          SL=0.
48700 C         CALCULATE D
48800 C
48900          DO 730 I=1,CELLN
49000          SL=SL+SLINK(I)*(SLINK(I)-1.0)
49100   730    CONTINUE
49200          D=0.5*SL
49300          SL=0.
49400 C         CALCULATE W,S1,S2
49500 C
49600 C        SET SLINK TO ZERO
49700          DO 760 I=1,CELLN
49800   760    SLINK(I)=0.0
49900          W=2.*A
50000          S1=4.*A
50100          S2=8.*(A+D)
50200   750    RETURN
50300          END
50400 C         ***************************************************
50500          SUBROUTINE LINK
50600 C         ***************************************************
50700         COMMON CS2(40),SUM2(40),SUM4(40),CMOME2(40),ZERO(20,40),
50800        $CMOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
50900        $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
51000        $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
51100        $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
51200        $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
51300         READ(5,1)CODE,V
51400     1   FORMAT(/2F1.0)
51500          IF(V.EQ.0.0) V=1.0
51600          IF(CODE.EQ.0.0) CALL QUEEN
51700          IF(CODE.EQ.1.0) CALL ROOK
51800          IF(CODE.EQ.2.0) CALL BISHOP
51900          IF(CODE.EQ.3.0) CALL QUEEN
52000          RETURN
52100          END
52200 C         ***************************************************
52300          SUBROUTINE QUEEN
52400 C         ***************************************************
52500          DIMENSION S2W(100)
52600          COMMON CS2(40),SUM2(40),SUM4(40),CMOME2(40),ZERO(20,40),
52700        $CMOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
52800        $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
52900        $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
53000        $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
53100        $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
53200 C
53300 C      SET WEIGHT MATRIX TO ZERO
53400        DO 770 I=1,CELLN
53500        DO 770 J=1,CELLN
53600   770  WEIGHT(I,J)=0.0
53700 C       DETERMINE WEIGHTING COEFFICIENTS
53800 C       BISHOP'S CASE FIRST
53900        COL1=COL
54000        DO 1 CELL=1,CELLN
54100        IF(CELL.LE.COL1-V.AND.CELL+V*COL+V.LE.CELLN)
54200       $WEIGHT(CELL,CELL+V*COL+V)=1.0/(V*SQRT(2.0))
54300        IF(CELL.LE.COL1-V.AND.CELL-V*COL+V.GE.1.0)
54400       $WEIGHT(CELL,CELL-V*COL+V)=1.0/(V*SQRT(2.0))
54500        IF(CELL.GE.COL1-COL+V+1.0.AND.CELL+V*COL-V.LE.CELLN)
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54600       $WEIGHT(CELL,CELL+V*COL-V)=1.0/(V*SQRT(2.0))
54700        IF(CELL.GE.COL1-COL+V+1.0.AND.CELL-V*COL-V.GE.1.0)
54800       $WEIGHT(CELL,CELL-V*COL-V)=1.0/(V*SQRT(2.0))
54900        IF(AMOD(CELL,COL).EQ.0.0) COL1=COL1+COL
55000      1 CONTINUE
55100 C       NOW ROOK'S CASE
55200        COL1=1.0
55300        DO 700 CELL=1,CELLN
55400        IF(CELL.GT.V*COL) WEIGHT(CELL,CELL-V*COL)=1.0
55500        IF(CELL.LT.CELLN-V*COL+1.0) WEIGHT(CELL,CELL+V*COL)=1.0
55600        IF(COL1+V-1.0.LT.CELL) WEIGHT(CELL,CELL-V)=1.0
55700        IF(CELL.LT.COL1+COL-V) WEIGHT(CELL,CELL+V)=1.0
55800        IF(AMOD(CELL,COL).EQ.0.0) COL1=COL1+COL
55900    700 CONTINUE
56000 C       CALCULATE W & S1 FOR NONBINARY WEIGHTING
56100 C      SET W,S1,S2 AND S2W TO ZERO
56200        W=0.0;S1=0.0;S2=0.0
56300        DO 760 I=1,CELLN
56400    760 S2W(I)=0.0
56500        DO 901 CELL1=1,CELLN
56600        DO 901 CELL2=1,CELLN
56700        W=W+WEIGHT(CELL1,CELL2)
56800    901 S1=S1+(2.*WEIGHT(CELL1,CELL2))**2
56900        S1=S1*0.5
57000 C       CALCULATE S2 FOR NONBINARY WEIGHTING
57100        DO 902 CELL1=1,CELLN
57200        DO 902 CELL2=1,CELLN
57300    902 S2W(CELL1)=S2W(CELL1)+WEIGHT(CELL1,CELL2)
57400        DO 903 CELL=1,CELLN
57500    903 S2=S2+(2.*S2W(CELL))**2
57600        RETURN
57700        END
57800 C       ************************************
57900        SUBROUTINE CGRAM
58000 C       ************************************
58100        DIMENSION GRAM(20),WRK(10),S1RK(10),S2RK(10),CRK(10,20,40),
58200       $WBSH(10),S1BSH(10),S2BSH(10),CBSH(10,20,40),TRK(10,20),TBSH(10,20)
58300        COMMON CS2(40),SUM2(40),SUM4(40),CHOME2(40),ZERO(20,40),
58400       $CHOME4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
58500       $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
58600       $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
58700       $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
58800       $TZO(20),CODE,SD(20,40),TMEAN(20),TSD(20),CMEAN(20,40),SUM(20,40)
58900        BIG=COL;IF(ROW.GT.COL) BIG=ROW
59000        READ(5,108) (GRAM(I),I=1,20)
59100    108 FORMAT(20F1.0)
59200 C       READ DATA FOR SPECIES
59300        REWIND 4
59400 C      INITIALISE SUMZ2 AND TSUMZ2
59500        DO 227 I=1,SPN
59600        TSUMZ2(I)=0.0
59700        DO227 J=1,CLASS(I)
59800    227 SUMZ2(I,J)=0.0
59900        DO 216 SP=1,SPN
60000 C
60100        READ(4,111)(SNAME(SP,I),I=1,80)
60200    111 FORMAT(80A1)
60300        DO 201 SSALC=1,CLASS(SP)
60400        DO 201 WOR=1,ROW
60500        READ(4,/)(DATA(SSALC,WOR,LOC),LOC=1,COL)
60600    201 CONTINUE
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60700       IF(GRAM(SP).EQ.0.0) GOTO 228
60800 C      CONVERT GRID INTO VECTOR
60900 C
61000       DO 202 SSALC=1,CLASS(SP)
61100       DO 202 WOR=1,ROW
61200       DO 202 LOC=1,COL
61300       VECT(SSALC,(WOR-1)*COL+LOC)=DATA(SSALC,WOR,LOC)
61400   202 CONTINUE
61500 C      CALCULATE MEAN AND MOMENTS OF EACH CLASS
61600 C
61700       IF(GRAM(SP).EQ.1.0) GOTO 229
61800       DO 203 SSALC=1,CLASS(SP)
61900       DO 203 CELL=1,CELLN
62000       SUM(SP,SSALC)=SUM(SP,SSALC)+VECT(SSALC,CELL)
62100   203 CONTINUE
62200       DO 204 SSALC=1,CLASS(SP)
62300       CMEAN(SP,SSALC)=SUM(SP,SSALC)/CELLN
62400       DO 205 CELL=1,CELLN
62500       SUM2(SSALC)=SUM2(SSALC)+(VECT(SSALC,CELL)-CMEAN(SP,SSALC))**2
62600       SUM4(SSALC)=SUM4(SSALC)+(VECT(SSALC,CELL)-CMEAN(SP,SSALC))**4
62700   205 CONTINUE
62800       CMOME2(SSALC)=SUM2(SSALC)/CELLN
62900       CMOME4(SSALC)=SUM4(SSALC)/CELLN
63000   204 CONTINUE
63100 C      CALCULATE B SQUARES
63200 C
63300       DO 206 SSALC=1,CLASS(SP)
63400       IF(SUM(SP,SSALC).EQ.0.0) GOTO 206
63500       BTWO(SP,SSALC)=CMOME4(SSALC)/CMOME2(SSALC)**2
63600   206 CONTINUE
63700 C      CALCULATE Z VALUES
63800 C
63900       DO 207 SSALC=1,CLASS(SP)
64000       DO 207 CELL=1,CELLN
64100       Z(SSALC,CELL)=VECT(SSALC,CELL)-CMEAN(SP,SSALC)
64200   207 CONTINUE
64300 C      CALCULATE SUM OF Z-PRODUCT
64400 C
64500       DO 217 V=1,BIG-1.0
64600       CALL ROOK
64700       WRK(V)=W;S1RK(V)=S1;S2RK(V)=S2
64800       DO 217 SSALC=1,CLASS(SP)
64900       IF(SUM(SP,SSALC).EQ.0.0) GOTO 217
65000       DO 217 CELL1=1,CELLN
65100       DO 217 CELL2=1,CELLN
65200       ROT=Z(SSALC,CELL1)*Z(SSALC,CELL2)*WEIGHT(CELL1,CELL2)
65300       CRK(V,SP,SSALC)=CRK(V,SP,SSALC)+ROT
65400   217 CONTINUE
65500       DO219 V=1,BIG-1.0
65600       CALL BISHOP
65700       WBSH(V)=W;S1BSH(V)=S1;S2BSH(V)=S2
65800       DO 219 SSALC=1,CLASS(SP)
65900       IF(SUM(SP,SSALC).EQ.0.0) GOTO 219
66000       DO 219 CELL1=1,CELLN
66100       DO 219 CELL2=1,CELLN
66200       ROT=Z(SSALC,CELL1)*Z(SSALC,CELL2)*WEIGHT(CELL1,CELL2)
66300       CBSH(V,SP,SSALC)=CBSH(V,SP,SSALC)+ROT
66400   219 CONTINUE
66500 C      CALCULATE SUM OF Z SQUARES
66600 C
66700       DO 208 SSALC=1,CLASS(SP)
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66800         DO 208 CELL=1,CELLN
66900         SUMZ2(SP,SSALC)=SUMZ2(SP,SSALC)+Z(SSALC,CELL)**2
67000     208 CONTINUE
67100     229 CONTINUE
67200 C        CALCULATE TOTAL OF CLASSES
67300 C
67400         DO 209 CELL=1,CELLN
67500         DO 209 SSALC=1,CLASS(SP)
67600         TOTAL(CELL)=TOTAL(CELL)+VECT(SSALC,CELL)
67700     209 CONTINUE
67800 C        CALCULATE MEAN OF TOTAL
67900 C
68000         DO 210 CELL=1,CELLN
68100         TMEAN(SP)=TMEAN(SP)+TOTAL(CELL)
68200     210 CONTINUE
68300         TMEAN(SP)=TMEAN(SP)/CELLN
68400 C        CALCULATE 2ND AND 4TH MOMENTS OF TOTAL
68500 C
68600         DO 211 CELL=1,CELLN
68700         TSUM2=TSUM2+(TOTAL(CELL)-TMEAN(SP))**2
68800         TSUM4=TSUM4+(TOTAL(CELL)-TMEAN(SP))**4
68900     211 CONTINUE
69000         TMOME2=TSUM2/CELLN
69100         TMOME4=TSUM4/CELLN
69200 C        CALCULATE B SQUARED FOR TOTAL
69300 C
69400         IF(TMEAN(SP).EQ.0.0) GOTO 213
69500         TBTWO(SP)=TMOME4/TMOME2**2
69600 C        CALCULATE Z VALUES FOR TOTAL
69700 C
69800         DO 212 CELL=1,CELLN
69900         TZ(CELL)=TOTAL(CELL)-TMEAN(SP)
70000     212 CONTINUE
70100 C        CALCULATE SUM OF Z-PRODUCT
70200         DO218 V=1,BIG-1.0
70300         CALL ROOK
70400         DO 218 CELL1=1,CELLN
70500         DO 218 CELL2=1,CELLN
70600         TRK(V,SP)=TRK(V,SP)+TZ(CELL1)*TZ(CELL2)*WEIGHT(CELL1,CELL2)
70700     218 CONTINUE
70800         DO220 V=1,BIG-1.0
70900         CALL BISHOP
71000         DO 220 CELL1=1,CELLN
71100         DO 220 CELL2=1,CELLN
71200         TBSH(V,SP)=TBSH(V,SP)+TZ(CELL1)*TZ(CELL2)*WEIGHT(CELL1,CELL2)
71300     220 CONTINUE
71400 C        CALCULATE SUM OF Z SQUARES
71500         DO 213 CELL=1,CELLN
71600         TSUMZ2(SP)=TSUMZ2(SP)+TZ(CELL)**2
71700     213 CONTINUE
71800 C        SET VARIABLES TO ZERO
71900     104 FORMAT(11X,I3,3X,F5.2,5X,F7.4,2X,F7.4,2X,F9.4,4X,F9.4,8X,
72000        -F9.4,10X,F9.4)
72100         DO 214 SSALC=1,CLASS(SP)
72200         SUM2(SSALC)=0.0
72300         SUM4(SSALC)=0.0
72400     214 CONTINUE
72500         DO 215 CELL=1,CELLN
72600         TOTAL(CELL)=0.0
72700     215 CONTINUE
72800         TSUM2=0.0;TSUM4=0.0
```

```
C      RETURN AND REPEAT FOR NEXT SPECIES
C
  228 CONTINUE
  216 CONTINUE
      WRITE(6,50)
   50 FORMAT(//55X,'CORRELOGRAM'/55X,11('*')//)
C
      DO 221 SP=1,SPN
      IF(TMEAN(SP).EQ.0.0) GOTO 221
      IF(GRAM(SP).EQ.0.0) GO TO 221
      WRITE(6,110)
  110 FORMAT(108('-'))
      WRITE(6,101) (SNAME(SP,I),I=1,80)
  101 FORMAT(3X,'SPECIES',2X,80A1//)
      IF(GRAM(SP).EQ.1.0) GOTO 106
      DO 222 SSALC=1,CLASS(SP)
      IF(SUM(SP,SSALC).EQ.0.0) GOTO 222
      WRITE(6,102) SSALC
  102 FORMAT(6X,'CLASS',2X,I3//)
      B2=BTWO(SP,SSALC)
      Z2=SUMZ2(SP,SSALC)
C          ROOKS FIRST
      WRITE(6,103)
  103 FORMAT(10X,'ROOK',2X,'DISTANCE',5X,'E(I)',5X,'I',
     -5X,'SD(I)(NORM)',2X,'SD(I)(RAND)',2X,'ST.NORM.DEV.(NORM)',
     -2X,'ST.NORM.DEV.(RAND)')
      DO 223 V=1,BIG-1.0
      ZP=CRK(V,SP,SSALC)
      W=WRK(V)
      S1=S1RK(V)
      S2=S2RK(V)
      CALL MORAN
      WRITE(6,104)V,V,EXPI,AIS,SQRT(ENI2),SQRT(ERI2),DEVN,DEVR
  223 CONTINUE
C     NOW BISHOPS
      WRITE(6,105)
  105 FORMAT(9X,'BISHOP',1X,'DISTANCE',5X,'E(I)',5X,'I',5X,
     -'SD(I)(NORM)',2X,'SD(I)(RAND)',2X,'ST.NORM.DEV.(NORM)',
     -2X,'ST.NORM.DEV.(RAND)')
      DO 224 V=1,BIG-1.0
      ZP=CBSH(V,SP,SSALC)
      W=WBSH(V)
      S1=S1BSH(V)
      S2=S2BSH(V)
      CALL MORAN
      WRITE(6,104)V,V*SQRT(2.0),EXPI,AIS,SQRT(ENI2),SQRT(ERI2),
     -DEVN,DEVR
  224 CONTINUE
  222 CONTINUE
C     NOW TOTALS
  106 WRITE(6,107)
  107 FORMAT(6X,'TOTAL'/)
C     ROOKS FIRST
      WRITE(6,103)
      B2=TBTWO(SP)
      Z2=TSUMZ2(SP)
      DO 225 V=1,BIG-1.0
      ZP=TRK(V,SP)
      W=WRK(V)
      S1=S1RK(V)
      S2=S2RK(V)
```

```
79000       CALL MORAN
79100       WRITE(6,104)W,V,EXPI,AIS,SQRT(ENI2),SQRT(ERI2),DEVN,DEVR
79200   225 CONTINUE
79300 C     NOW BISHOPS
79400       WRITE(6,105)
79500       DO 226 V=1,BIG-1.0
79600       ZP=TBSH(V,SP)
79700       W=WBSH(V)
79800       S1=S1BSH(V)
79900       S2=S2BSH(V)
80000       CALL MORAN
80100       WRITE(6,104)W,V*SQRT(2.0),EXPI,AIS,SQRT(ENI2),SQRT(ERI2),
80200      -DEVN,DEVR
80300   226 CONTINUE
80400   221 CONTINUE
80500       RETURN
80600       END
80700 C      ************************************************
80800       SUBROUTINE GRID
80900 C      ************************************************
81000 C     SUBROUTINE GRID READS IN GRID SPECIFICATIONS AND DATA STRUCTURE
81100 C
81200       COMMON CS2(40),SUM2(40),SUM4(40),CMONE2(40),ZERO(20,40),
81300      $CMONE4(40),Z(40,100),SUMZ2(20,40),TOTAL(100),TZ(100),TSUMZ2(20)
81400      $,SNAME(20,80),CLASS(20),DATA(40,10,10),VECT(40,100),WANT(20),
81500      $WEIGHT(100,100),BTWO(20,40),SUMZP(20,40),TBTWO(40),TSUMZP(20),
81600      $COL,ROW,CELLN,W,S1,S2,ZP,Z2,AIS,EXPI,ERI2,ENI2,DEVR,DEVN,B2,SPN,V,
81700      $TZO(20),CODE,SO(20,40),TMEAN(20),TSO(20),CMEAN(20,40),SUM(20,40)
81800       READ(5,101)ROW,COL,SPN,(CLASS(I),I=1,SPN)
81900   101 FORMAT(23F3.0)
82000       CELLN=ROW*COL
82100       RETURN
82200       END
```

WALNUT jobs

WALNUT is less flexible than the other analysis programs in that it does not allow for variations of parameters through the driving job. The default is for correlations to be calculated between all possible pairs of species groups. For the analysis of grids (which must be square) other than 8 x 8, and species numbers and groups other than those used in this work, the source program must be modified. This involves replacing 64 by the number of cells in the grid and 16 by the number of species, for all occurences of those variables. The number of groups in each species can be modified by changing the DATA statement.

Example of job for planar cross-correlation analysis

```
?BEGIN JOB WALNUT/200381/100M;
QUEUE=23;
RUN OBJECT/WALNUT;
FILE 4(KIND=READER);
FILE FILE5=GROUP/GRID/200381/100M;
DATA
WALNUT/200381/100M
?
?END JOB
```

```
LIST WALNUT

100 $RESET FREE
200 FILE  4(KIND=READER,TITLE='COMMANDS')
300 FILE  5(KIND=DISK)
400 FILE  6(KIND=PRINTER,PROTECTION=SAVE)
500         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
600        $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
700        $CLASS1,CLASS2,ZMULT1,ZMULT2
800         COMMON/B/ZI(16,6,16,6,0:1,0:1)
900         COMMON/C/SNORR(16,6,16,6,0:1,0:1)
1000         COMMON/D/SNORI(16,6,16,6,0:1,0:1)
1100         DIMENSION TITLE(80)
1200         DATA CLASS/5,4,3,5,2,1,1,1,1,1,1,1,1,1,1,1/
1300         READ(4,1)(TITLE(I),I=1,80)
1400         WRITE(6,2)(TITLE(I),I=1,80)
1500      1  FORMAT(80A1)
1600      2  FORMAT(1X,80A1)
1700         CALL READ
1800         CALL NOISE
1900         CALL CROSS
2000         CLOSE(6,DISP=CRUNCH)
2100         END
2200         SUBROUTINE READ
2300         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
2400        $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
2500        $CLASS1,CLASS2,ZMULT1,ZMULT2
2600         COMMON/B/ZI(16,6,16,6,0:1,0:1)
2700         COMMON/C/SNORR(16,6,16,6,0:1,0:1)
2800         COMMON/D/SNORI(16,6,16,6,0:1,0:1)
2900         DIMENSION DATA(64,16,6),ZMEAN(16,6)
3000 C        READ IN AND TOTAL DATA
3100         DO 1 CELL=1,64
3200         DO 1 SP=1,16
3300      1  READ(5,/)(DATA(CELL,SP,CLASSN),CLASSN=1,CLASS(SP))
3400         DO 2 CELL=1,64
3500         DO 2 SP=1,16
3600         DO 2 CLASSN=1,CLASS(SP)
3700         DATA(CELL,SP,CLASS(SP)+1)=DATA(CELL,SP,CLASS(SP)+1)+
3800        $DATA(CELL,SP,CLASSN)
3900      2  CONTINUE
4000 C        CONVERT DATA MATRIX INTO VECTOR
4100         DO 3 SP=1,16
4200         DO 3 CLASSN=1,CLASS(SP)+1
4300         DO 3 CELL=1,64
4400      3  VECTOR(SP,CLASSN,CELL)=DATA(CELL,SP,CLASSN)
4500 C        CALCULATE MEANS OF VECTORS
4600         DO 4 SP=1,16
4700         DO 4 CLASSN=1,CLASS(SP)+1
4800         DO 4 CELL=1,64
4900      4  ZMEAN(SP,CLASSN)=ZMEAN(SP,CLASSN)+VECTOR(SP,CLASSN,CELL)
```

```
5000          DO 5 SP=1,16
5100          DO 5 CLASSN=1,CLASS(SP)+1
5200       5  ZMEAN(SP,CLASSN)=ZMEAN(SP,CLASSN)/64.0
5300 C         CENTRE VECTORS
5400          DO 6 SP=1,16
5500          DO 6 CLASSN=1,CLASS(SP)+1
5600          DO 6 CELL=1,64
5700       6  VECTOR(SP,CLASSN,CELL)=VECTOR(SP,CLASSN,CELL)-ZMEAN(SP,CLASSN)
5800          RETURN
5900          END
6000          SUBROUTINE NONE
6100          COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
6200         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
6300         $CLASS1,CLASS2,ZMULT1,ZMULT2
6400          COMMON/B/ZI(16,6,16,6,0:1,0:1)
6500          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
6600          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
6700 C         CALCULATE VARIANCE OF CENTRED VECTORS
6800          DO 1 SP=1,16
6900          DO 1 CLASSN=1,CLASS(SP)+1
7000          DO 1 CELL=1,64
7100       1  VAR(SP,CLASSN)=VAR(SP,CLASSN)+VECTOR(SP,CLASSN,CELL)**2
7200          DO 2 SP=1,16
7300          DO 2 CLASSN=1,CLASS(SP)+1
7400       2  VAR(SP,CLASSN)=VAR(SP,CLASSN)/64.0
7500          RETURN
7600          END
7700          SUBROUTINE CROSS
7800          COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
7900         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
8000         $CLASS1,CLASS2,ZMULT1,ZMULT2
8100          COMMON/B/ZI(16,6,16,6,0:1,0:1)
8200          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
8300          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
8400 C         INITIALLY DO FOR ZERO SPACING
8500          CHESS=0
8600          SPACE=0
8700          DO 101 I=1,64
8800          DO 101 J=1,64
8900     101  WEIGHT(I,J)=0
9000          DO 102 I=1,64
9100     102  WEIGHT(I,I)=1
9200          DO 103 SP1=1,16
9300          DO 103 CLASS1=1,CLASS(SP1)+1
9400          IF(CLASS(SP1).EQ.1.AND.CLASS1.EQ.2) GOTO 888
9500          DO 104 SP2=SP1,16
9600          IF(SP1.EQ.SP2.AND.CLASS(SP1).EQ.1) GOTO 777
9700          IF(SP1.EQ.SP2)X=CLASS1
9800          IF(SP1.NE.SP2)X=0
9900          IF(X.EQ.CLASS(SP1)+1) GOTO 777
10000          DO 105 CLASS2=X+1,CLASS(SP2)+1
10100          IF(CLASS(SP2).EQ.1.AND.CLASS2.EQ.2) GOTO 666
```

```
10200          CALL MULT1
10300          CALL MULT2
10400          CALL MORAN
10500          CALL EXPI2
10600          CALL STNORD
10700    666   CONTINUE
10800    105   CONTINUE
10900    777   CONTINUE
11000    104   CONTINUE
11200    103   CONTINUE
11300          CALL PRINT
11400 C         FIRST ROOK
11500          CHESS=1
11600          DO 2 SPACE=1,2
11700          CALL ROOK
11800          DO 1 SP1=1,16
11900          DO 1 CLASS1=1,CLASS(SP1)+1
12000          IF(CLASS(SP1).EQ.1.AND.CLASS1.EQ.2)GOTO 11
12100          DO 33 SP2=SP1,16
12200          IF(SP1.EQ.SP2.AND.CLASS(SP1).EQ.1) GOTO 111
12300          IF(SP1.EQ.SP2)X=CLASS1
12400          IF(SP1.NE.SP2)X=0
12500          IF(X.EQ.CLASS(SP1)+1) GOTO 111
12600          DO 34 CLASS2=X+1,CLASS(SP2)+1
12700          IF(CLASS(SP2).EQ.1.AND.CLASS2.EQ.2)GOTO 222
12800          CALL MULT1
12900          CALL MULT2
13000          CALL MORAN
13100          CALL EXPI2
13200          CALL STNORD
13300    222   CONTINUE
13400     34   CONTINUE
13500    111   CONTINUE
13600     33   CONTINUE
13700     11   CONTINUE
13800      1   CONTINUE
13900          CALL PRINT
14000      2   CONTINUE
14100 C        NOW BISHOP
14200          CHESS=2
14300          DO 22 SPACE=1,2
14400          CALL BISHOP
14500          DO 10 SP1=1,16
14600          DO 10 CLASS1=1,CLASS(SP1)+1
14700          IF(CLASS(SP1).EQ.1.AND.CLASS1.EQ.2)GOTO 1010
14800          DO 303 SP2=SP1,16
14900          IF(SP1.EQ.SP2.AND.CLASS(SP1).EQ.1) GOTO 1011
15000          IF(SP1.EQ.SP2)X=CLASS1
```

```
15100          IF(SP1.NE.SP2)X=0
15200          IF(X.EQ.CLASS(SP1)+1) GOTO 1011
15300          DO 304 CLASS2=X+1,CLASS(SP2)+1
15400          IF(CLASS(SP2).EQ.1.AND.CLASS2.EQ.2)GOTO 2022
15500          CALL MULT1
15600          CALL MULT2
15700          CALL NORRN
15800          CALL EXPI2
15900          CALL STNORD
16000 2022     CONTINUE
16100   304    CONTINUE
16200  1011    CONTINUE
16300   303     CONTINUE
16400   101    CONTINUE
16500    10    CONTINUE
16600          CALL PRINT
16700    22    CONTINUE
16800          RETURN
16900          END
17000          SUBROUTINE ROOK
17100          COMMON/A/CLASS(16),VECTOR(16,6,64),VRR(16,6),WEIGHT(64,64),
17200         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
17300         $CLASS1,CLASS2,ZMULT1,ZMULT2
17400          COMMON/B/ZI(16,6,16,6,0:1,0:1)
17500          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
17600          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
17700          S=SPACE
17800          DO 1 I=1,64
17900          DO 1 J=1,64
18000      1   WEIGHT(I,J)=0
18100          C1=1
18200          DO 2 C=1,64
18300          IF(C.GT.S*8) WEIGHT(C,C-S*8)=1
18400          IF(C.LT.64-S*8+1) WEIGHT(C,C+S*8)=1
18500          IF(C1+S-1.LT.C) WEIGHT(C,C-S)=1
18600          IF(C.LT.C1+8-S) WEIGHT(C,C+S)=1
18700          IF(AMOD(C,8).EQ.0.0) C1=C1+8
18800      2   CONTINUE
18900          RETURN
19000          END
19100          SUBROUTINE BISHOP
19200          COMMON/A/CLASS(16),VECTOR(16,6,64),VRR(16,6),WEIGHT(64,64),
19300         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
19400         $CLASS1,CLASS2,ZMULT1,ZMULT2
19500          COMMON/B/ZI(16,6,16,6,0:1,0:1)
19600          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
19700          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
19800          S=SPACE
19900          DO 1 I=1,64
20000          DO 1 J=1,64
20100      1   WEIGHT(I,J)=0
20200          C1=8
20300          DO 2 C=1,64
20400          IF(C.LE.C1-S.AND.C+S*8+S.LE.64) WEIGHT(C,C+S*8+S)=1
20500          IF(C.LE.C1-S.AND.C-S*8+S.GE.1) WEIGHT(C,C-S*8+S)=1
20600          IF(C.GE.C1-8+S+1.AND.C+S*8-S.LE.64) WEIGHT(C,C+S*8-S)=1
20700          IF(C.GE.C1-8+S+1.AND.C-S*8-S.GE.1) WEIGHT(C,C-S*8-S)=1
20800          IF(AMOD(C,8).EQ.0.0) C1=C1+8
20900      2   CONTINUE
21000          RETURN
21100          END
```

```
21200         SUBROUTINE MULT1
21300         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
21400        $EXP12R(0:2,0:2),EXP12I(0:2,0:2),CHESS,SPACE,SP1,SP2,
21500        $CLASS1,CLASS2,ZMULT1,ZMULT2
21600         COMMON/B/ZI(16,6,16,6,0:1,0:1)
21700         COMMON/C/SNORR(16,6,16,6,0:1,0:1)
21800         COMMON/D/SNORI(16,6,16,6,0:1,0:1)
21900         DIMENSION ZMPROD(64)
22000 C        MATRIX MULTIPLICATION OF XK'WXL
22100         ZMULT1=0.0
22200 C        FIRST MULTIPLY ROW VECTOR XK' BY WEIGHT MATRIX
22300         DO 1 COL=1,64
22400         ZMPROD(COL)=0.0
22500         DO 1 ROW=1,64
22600      1     ZMPROD(COL)=ZMPROD(COL)+VECTOR(SP1,CLASS1,ROW)*WEIGHT(ROW,COL)
22700 C        NOW MULTIPLY ZMPROD BY COLUMN VECTOR XL
22800         DO 2 I=1,64
22900      2  ZMULT1=ZMULT1+ZMPROD(I)*VECTOR(SP2,CLASS2,I)
23000 C        LEFT WITH ZMULT1=XK'WXL
23100         RETURN
23200         END
23300         SUBROUTINE MULT2
23400         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
23500        $EXP12R(0:2,0:2),EXP12I(0:2,0:2),CHESS,SPACE,SP1,SP2,
23600        $CLASS1,CLASS2,ZMULT1,ZMULT2
23700         COMMON/B/ZI(16,6,16,6,0:1,0:1)
23800         COMMON/C/SNORR(16,6,16,6,0:1,0:1)
23900         COMMON/D/SNORI(16,6,16,6,0:1,0:1)
24000         DIMENSION ZMPROD(64)
24100 C        MATRIX MULTIPLICATION OF (I'W1)**-1
24200         ZMULT2=0.0
24300 C        FIRST MULT IS EQUIV TO SUMMING COLS
24400         DO 1 COL=1,64
24500         ZMPROD(COL)=0.0
24600         DO 1 ROW=1,64
24700      1  ZMPROD(COL)=ZMPROD(COL)+WEIGHT(ROW,COL)
24800 C        SECOND IS EQUIV TO SUMMING ZMPROD VECTOR
24900         DO 2 COL=1,64
25000      2  ZMULT2=ZMULT2+ZMPROD(COL)
25100         ZMULT2=1/ZMULT2
25200 C        LEFT WITH ZMULT2=(1'W1)**-1
25300         RETURN
25400         END
25500         SUBROUTINE MORAN
25600         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
25700        $EXP12R(0:2,0:2),EXP12I(0:2,0:2),CHESS,SPACE,SP1,SP2,
25800        $CLASS1,CLASS2,ZMULT1,ZMULT2
25900         COMMON/B/ZI(16,6,16,6,0:1,0:1)
26000         COMMON/C/SNORR(16,6,16,6,0:1,0:1)
26100         COMMON/D/SNORI(16,6,16,6,0:1,0:1)
26200 C        CALCULATE MORAN STATISTIC
26300         IF(VAR(SP1,CLASS1)*VAR(SP2,CLASS2).EQ.0.0)GOTO 1
26400         ZI(SP1,CLASS1,SP2,CLASS2,CHESS,SPACE)=
26500        $ZMULT1/SQRT(VAR(SP1,CLASS1)*VAR(SP2,CLASS2))*ZMULT2
26600      1  CONTINUE
26700         RETURN
26800         END
26900         SUBROUTINE EXP12
27000         COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
27100        $EXP12R(0:2,0:2),EXP12I(0:2,0:2),CHESS,SPACE,SP1,SP2,
27200        $CLASS1,CLASS2,ZMULT1,ZMULT2
```

```
27300          COMMON/B/ZI(16,6,16,6,0:1,0:1)
27400          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
27500          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
27600          DIMENSION COLT(64),ROWT(64)
27700 C         CALCULATE EXPECTED I2 FOR GIVEN WEIGHT MATRIX UNDER
27800 C         THE TWO ASSUMPTIONS
27900          WSUM=0;W2SUM=0;SUMC2=0;SUMR2=0
28000          DO 7 I=1,64
28100          COLT(I)=0
28200          ROWT(I)=0
28300        7 CONTINUE
28400 C         FIRST UNDER R ASSUMPTION
28500 C         CALCULATE SUM OF ALL WEIGHTS
28600          DO 1 I=1,64
28700          DO 1 J=1,64
28800        1 WSUM=WSUM+WEIGHT(I,J)
28900 C         CALCULATE SUM OF SQUARE WEIGHTS
29000          DO 2 I=1,64
29100          DO 2 J=1,64
29200        2 W2SUM=W2SUM+WEIGHT(I,J)**2
29300 C         CALCULATE SUMOF SQUARE COL TOTALS
29400          DO 3 COL=1,64
29500          DO 3 ROW=1,64
29600        3 COLT(COL)=COLT(COL)+WEIGHT(ROW,COL)
29700          DO 4 COL=1,64
29800        4 SUMC2=SUMC2+COLT(COL)**2
29900 C         CALCULATE SUM OF SQUARE ROW TOTALS
30000          DO 5 ROW=1,64
30100          DO 5 COL=1,64
30200        5 ROWT(ROW)=ROWT(ROW)+WEIGHT(ROW,COL)
30300          DO 6 ROW=1,64
30400        6 SUMR2=SUMR2+ROWT(ROW)**2
30500          EXPI2R(CHESS,SPACE)=(64.0**2*W2SUM/63.0**2)-
30600         $(64.0*(SUMC2+SUMR2)/63.0**2)+
30700         $(WSUM**2/63.0**2)
30800          EXPI2R(CHESS,SPACE)=EXPI2R(CHESS,SPACE)/WSUM**2
30900 C         NOW UNDER IID ASSUMPTION
31000          EXPI2I(CHESS,SPACE)=W2SUM/WSUM**2
31100          RETURN
31200          END
31300          SUBROUTINE STNORD
31400          COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
31500         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
31600         $CLASS1,CLASS2,ZMULT1,ZMULT2
31700          COMMON/B/ZI(16,6,16,6,0:1,0:1)
31800          COMMON/C/SNORR(16,6,16,6,0:1,0:1)
31900          COMMON/D/SNORI(16,6,16,6,0:1,0:1)
32000 C         CALCULATE STANDARD NORMAL DEVIATES
32100 C         FIRST STNORMDEV FOR R ASSUMPTION
32200          SNORR(SP1,CLASS1,SP2,CLASS2,CHESS,SPACE)=
32300         $(ZI(SP1,CLASS1,SP2,CLASS2,CHESS,SPACE))/
32400         $SQRT(EXPI2R(CHESS,SPACE))
32500 C           NOW FOR IID ASSUMPTION
32600          SNORI(SP1,CLASS1,SP2,CLASS2,CHESS,SPACE)=
32700         $(ZI(SP1,CLASS1,SP2,CLASS2,CHESS,SPACE))/
32800         $SQRT(EXPI2I(CHESS,SPACE))
32900          RETURN
33000          END
33100          SUBROUTINE PRINT
33200          COMMON/A/CLASS(16),VECTOR(16,6,64),VAR(16,6),WEIGHT(64,64),
33300         $EXPI2R(0:2,0:2),EXPI2I(0:2,0:2),CHESS,SPACE,SP1,SP2,
```

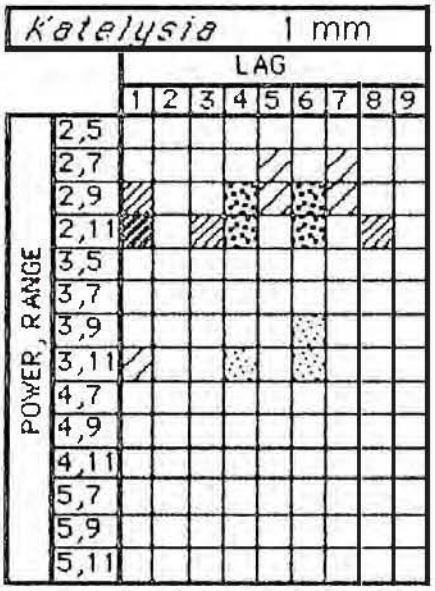
```
33400         $CLASS1,CLASS2,ZMULT1,ZMULT2
33500           COMMON/B/ZI(16,6,16,6,0:1,0:1)
33600           COMMON/C/SNORR(16,6,16,6,0:1,0:1)
33700           COMMON/D/SNORI(16,6,16,6,0:1,0:1)
33800           DO 1 SP1=1,16
33900           DO 1 CLASS1=1,CLASS(SP1)+1
34000           IF(CLASS(SP1).EQ.1.AND.CLASS1.EQ.2) GOTO 111
34100           WRITE(6,101)SP1,CLASS1
34200    101    FORMAT(1X,'SPECIES',1X,I2,1X,'CLASS',1X,I1,1X,'VS')
34300           DO 2 SP2=SP1,16
34400           IF(SP1.EQ.SP2)X=CLASS1
34500           IF(SP1.NE.SP2)X=0
34600           IF(X.EQ.CLASS(SP1)+1) GOTO 222
34700           DO 3 CLASS2=X+1,CLASS(SP2)+1
34800           IF(CLASS(SP2).EQ.1.AND.CLASS2.EQ.2) GOTO 333
34900           IF(CHESS.NE.0)GOTO 201
35000           WRITE(6,202)SP2,CLASS2,ZI(SP1,CLASS1,SP2,CLASS2,0,0),
35100         $SNORR(SP1,CLASS1,SP2,CLASS2,0,0),SNORI(SP1,CLASS1,SP2,CLASS2,0,0)
35200    202    FORMAT(9X,I2,7X,I1,5X,'0.00',5X,F7.4,2X,F7.4,2X,F7.4)
35300    201    IF(CHESS.NE.1.OR.SPACE.NE.1) GOTO 11
35400           WRITE(6,102)SP2,CLASS2,ZI(SP1,CLASS1,SP2,CLASS2,1,1),
35500         $SNORR(SP1,CLASS1,SP2,CLASS2,1,1),SNORI(SP1,CLASS1,SP2,CLASS2,1,1)
35600    102    FORMAT(9X,I2,7X,I1,5X,'1.00',5X,F7.4,2X,F7.4,2X,F7.4)
35700     11    IF(CHESS.NE.2.OR.SPACE.NE.1)GOTO 12
35800           WRITE(6,103)SP2,CLASS2,ZI(SP1,CLASS1,SP2,CLASS2,2,1),
35900         $SNORR(SP1,CLASS1,SP2,CLASS2,2,1),SNORI(SP1,CLASS1,SP2,CLASS2,2,1)
36000    103    FORMAT(9X,I2,7X,I1,5X,'1.41',5X,F7.4,2X,F7.4,2X,F7.4)
36100     12    IF(CHESS.NE.1.OR.SPACE.NE.2) GOTO 13
36200           WRITE(6,104)SP2,CLASS2,ZI(SP1,CLASS1,SP2,CLASS2,1,2),
36300         $SNORR(SP1,CLASS1,SP2,CLASS2,1,2),SNORI(SP1,CLASS1,SP2,CLASS2,1,2)
36400    104    FORMAT(9X,I2,7X,I1,5X,'2.00',5X,F7.4,2X,F7.4,2X,F7.4)
36500     13    IF(CHESS.NE.2.OR.SPACE.NE.2) GOTO 333
36600           WRITE(6,105)SP2,CLASS2,ZI(SP1,CLASS1,SP2,CLASS2,2,2),
36700         $SNORR(SP1,CLASS1,SP2,CLASS2,2,2),SNORI(SP1,CLASS1,SP2,CLASS2,2,2)
36800    105    FORMAT(9X,I2,7X,I1,5X,'2.83',5X,F7.4,2X,F7.4,2X,F7.4)
36900    333    CONTINUE
37000      3    CONTINUE
37100    222    CONTINUE
37200      2    CONTINUE
37300    111    CONTINUE
37400      1    CONTINUE
37500           RETURN
37600           END
```

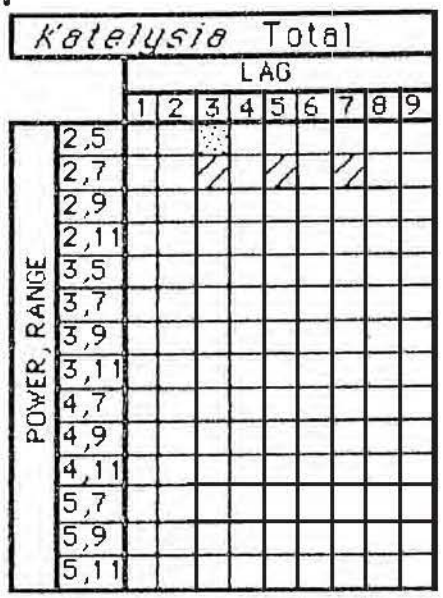
APPENDIX B

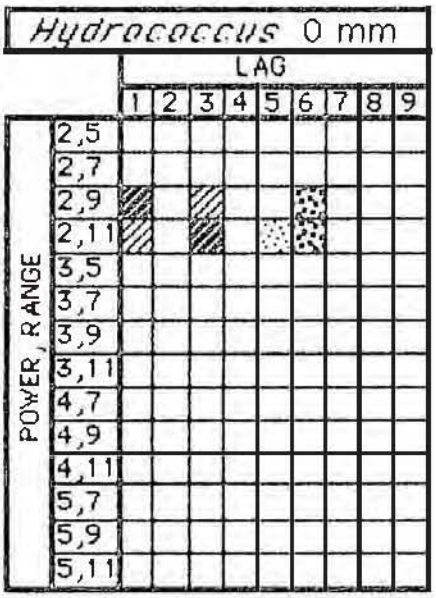
AUTOCORRELOGRAMS
FOR
SERIES AND PLANAR ANALYSIS

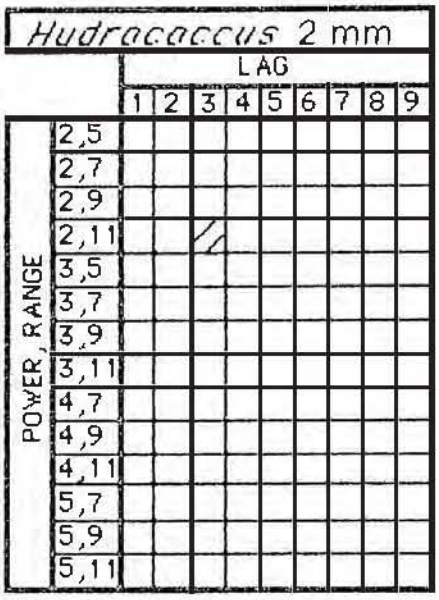
This appendix lists the correlograms for the autocorrelation analyses described in Chapters 5 and 6. Shading codings are as defined in Table 5.2.

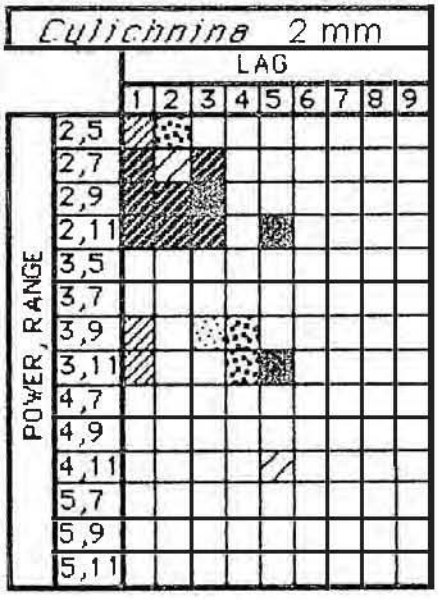
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
200381





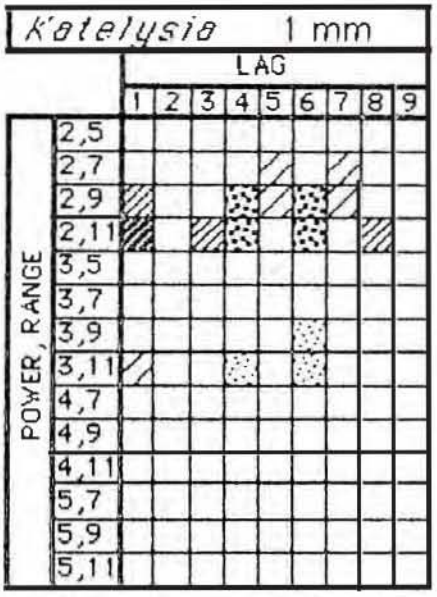




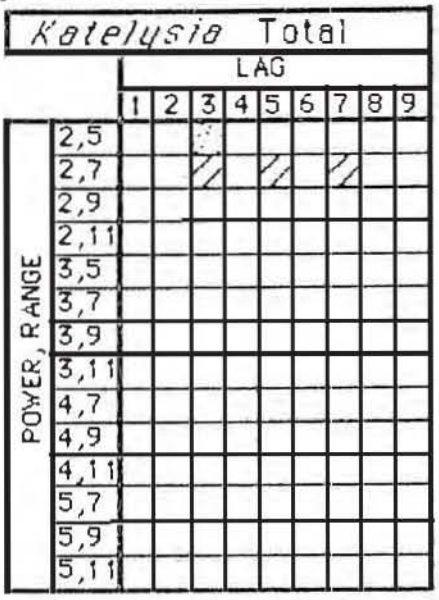


SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
200381

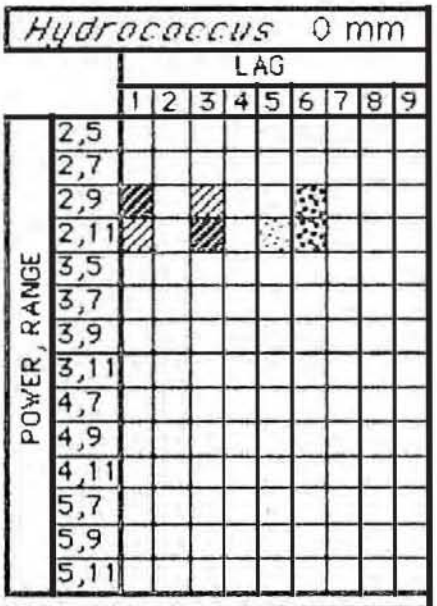
Katelysia 1 mm



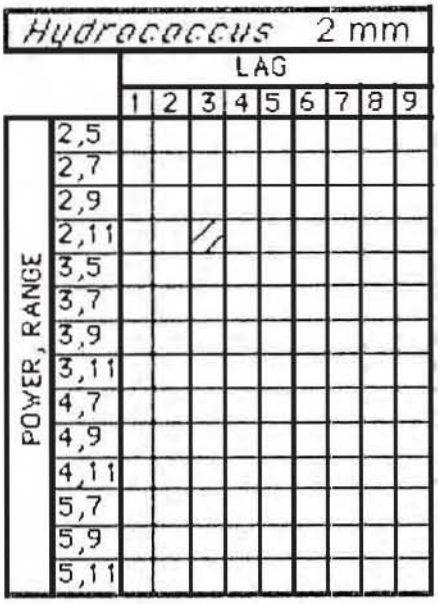
Katelysia Total



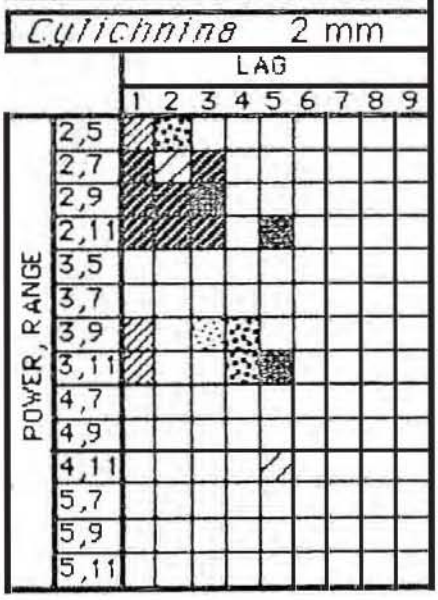
Hydrococcus 0 mm



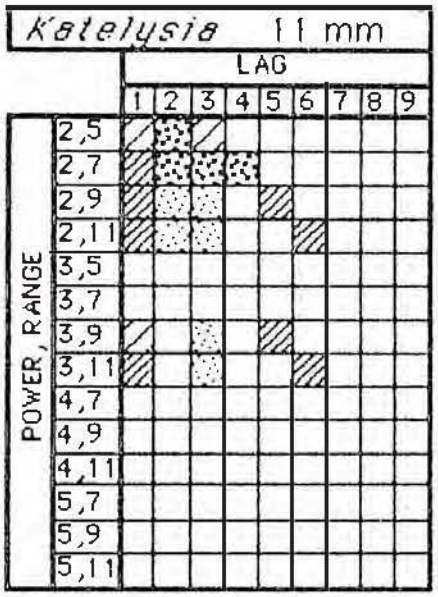
Hydrococcus 2 mm

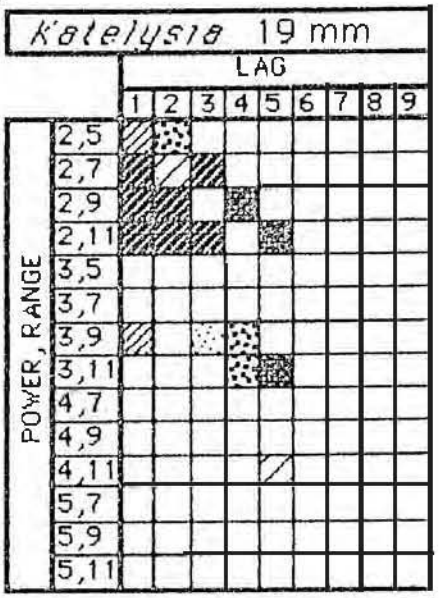


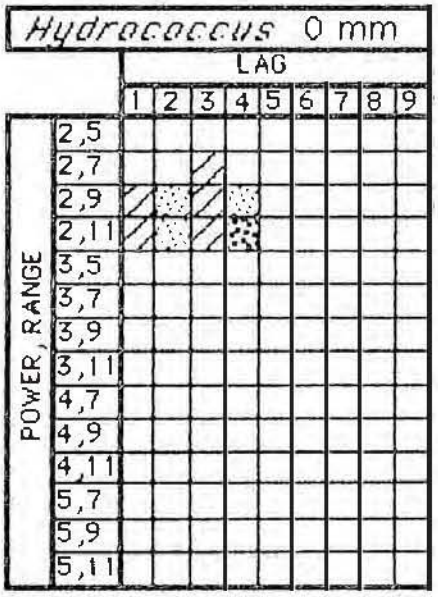
Cylichnina 2 mm

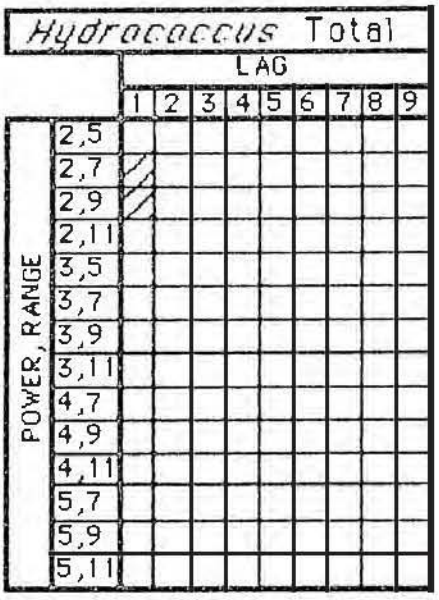


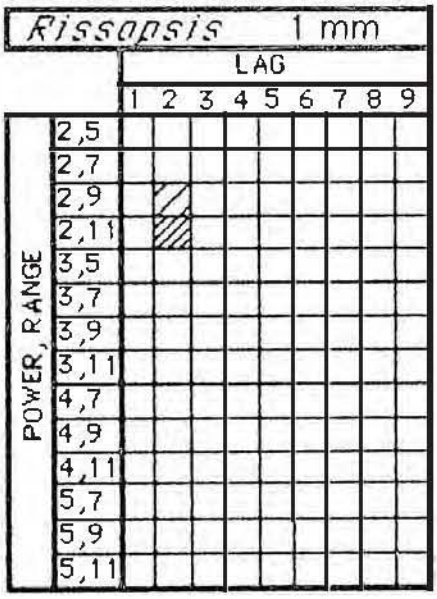
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
270681

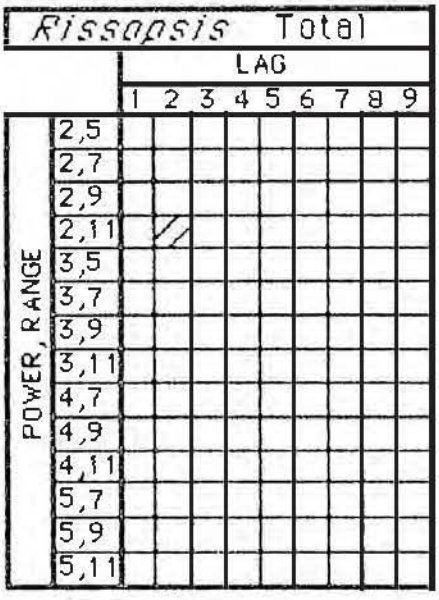




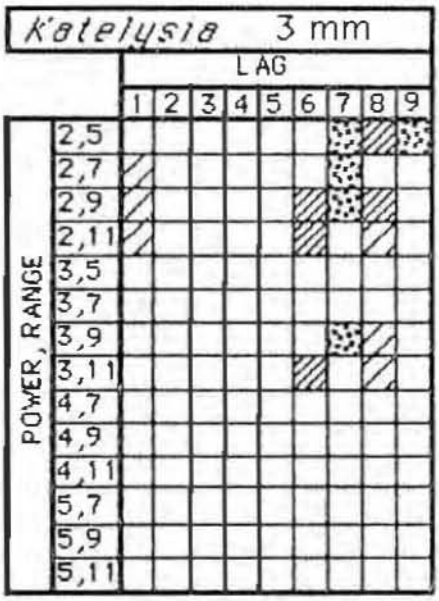


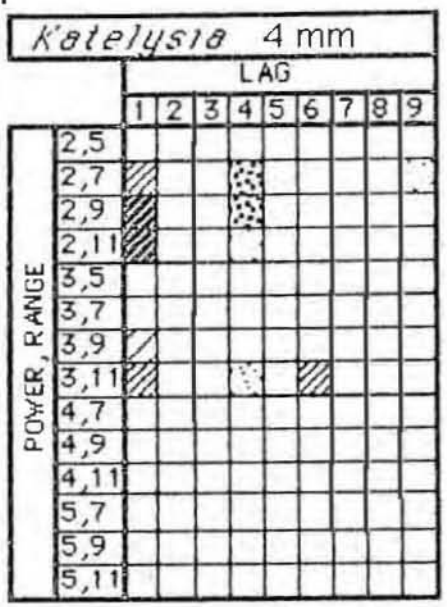


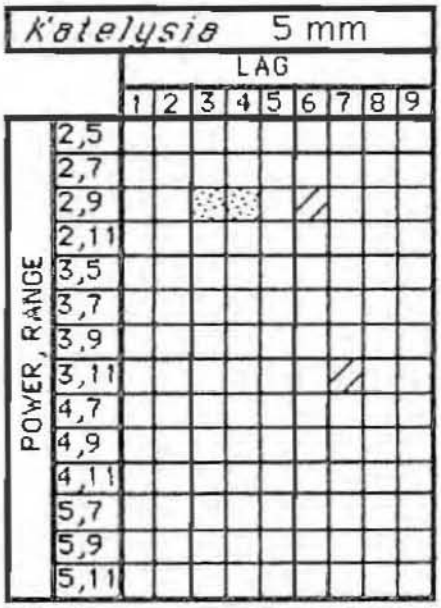


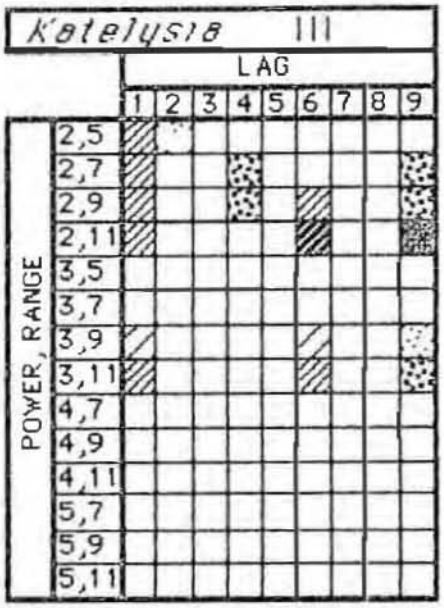


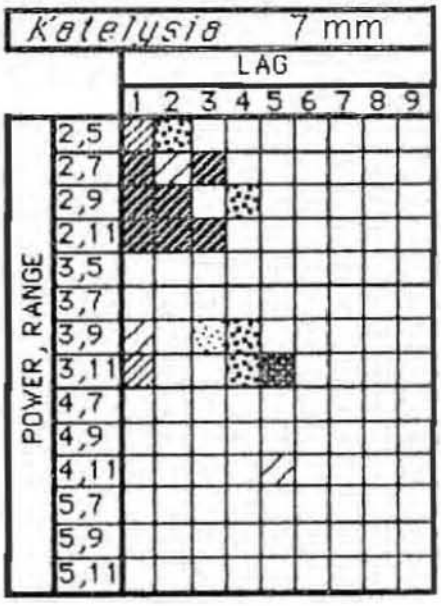
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
290981

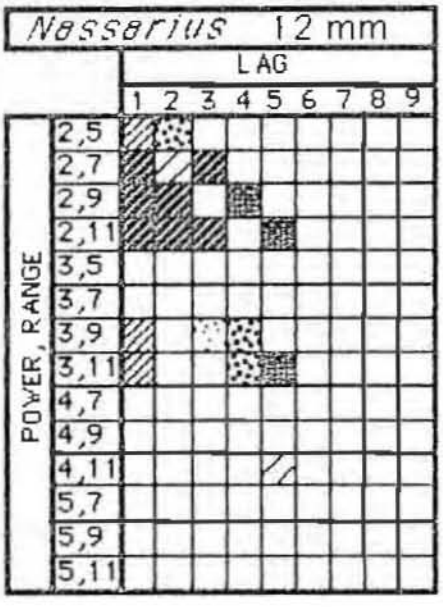








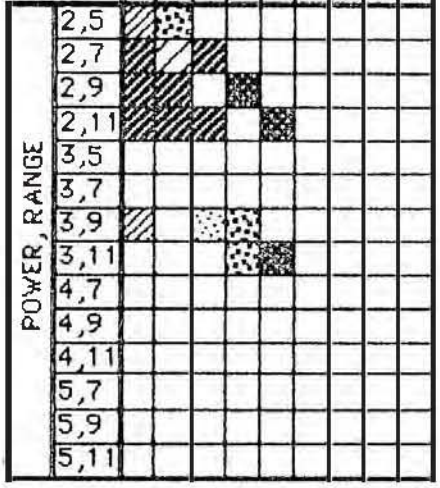




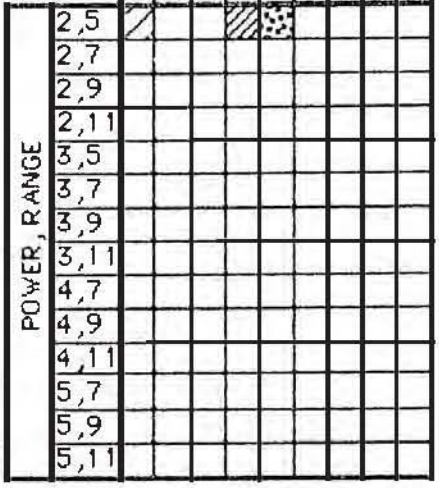
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS

290981

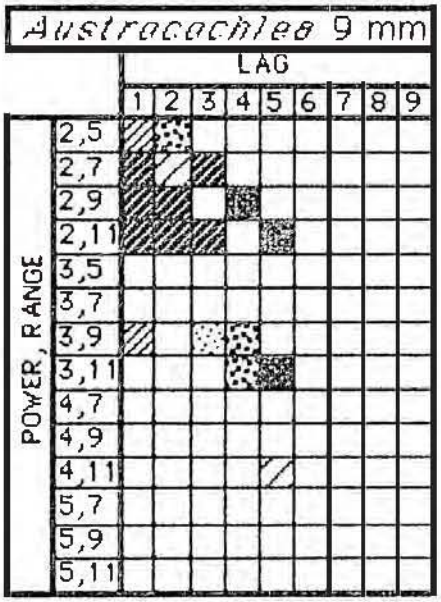
Austrocochlea 2 mm



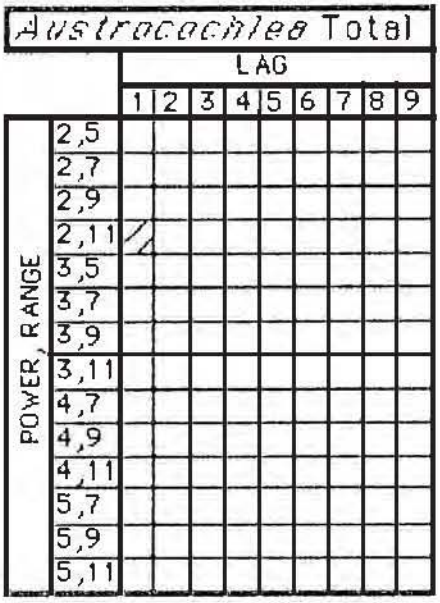
Austrocochlea 3 mm



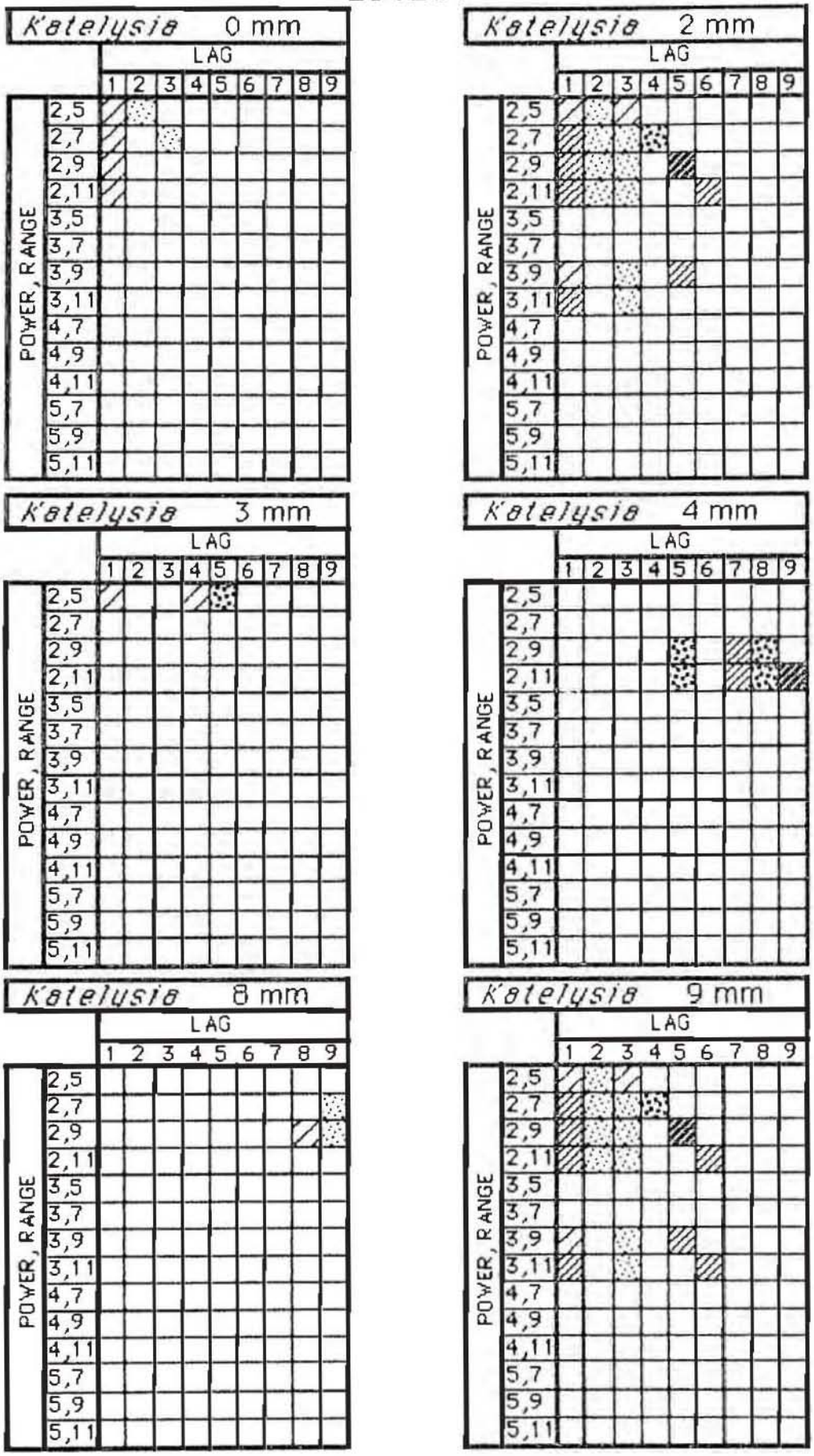
Austrocochlea 9 mm



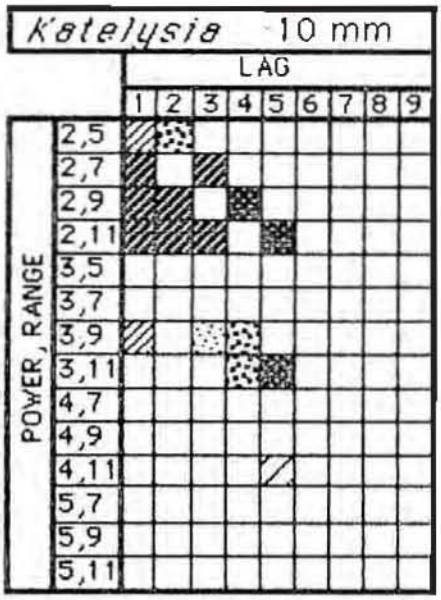
Austrocochlea Total

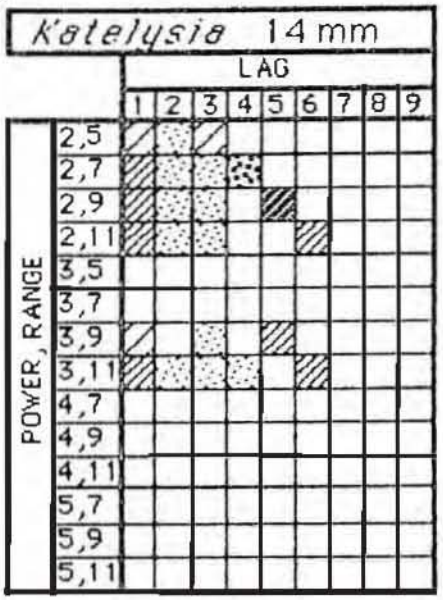


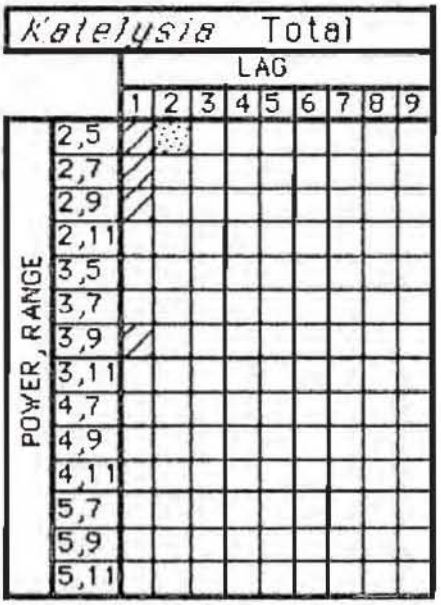
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
291281

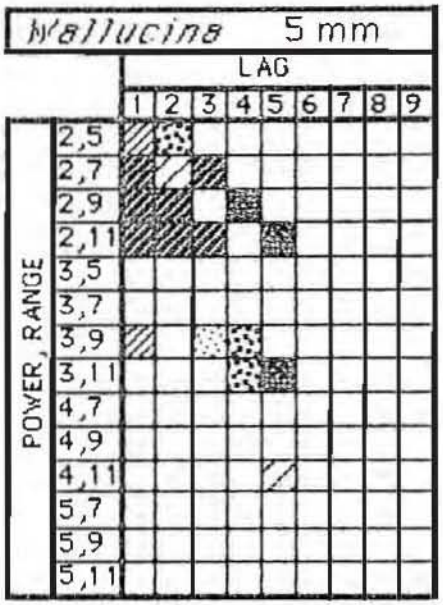


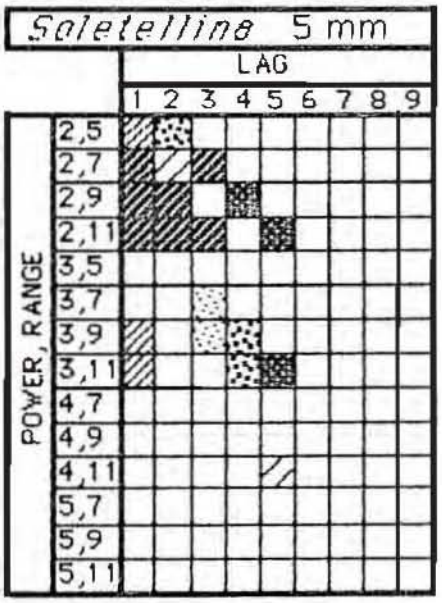
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
291281

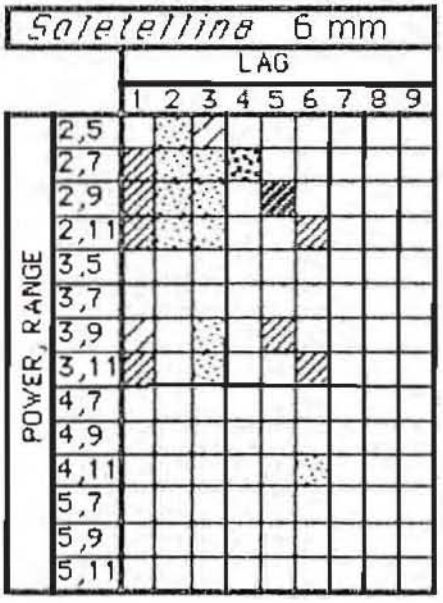






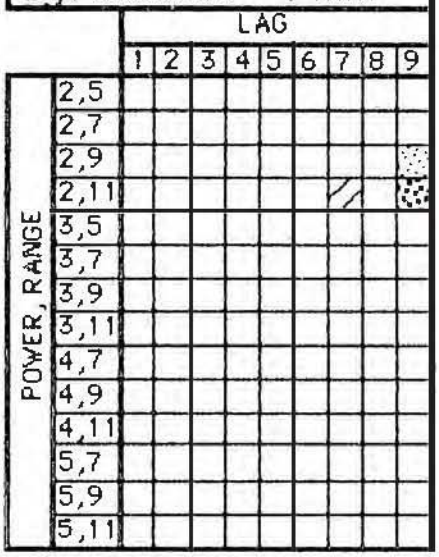




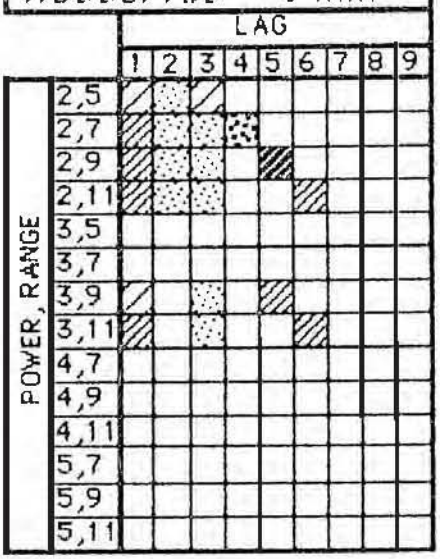


SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
291281

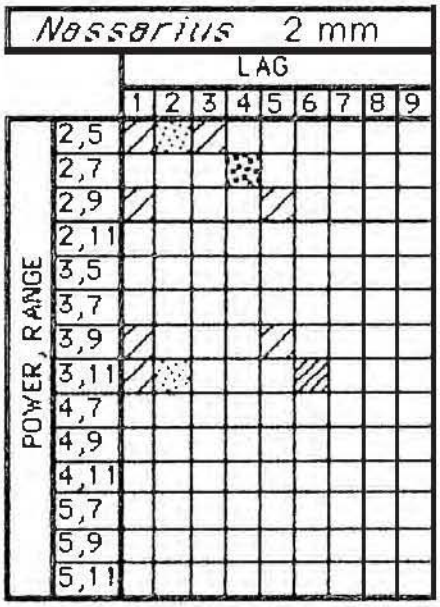
Cylichnina 1 mm



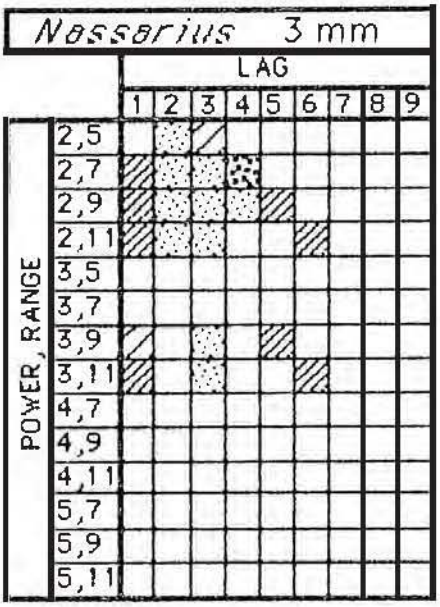
Nassarius 0 mm



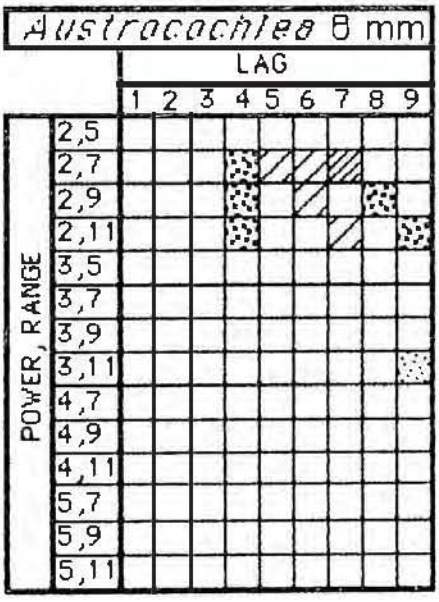
Nassarius 2 mm



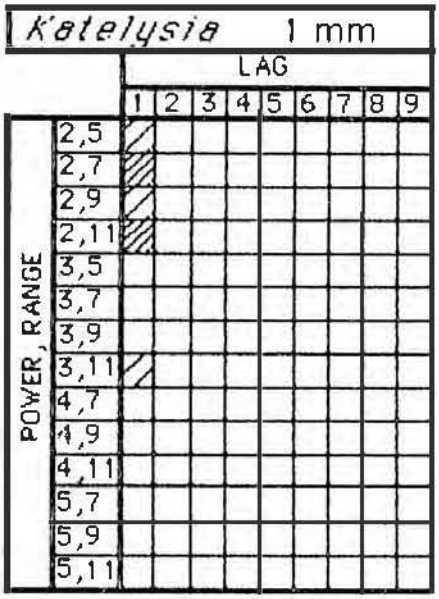
Nassarius 3 mm

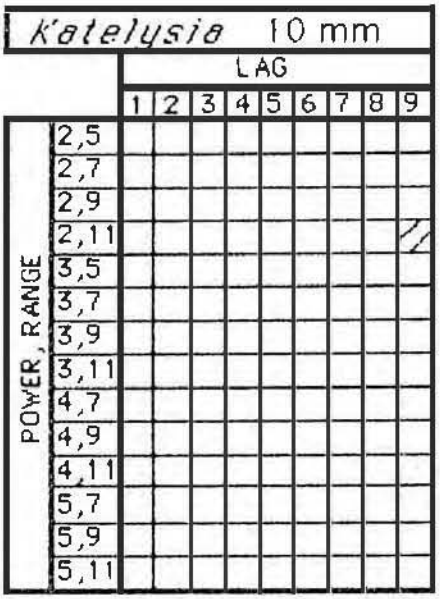


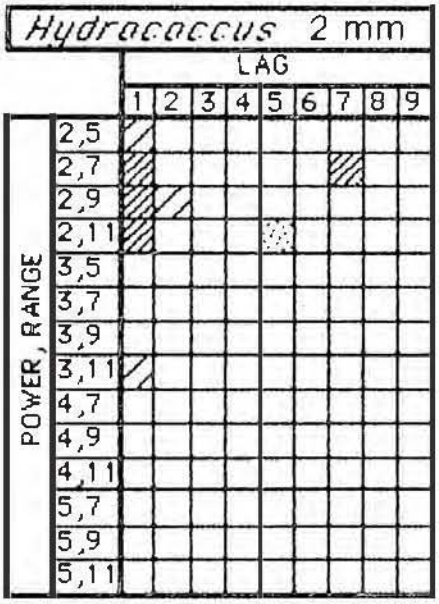
Austrocochlea 8 mm

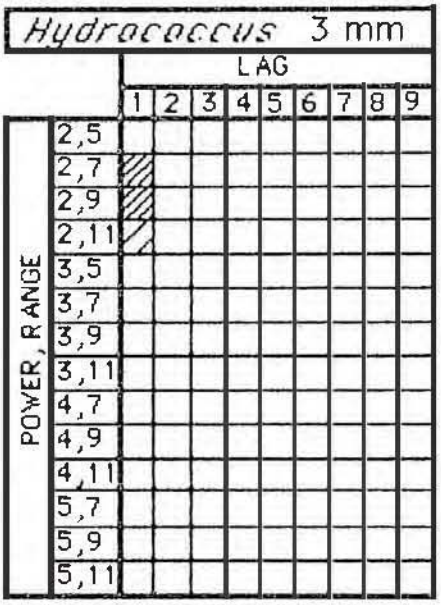


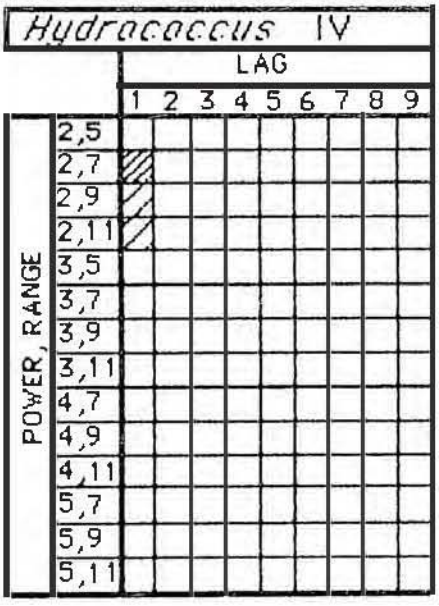
SERIES ANALYSIS OF SPECIES (GROUP) DISTRIBUTIONS
310382

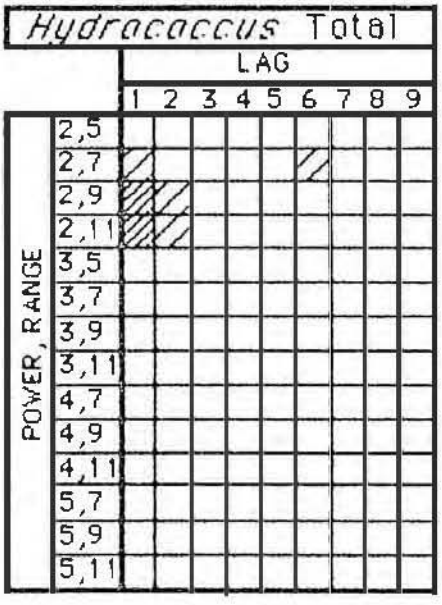


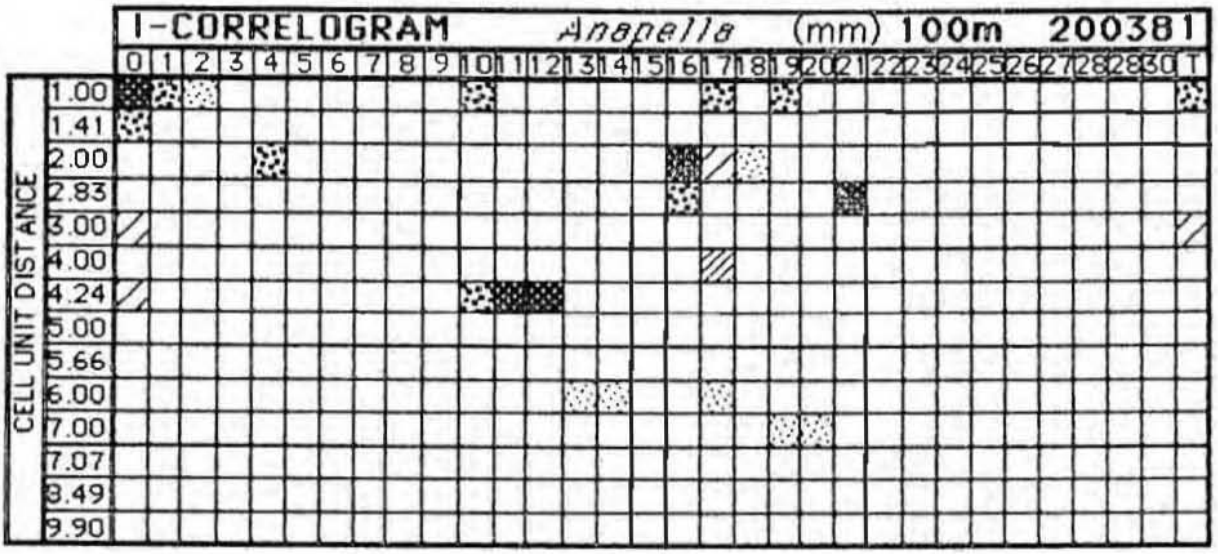











I-CORRELOGRAM Anapella (mm) 100m 200381
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 28 30 T
CELL UNIT DISTANCE
1.00
1.41
2.00
2.83
3.00
4.00
4.24
5.00
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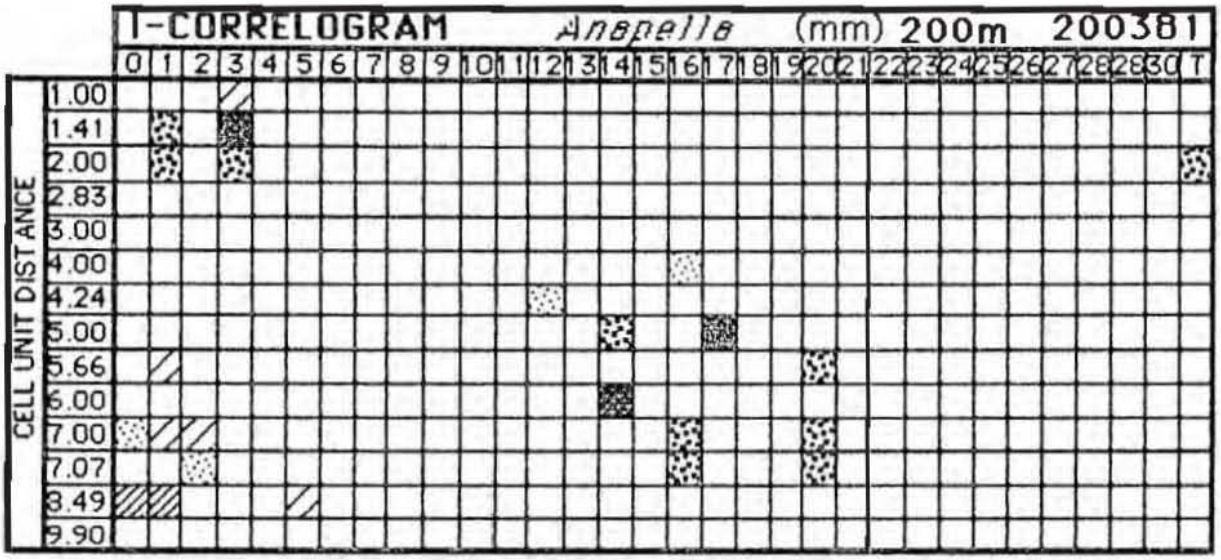
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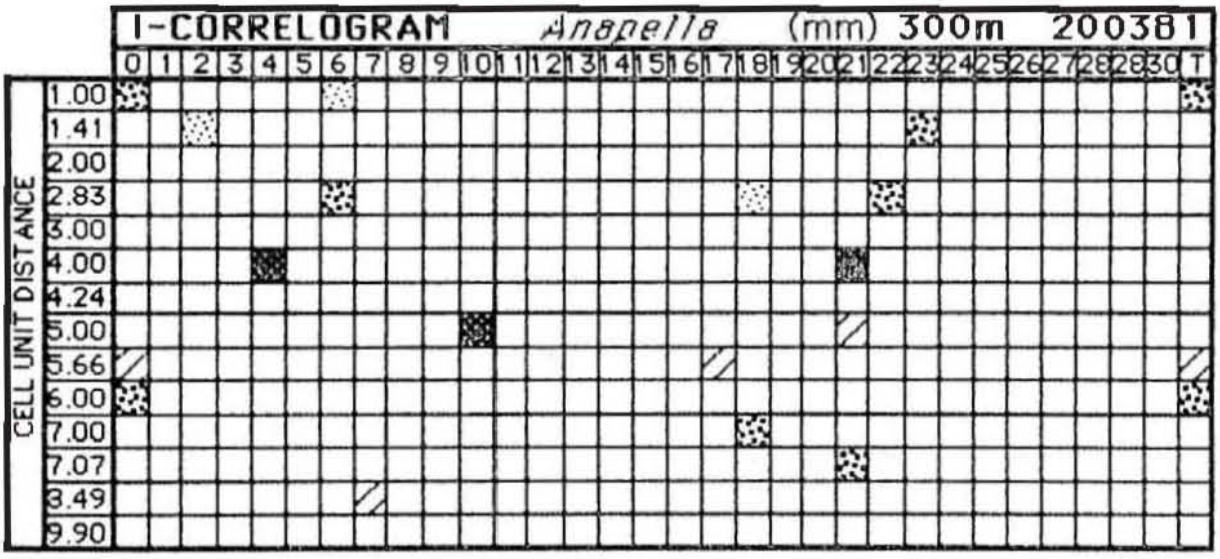
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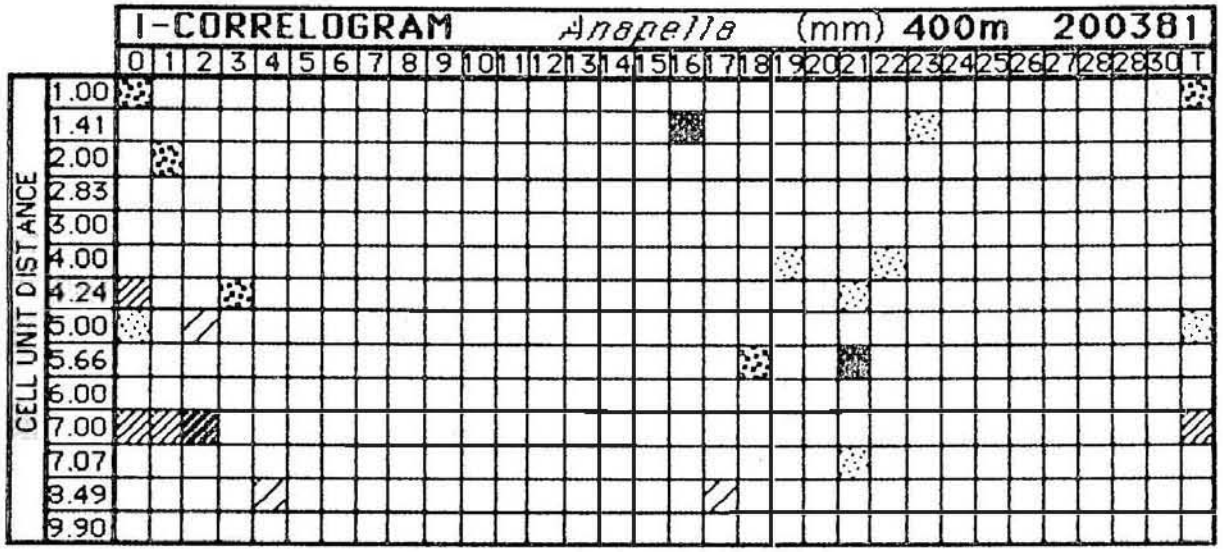
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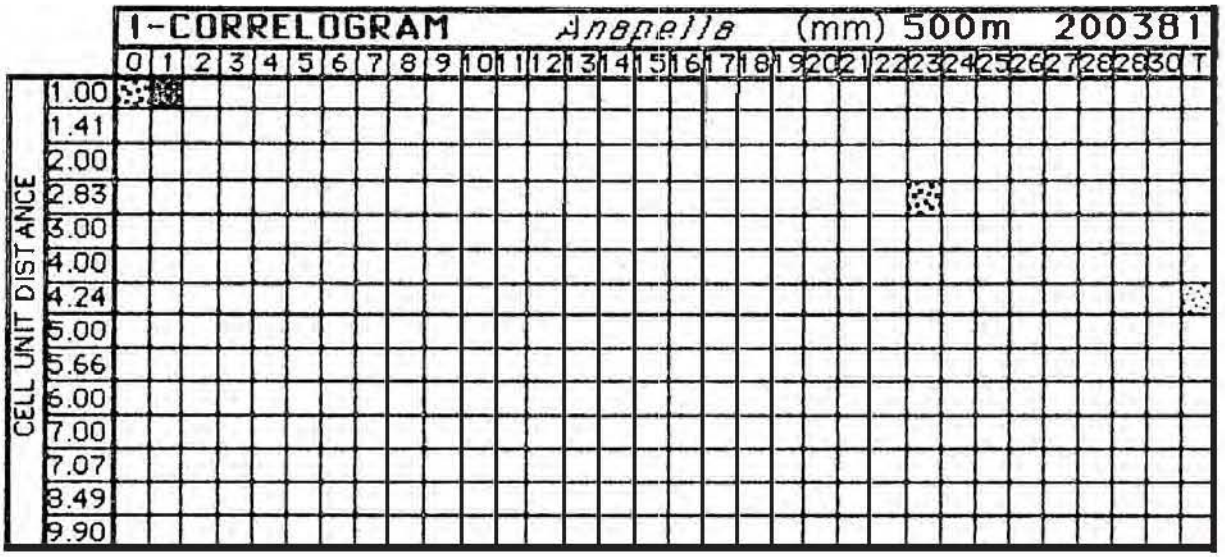
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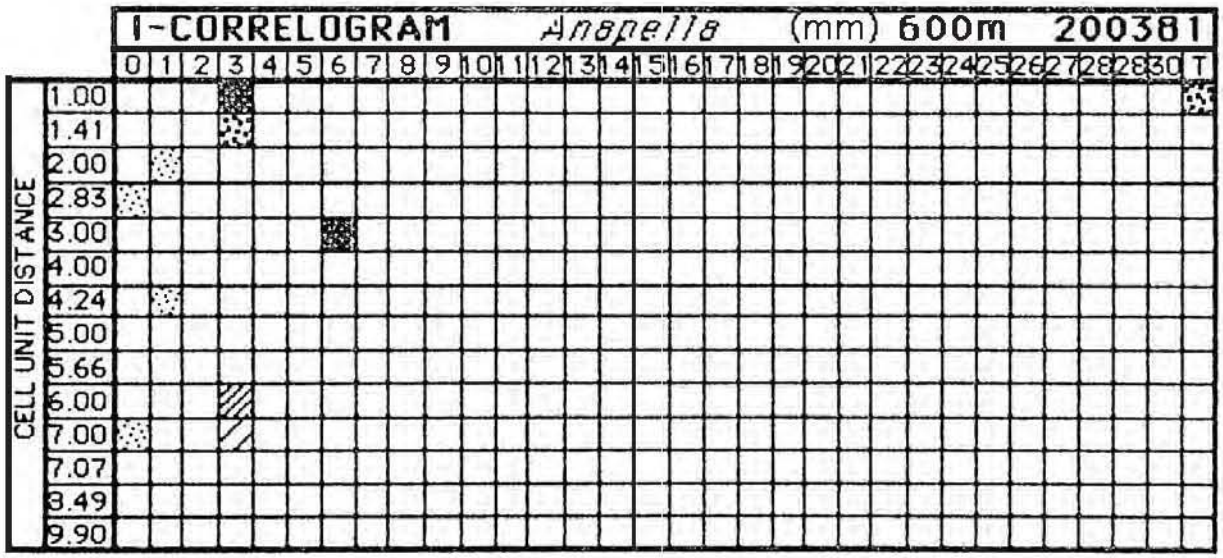
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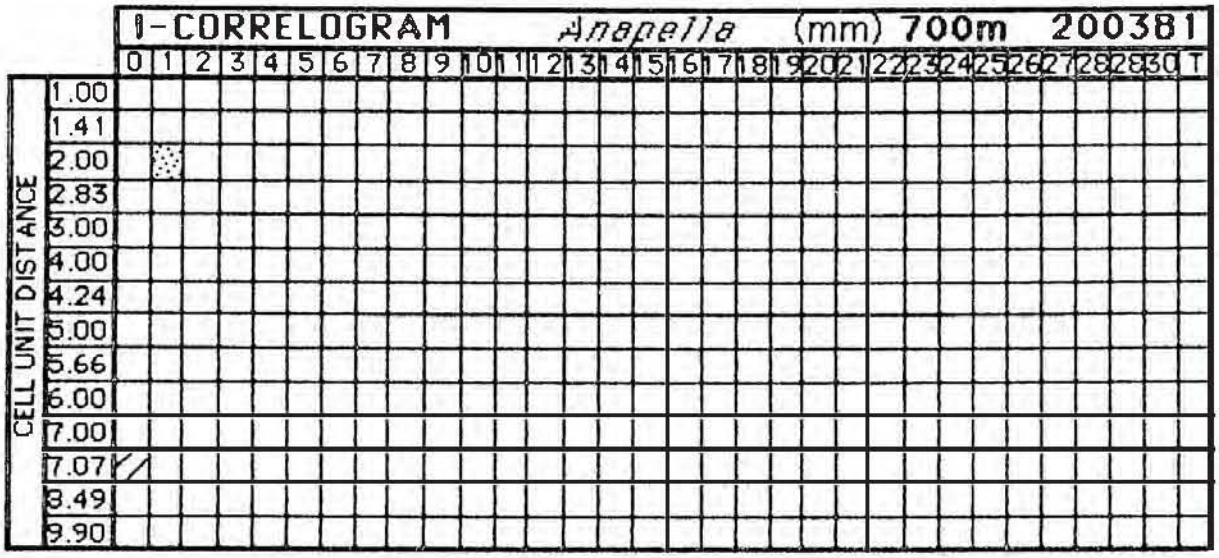
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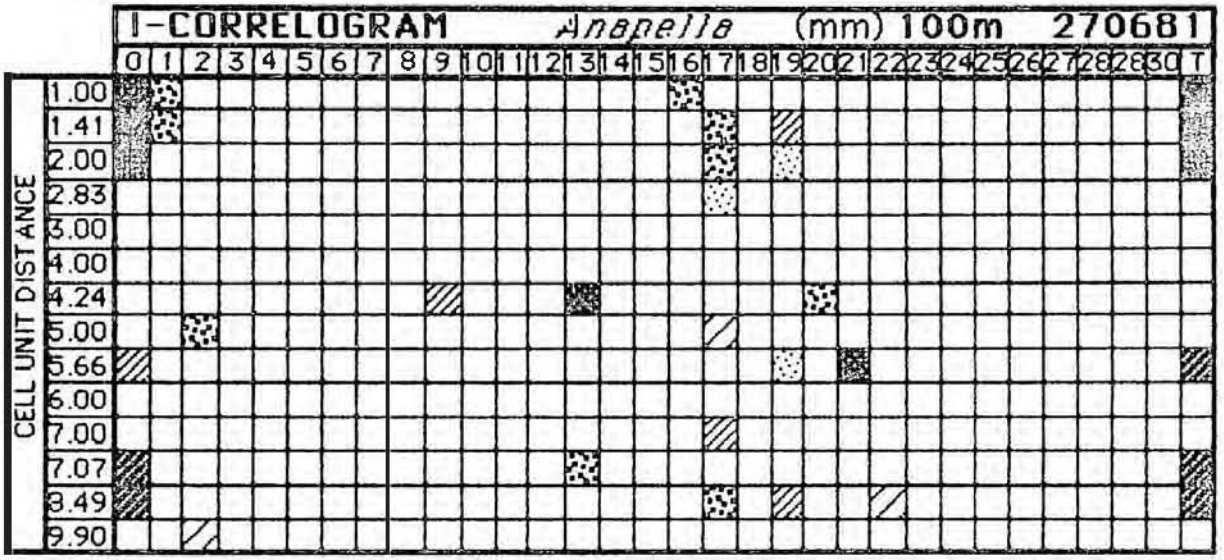
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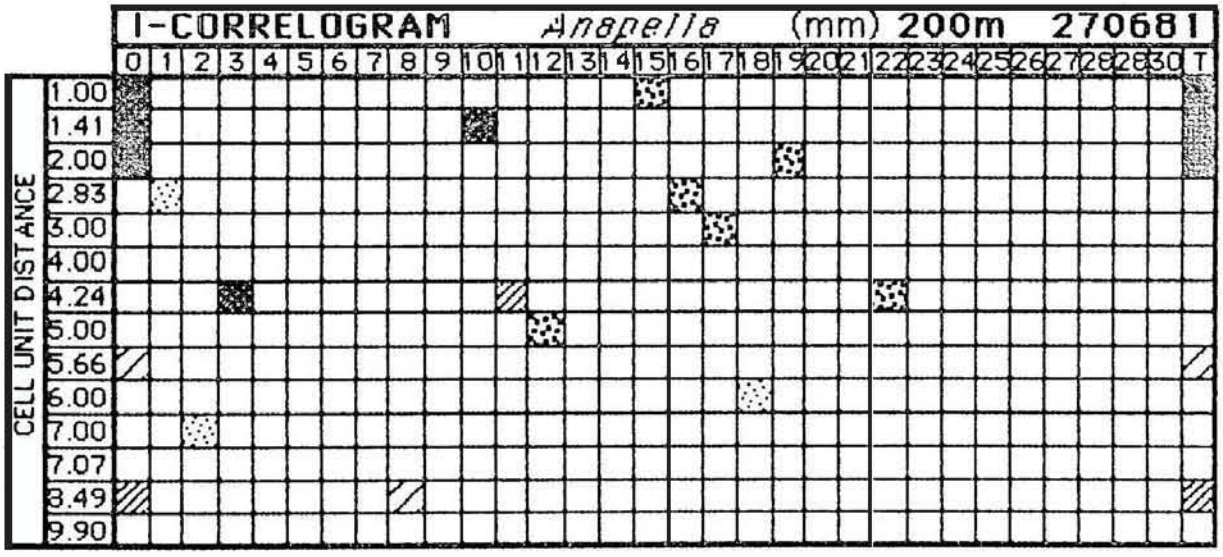
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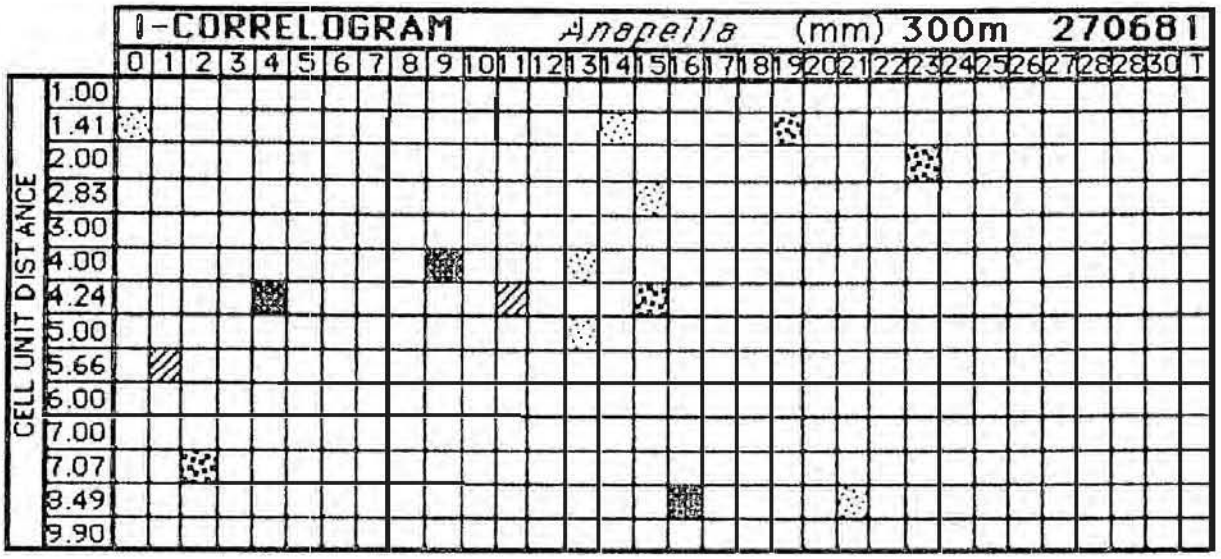
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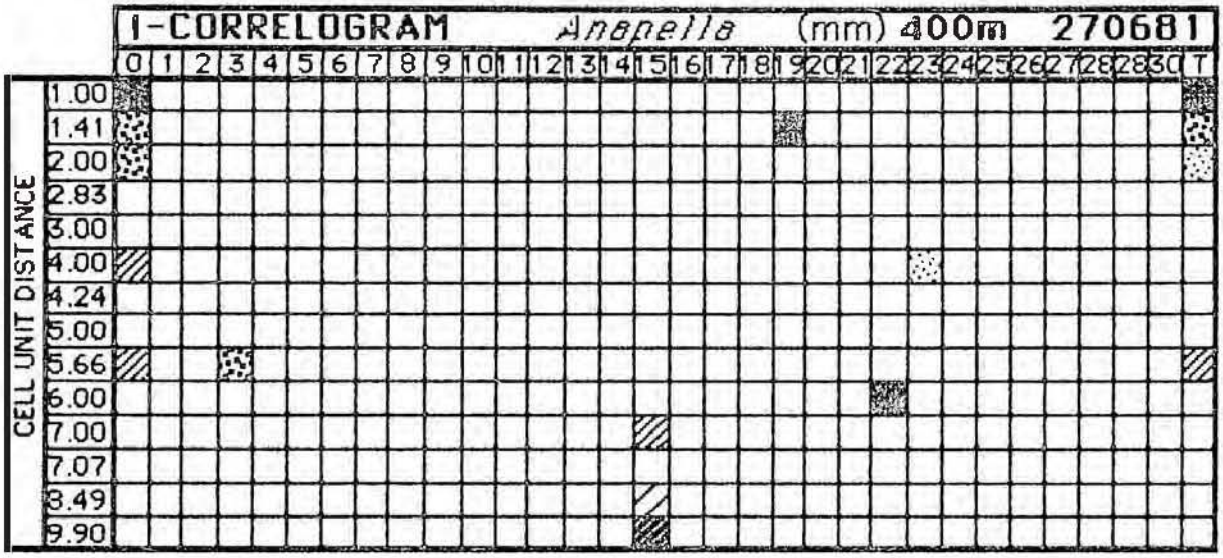
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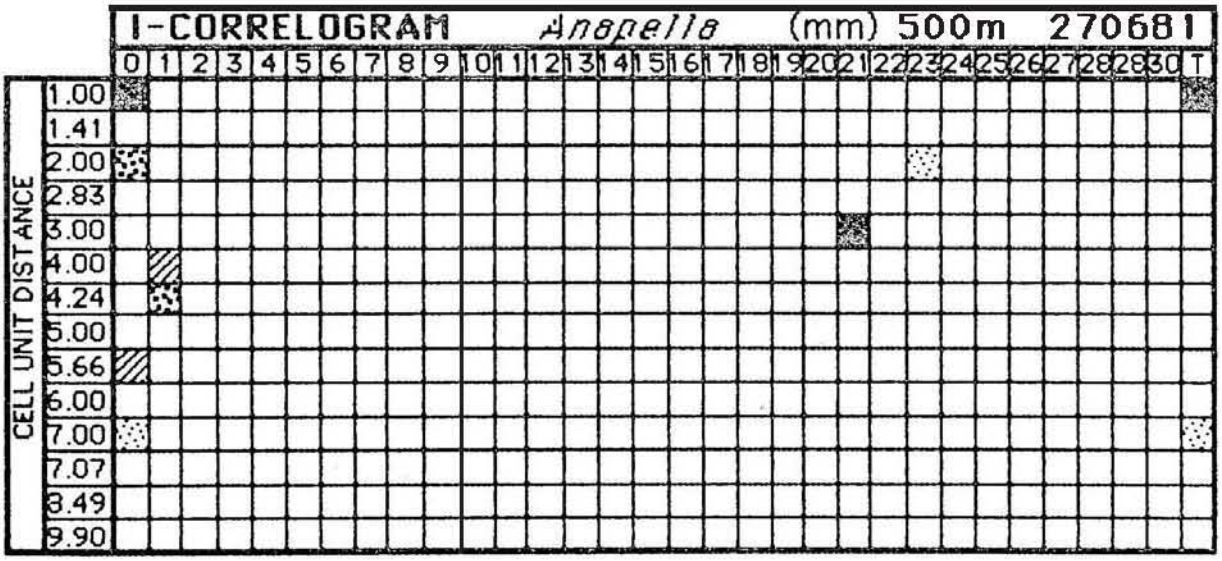
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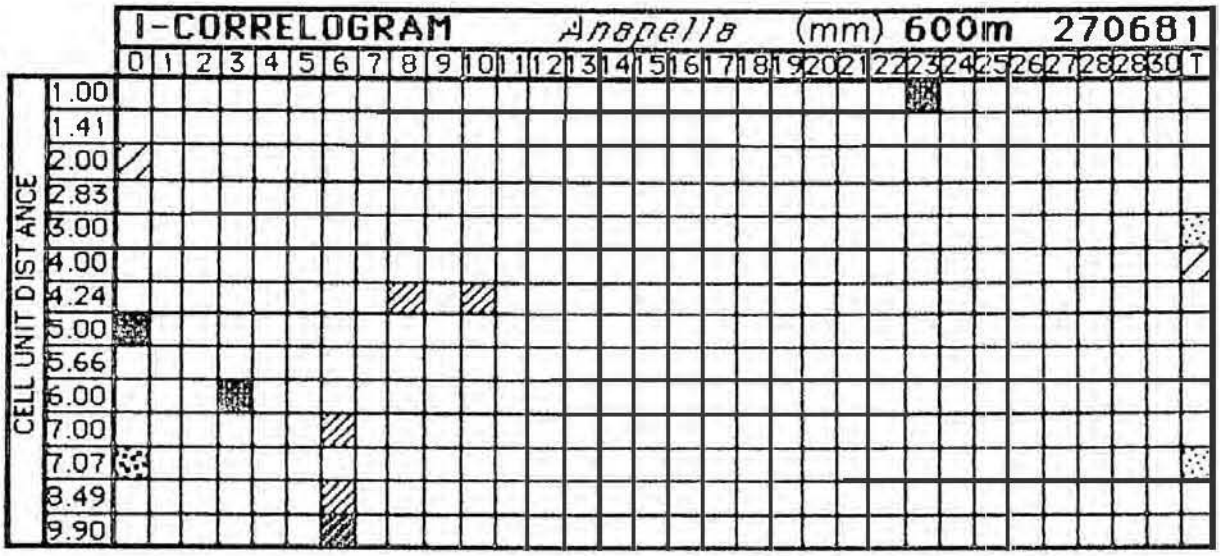
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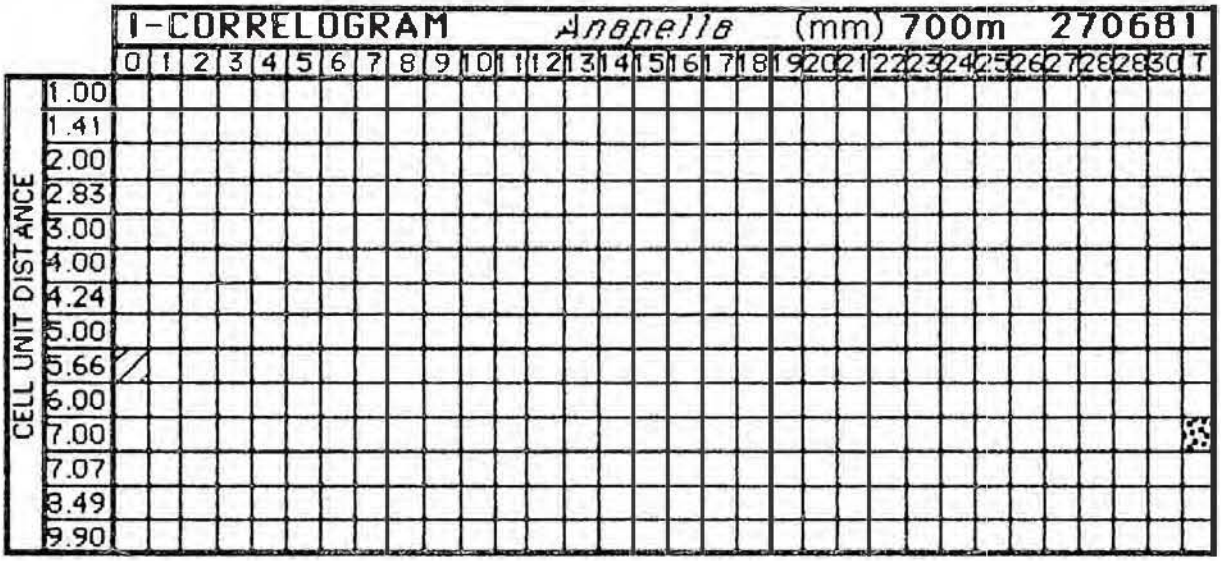
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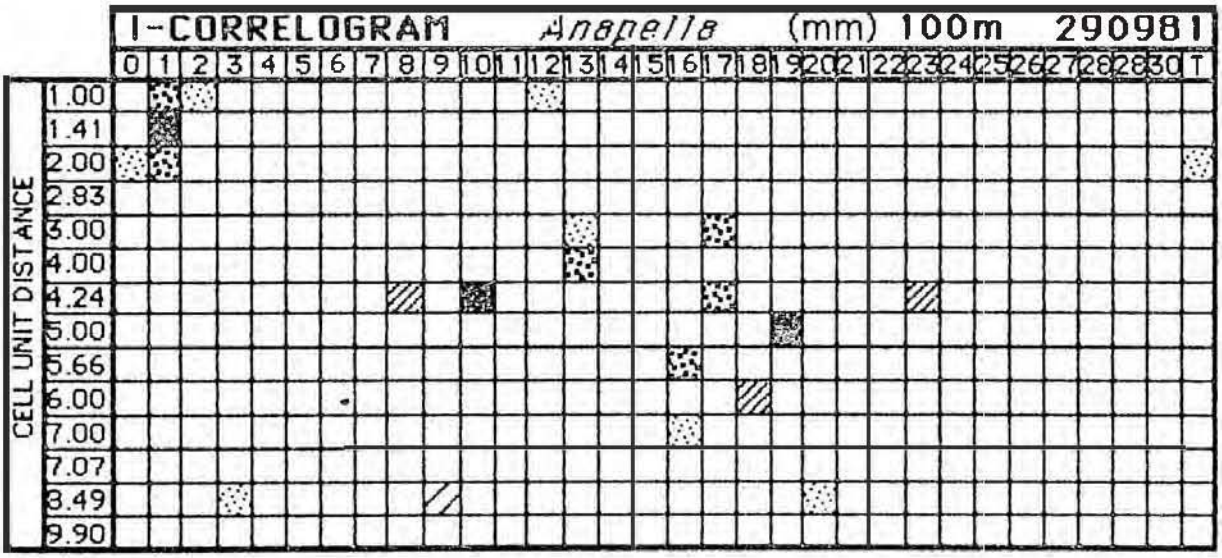
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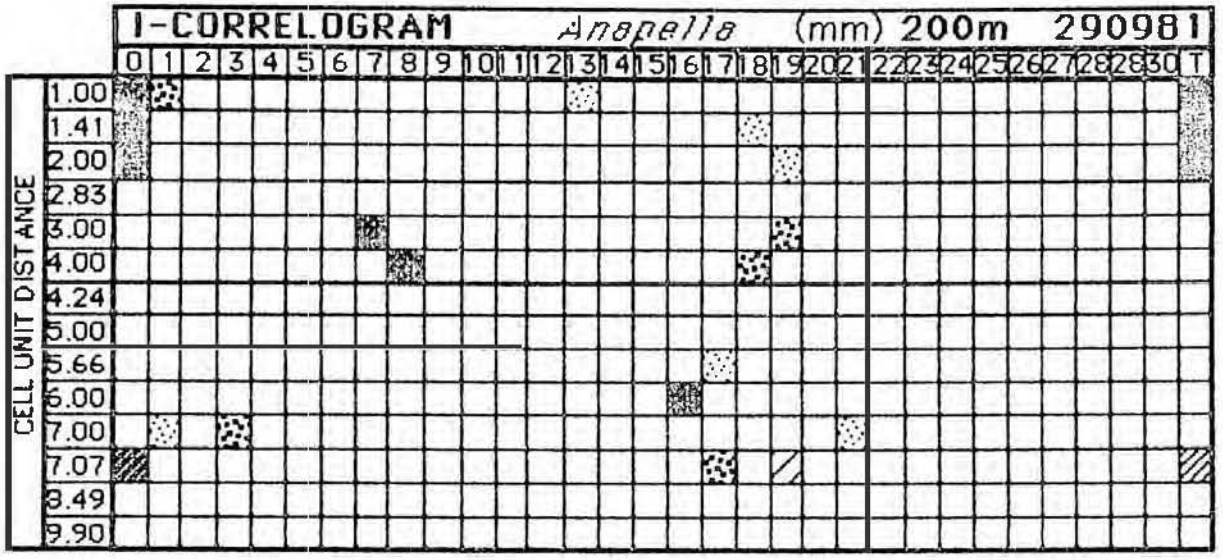
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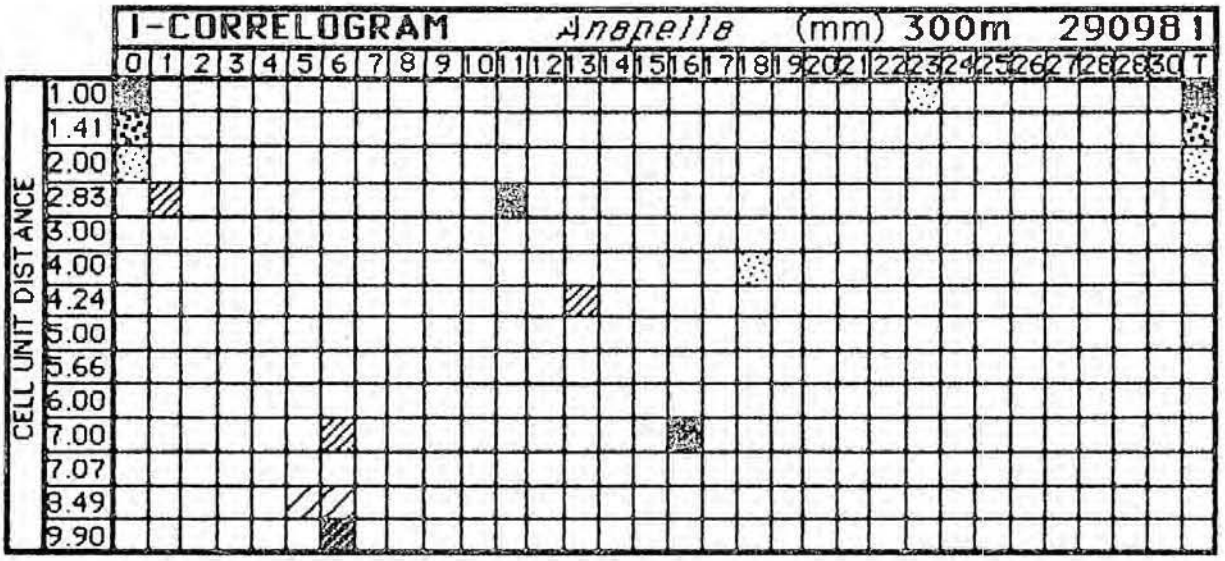
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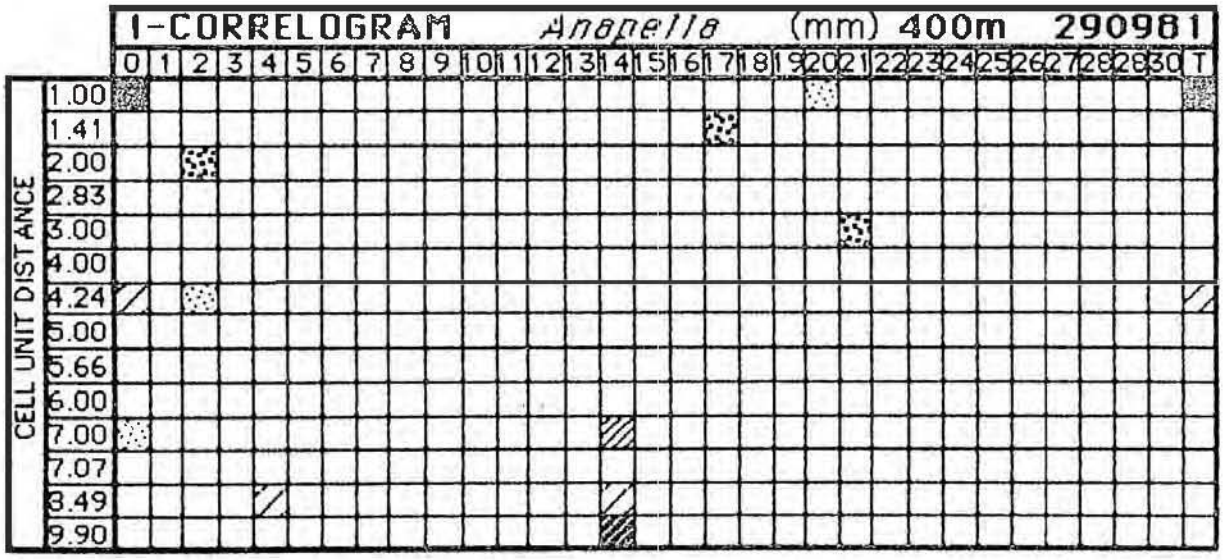
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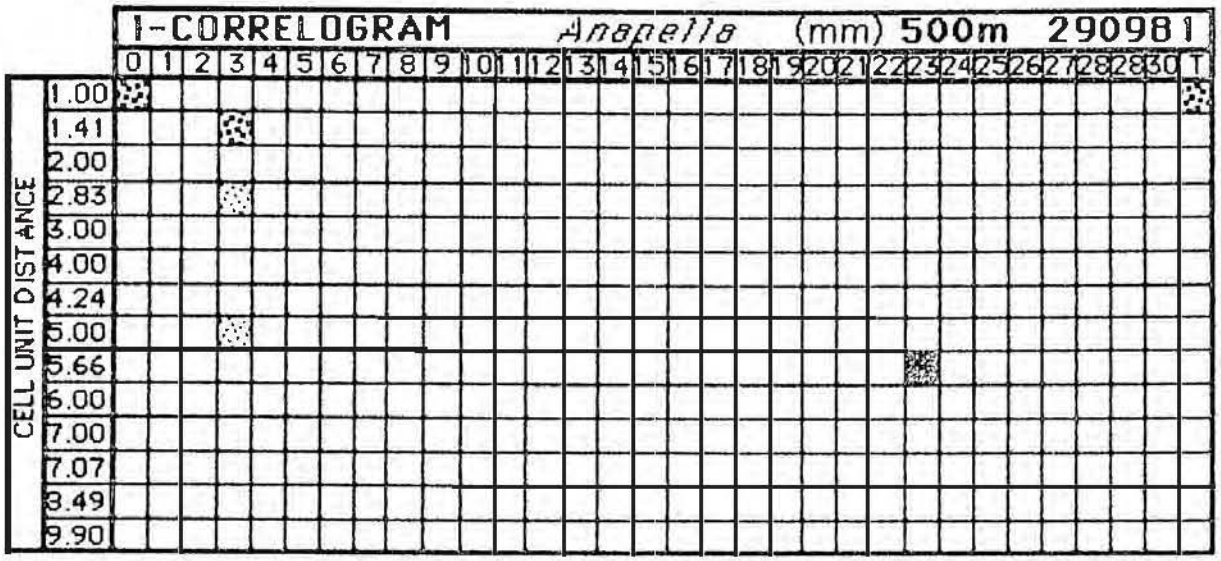
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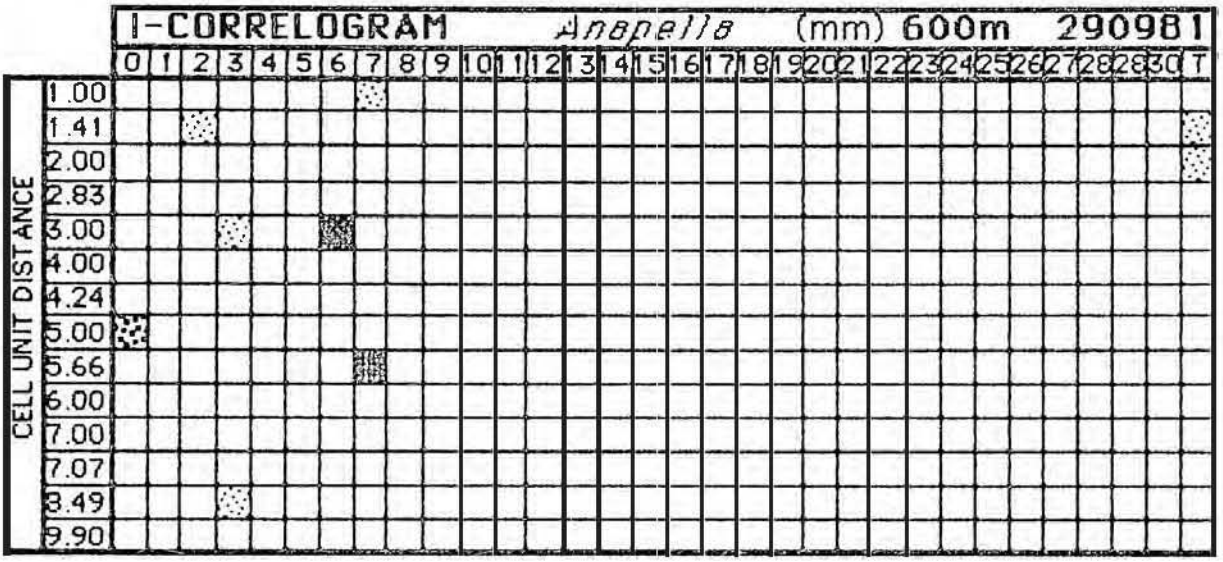
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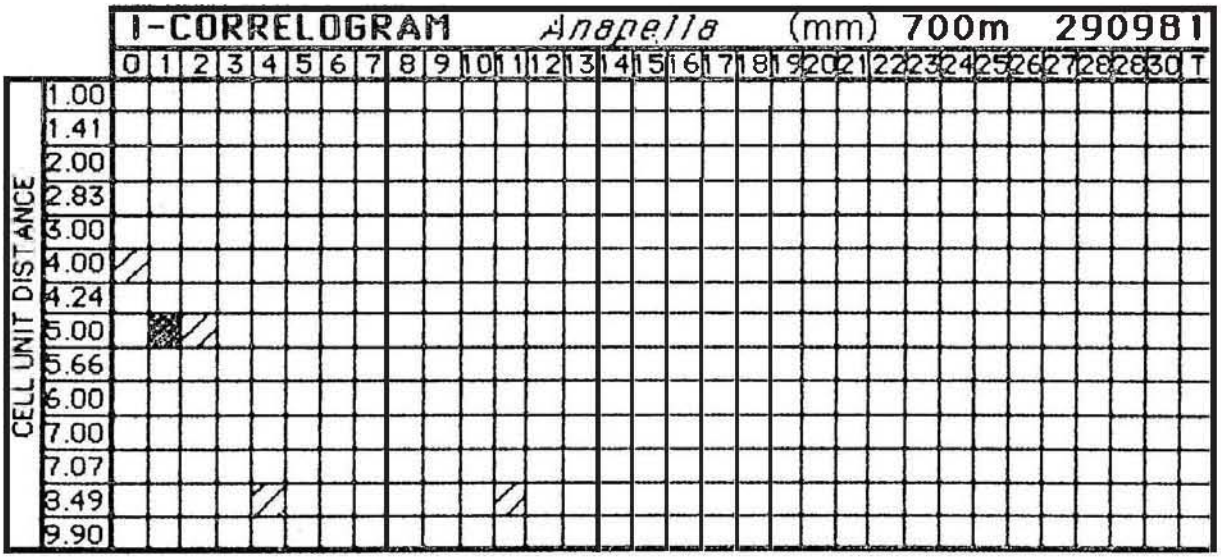
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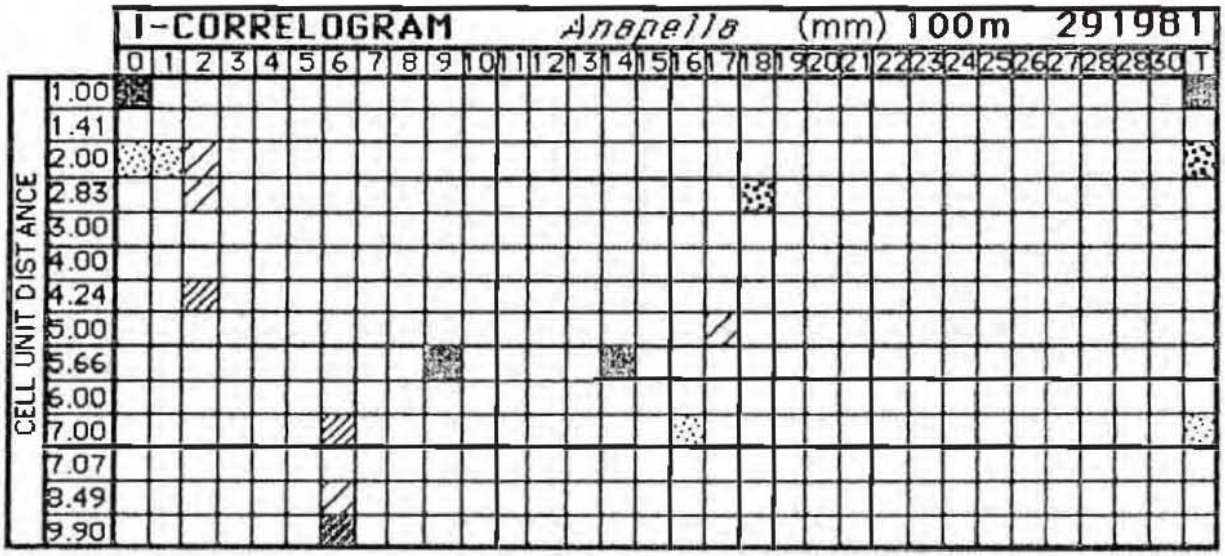
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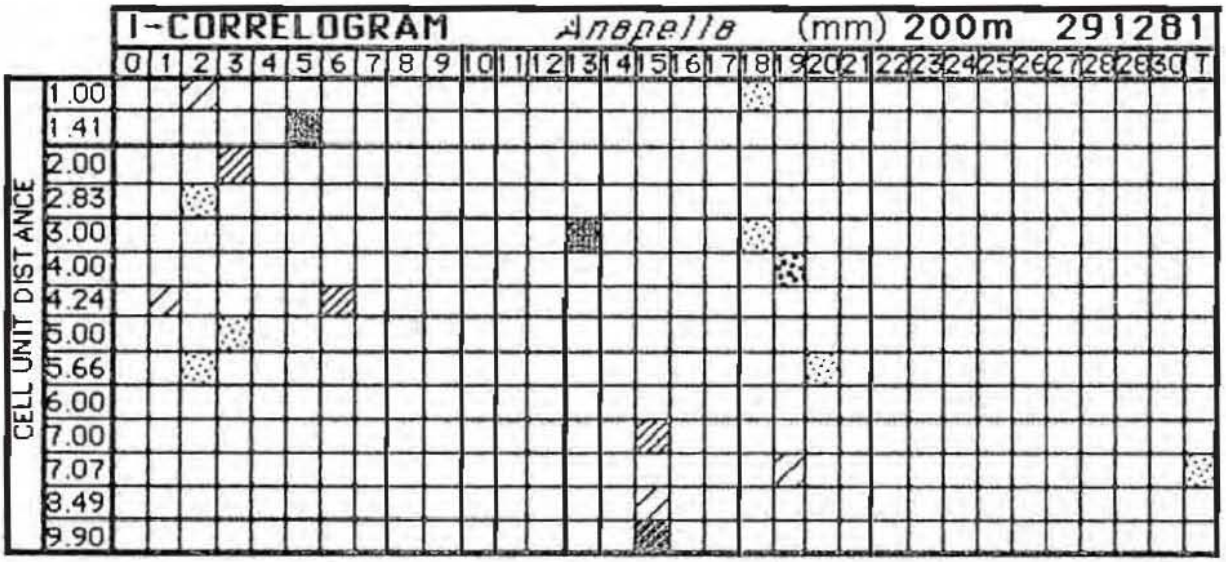
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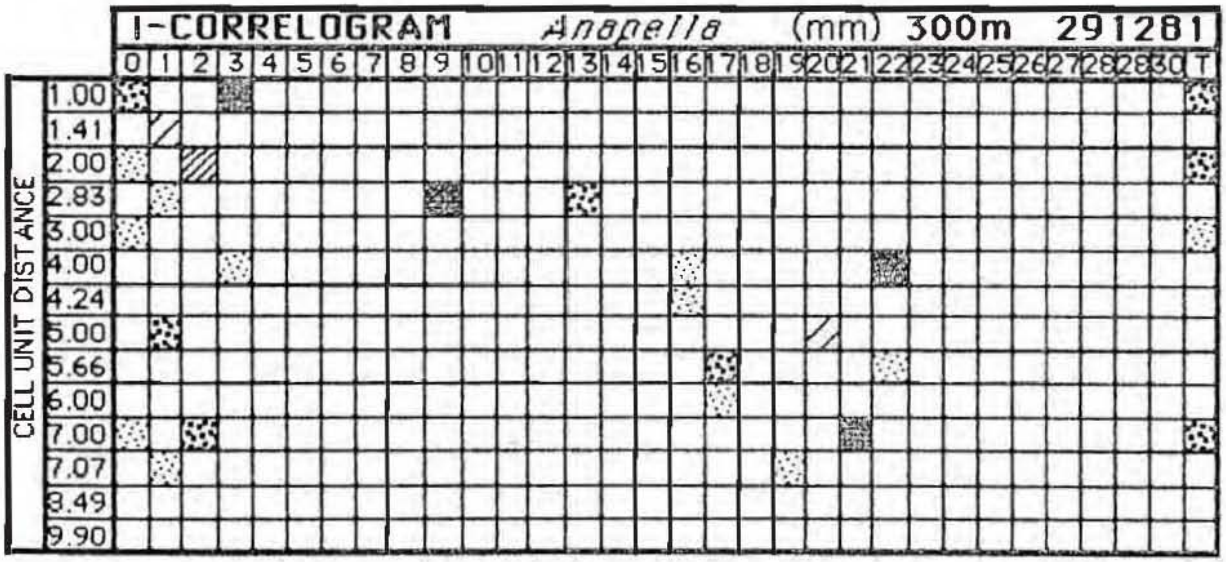
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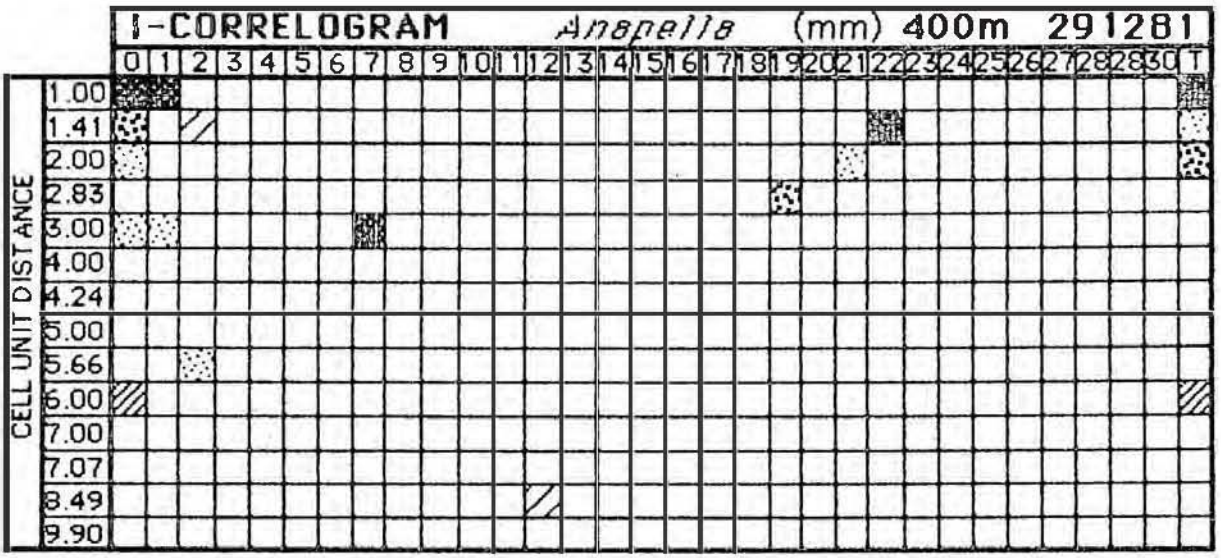
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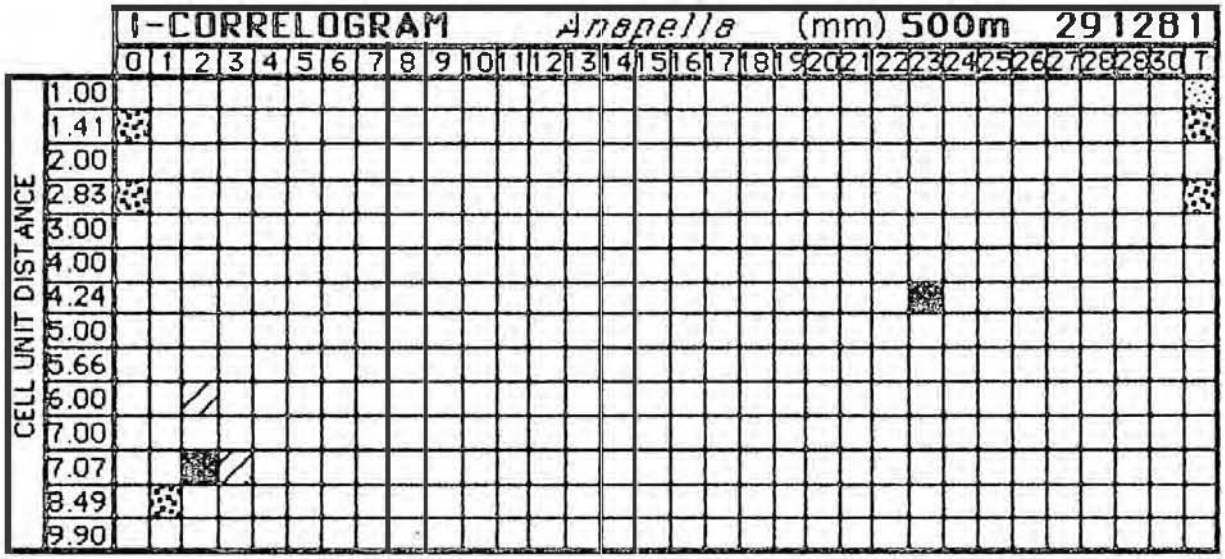
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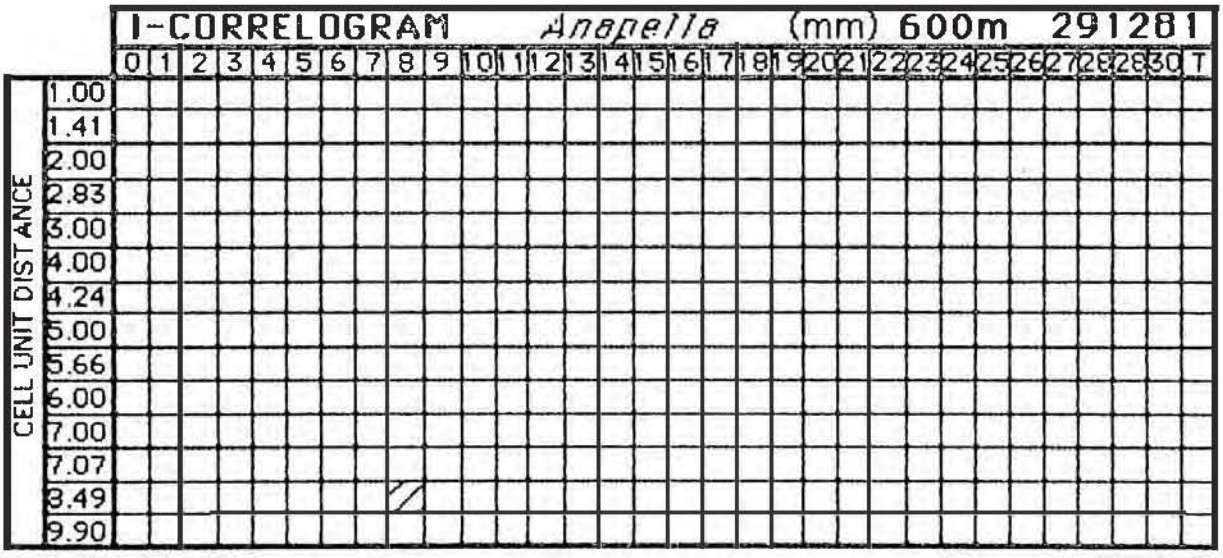
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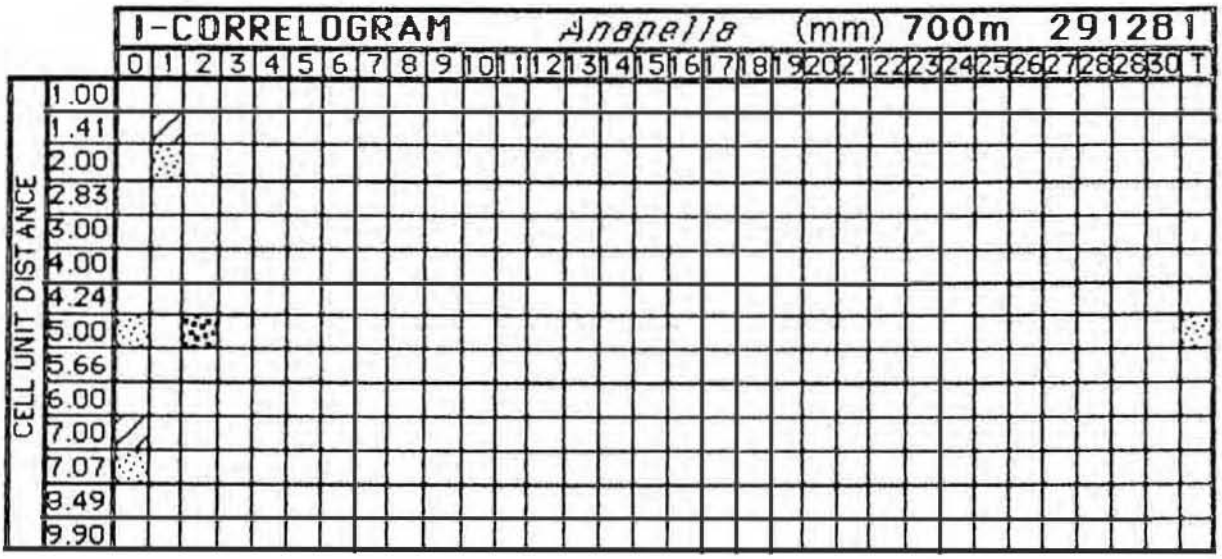
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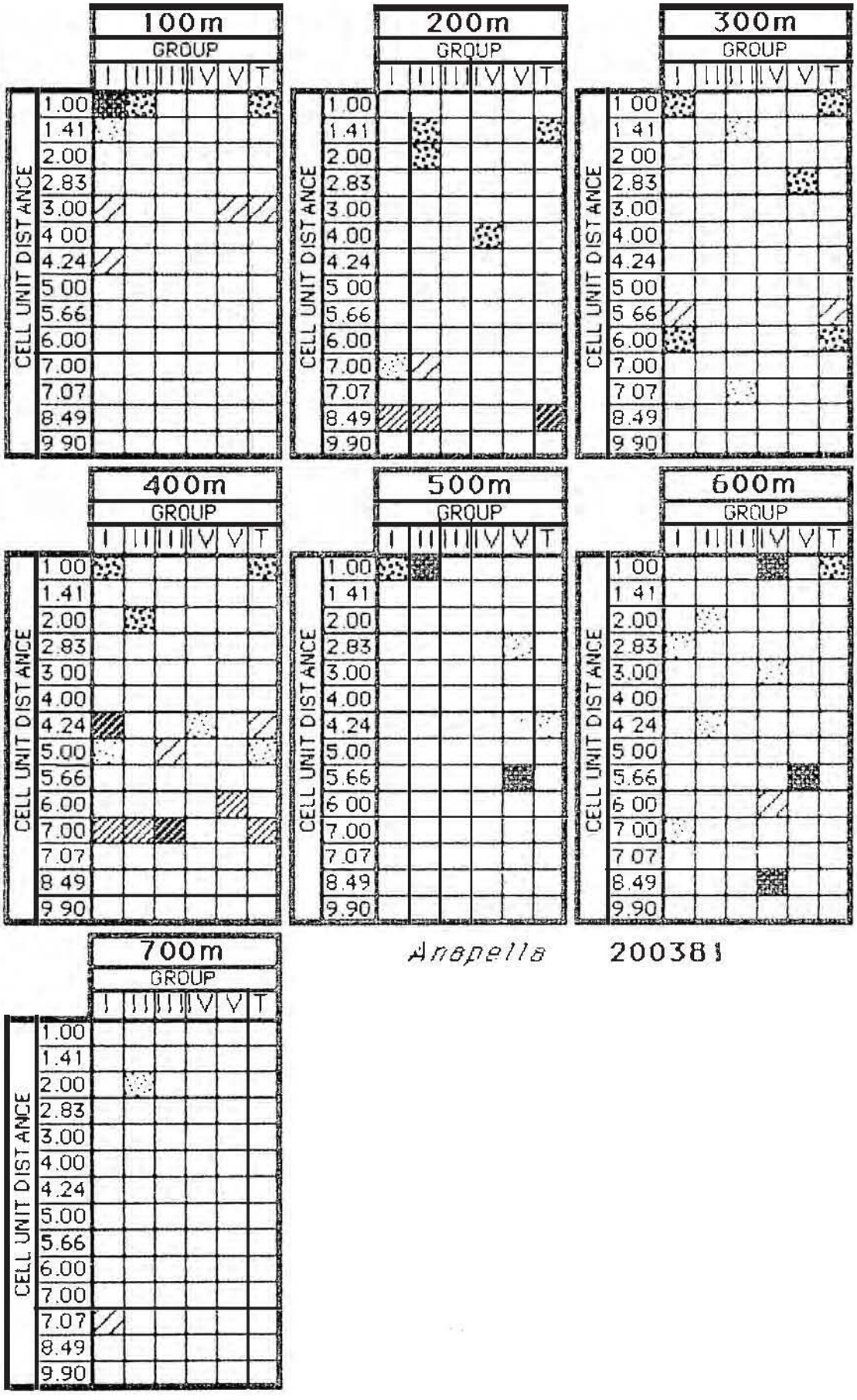
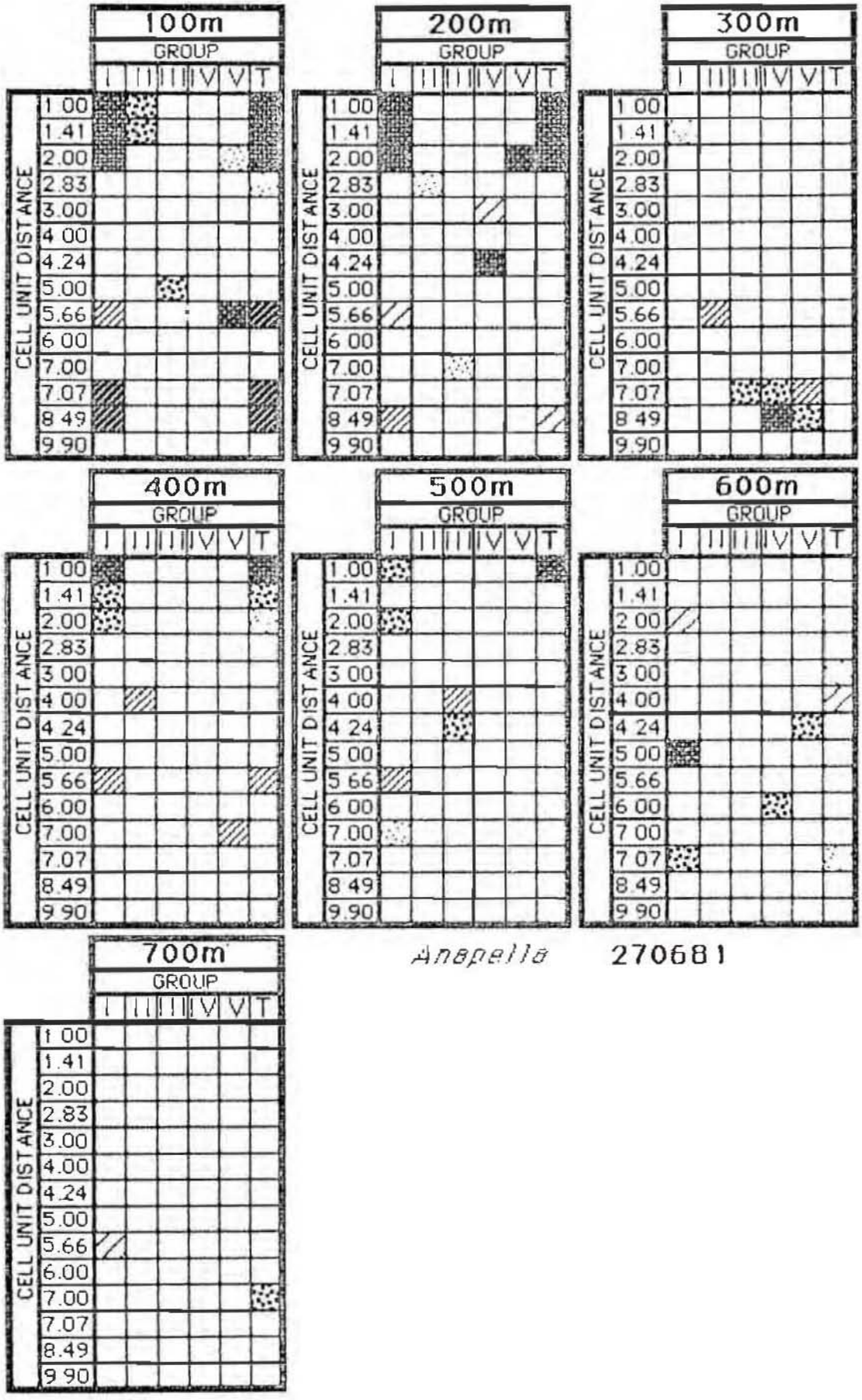


Anapella 200381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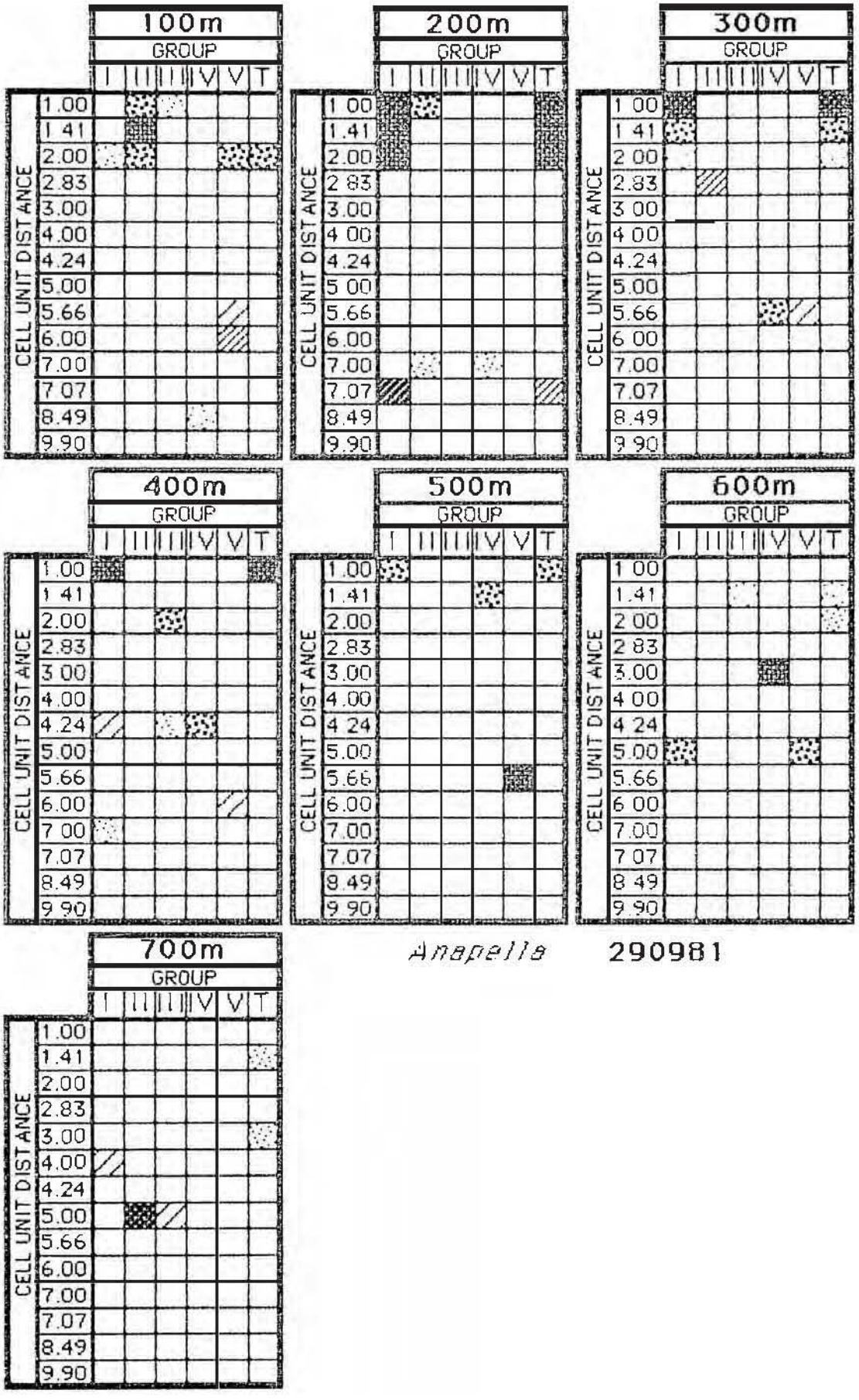

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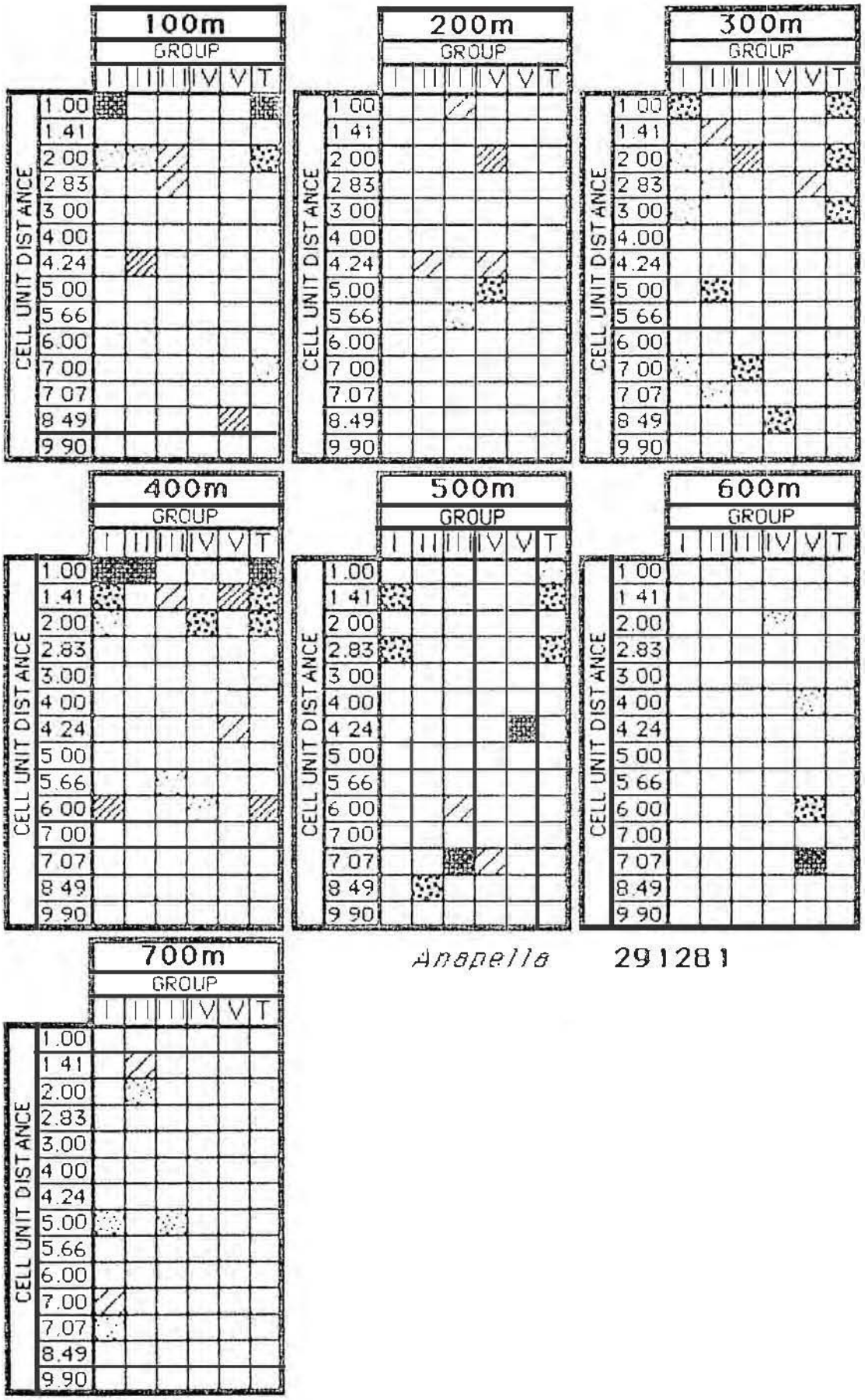
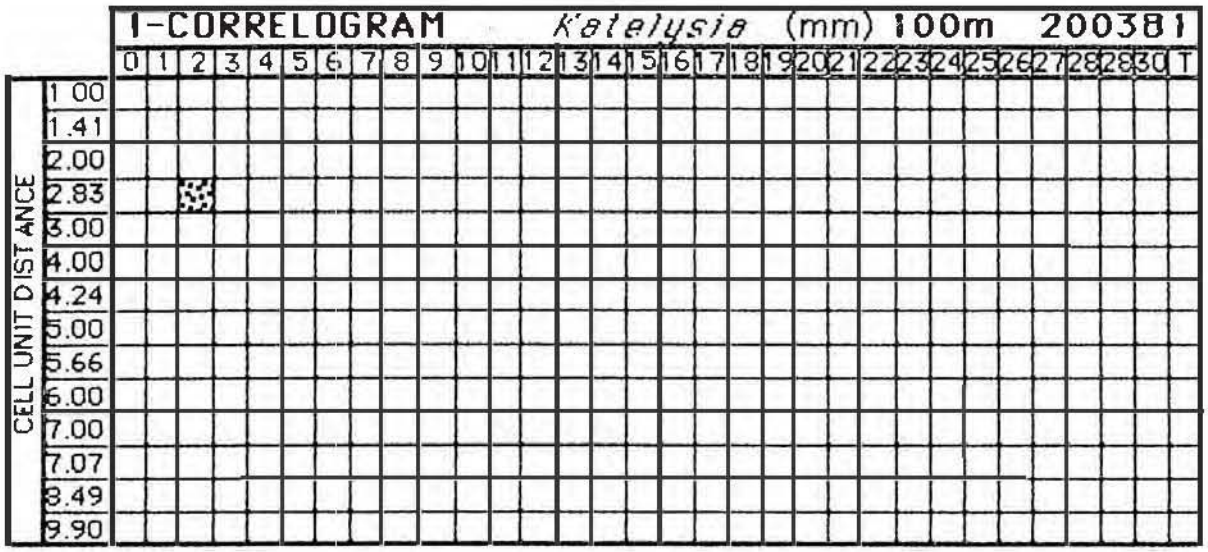


Anapella 291281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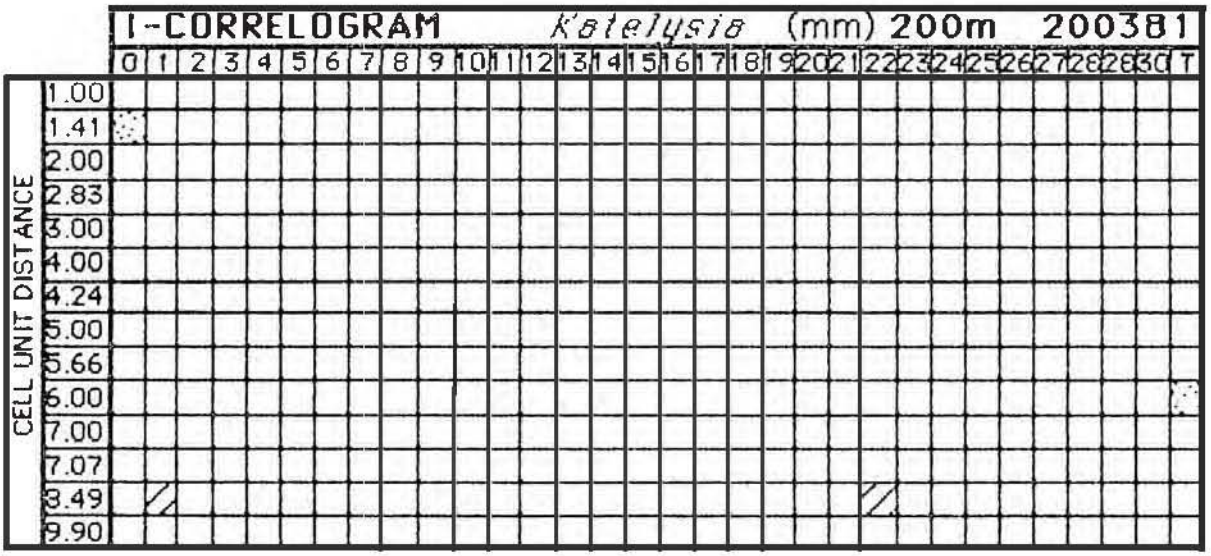
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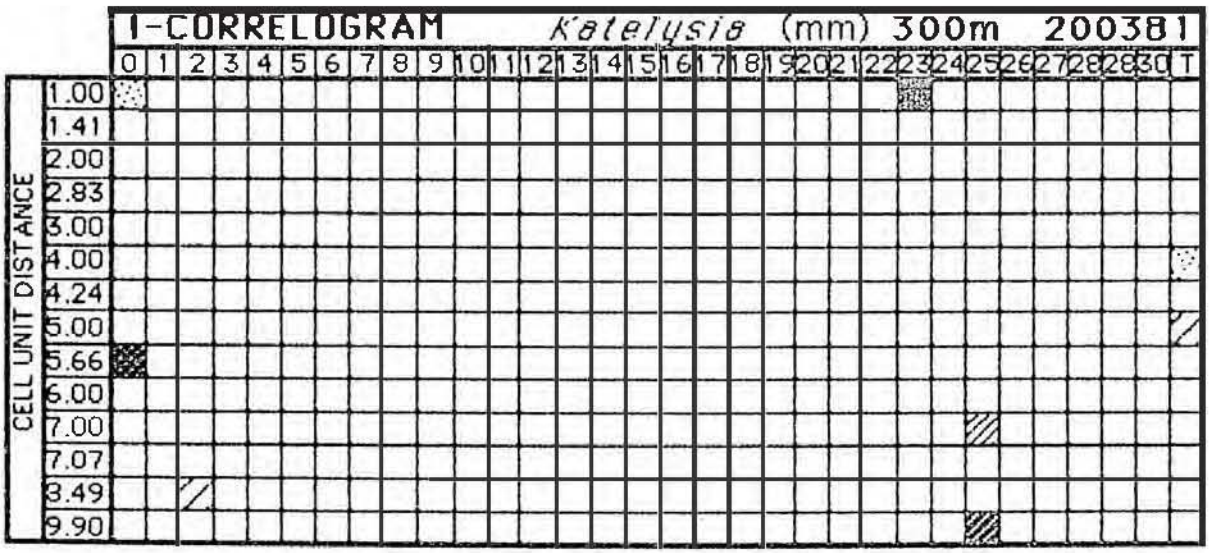
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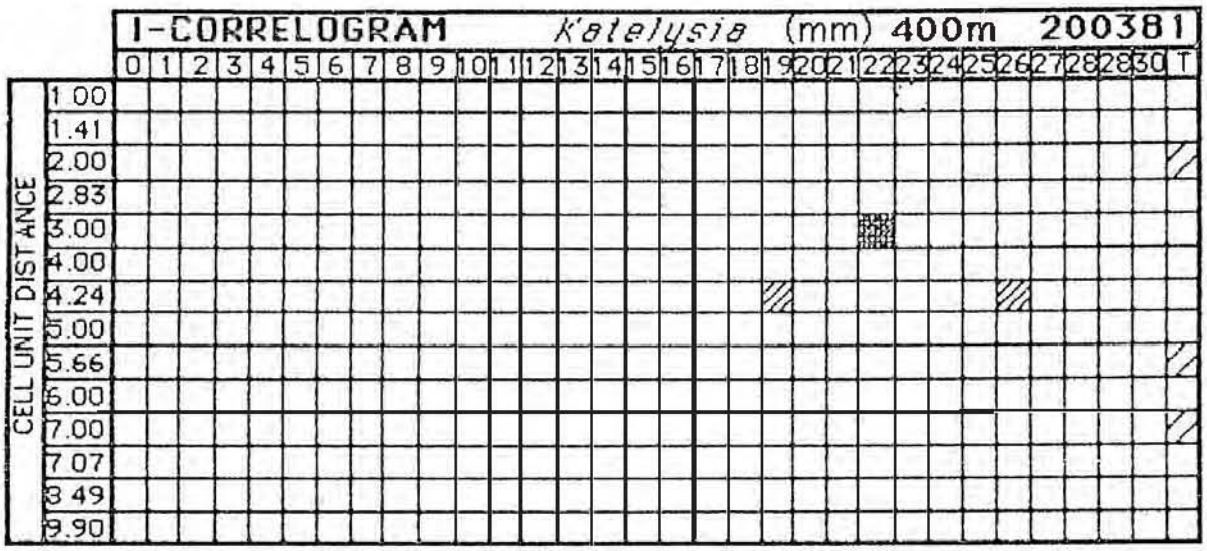
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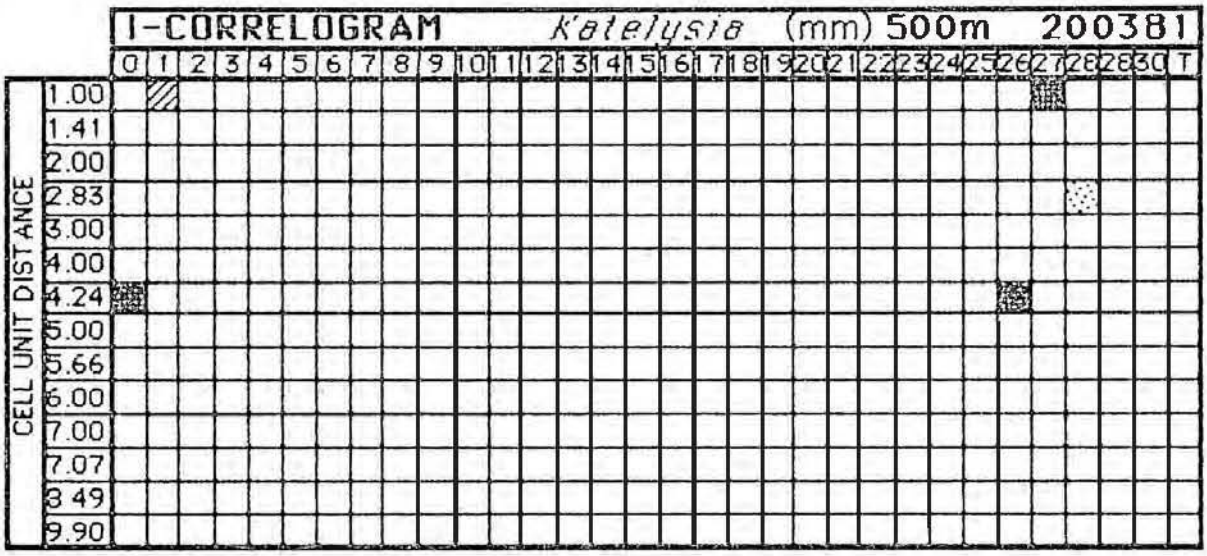
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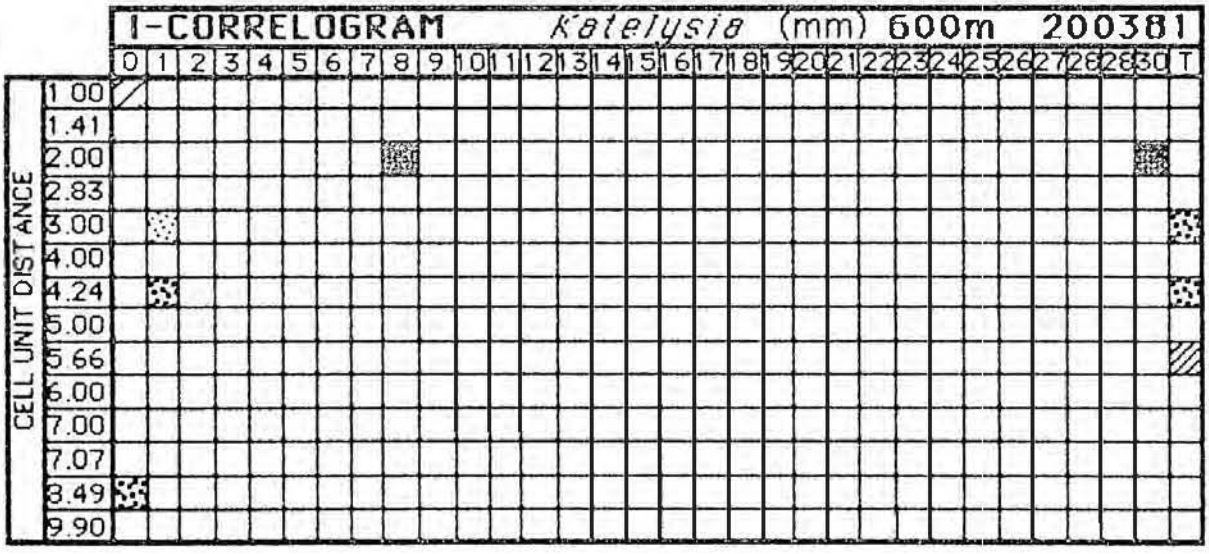
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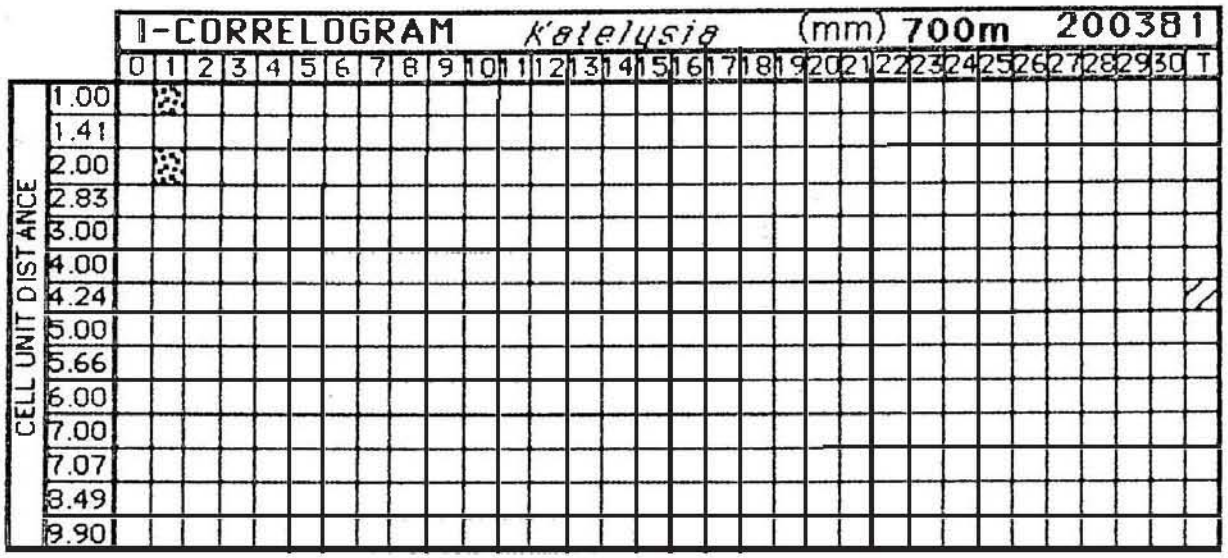
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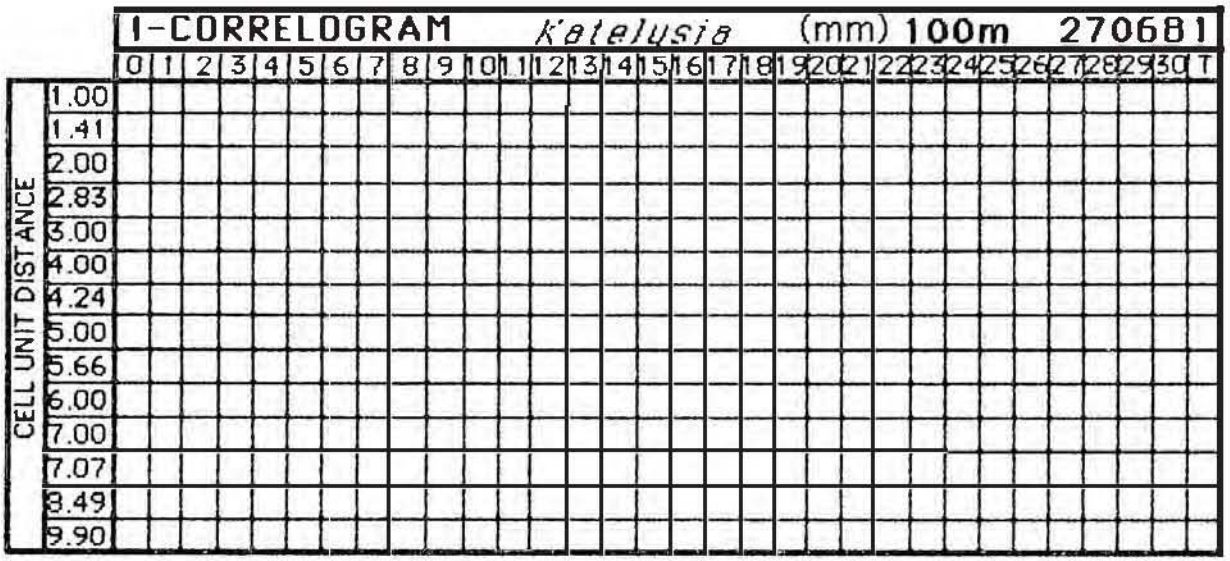
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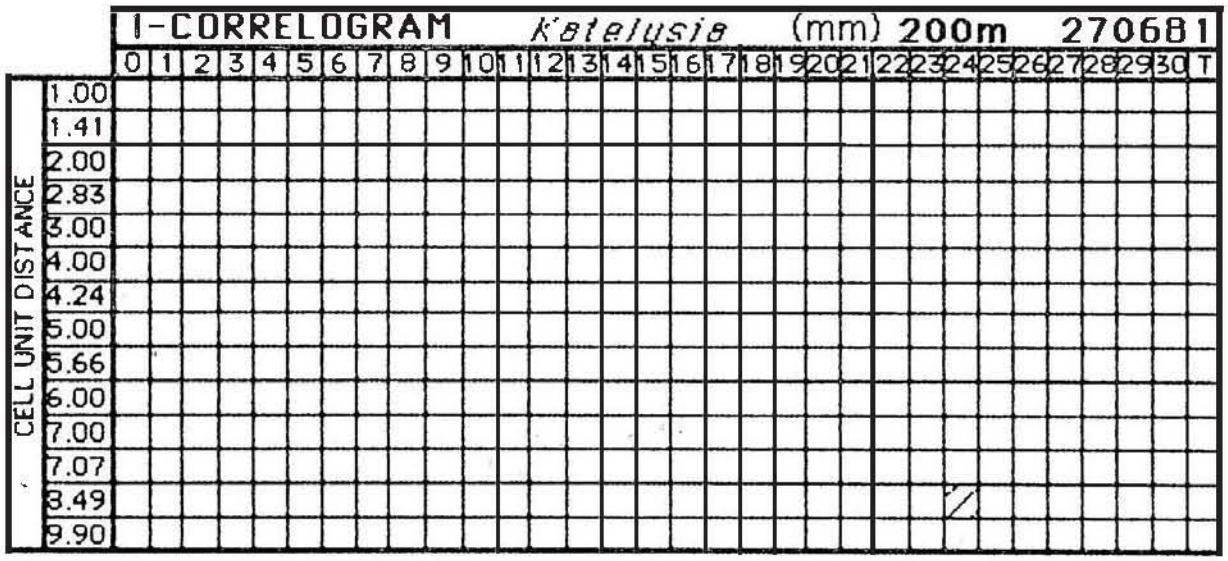
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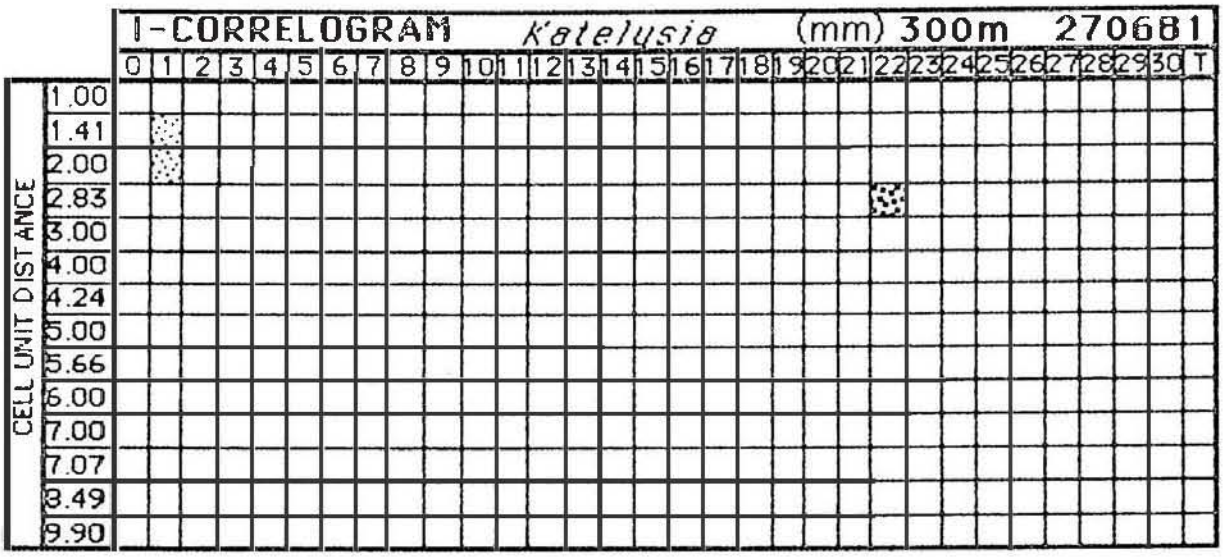
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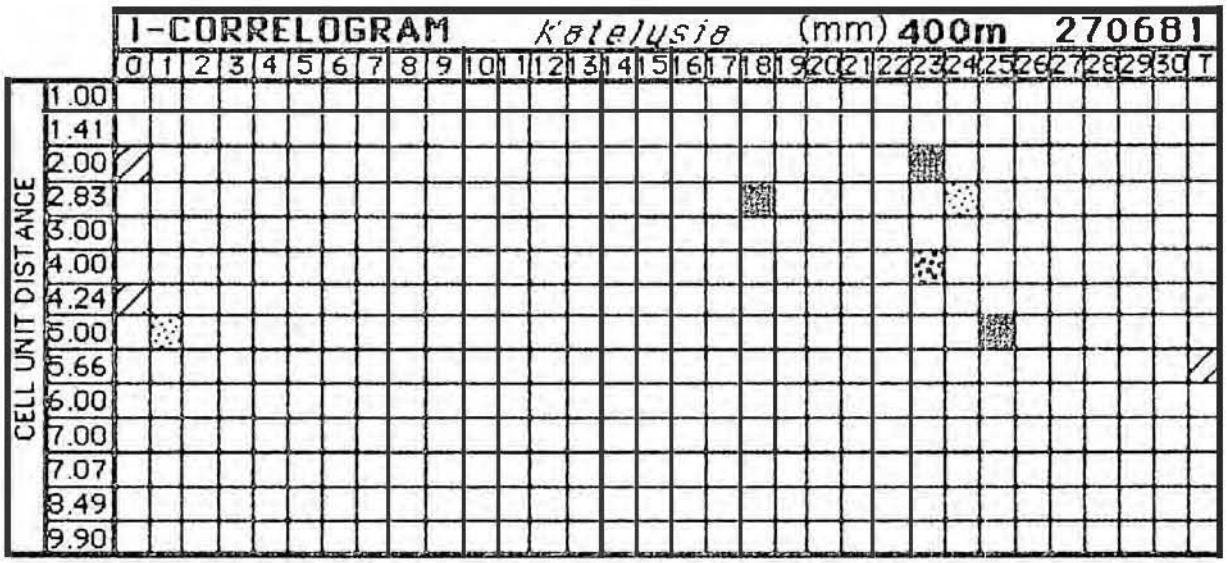
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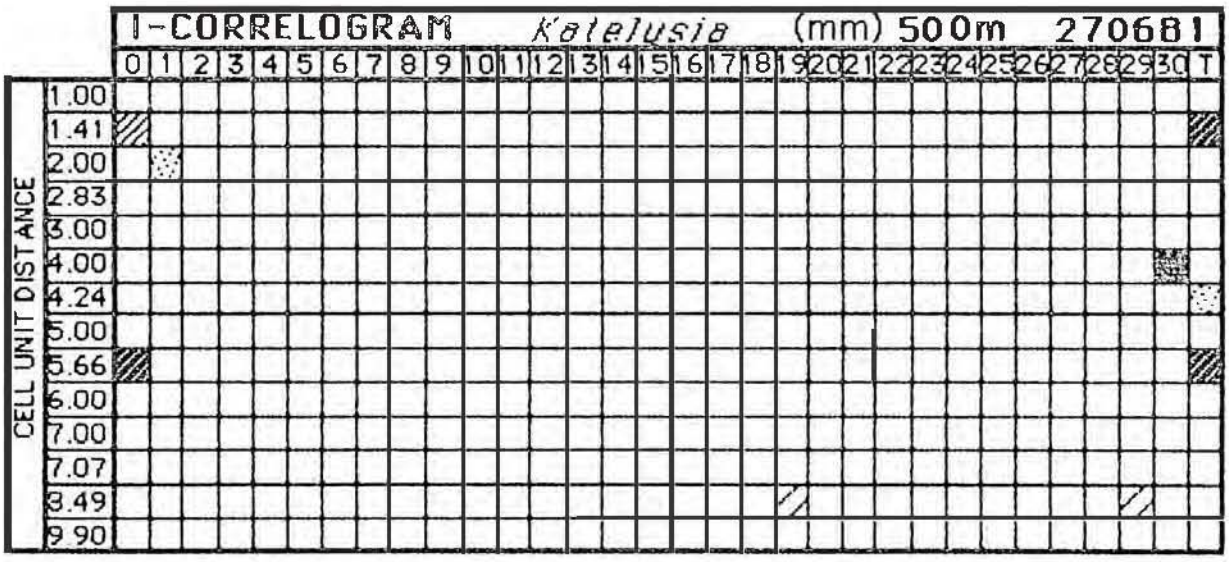
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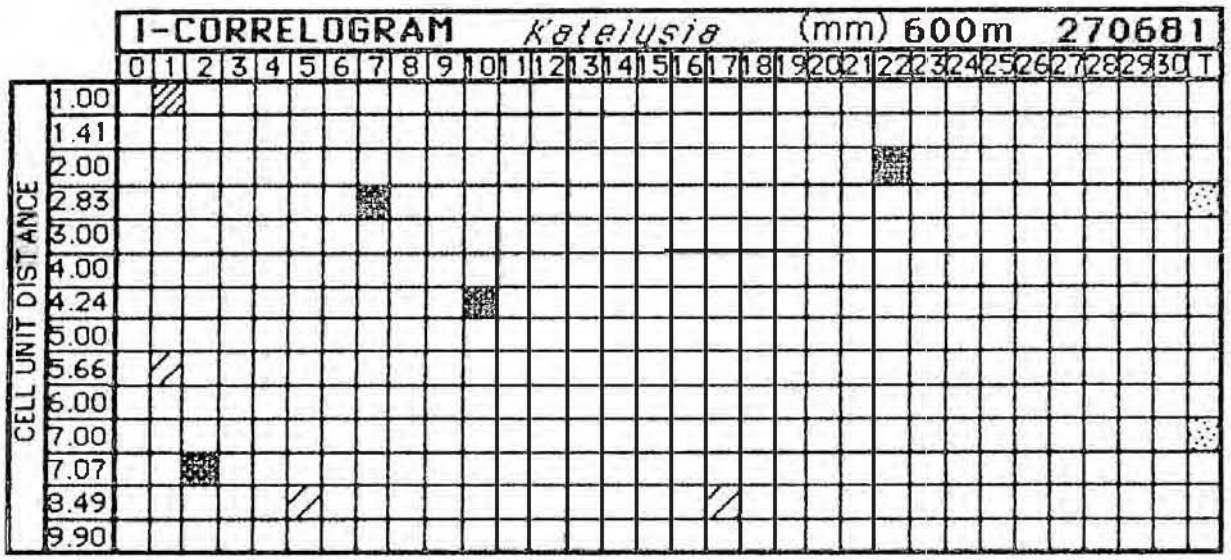
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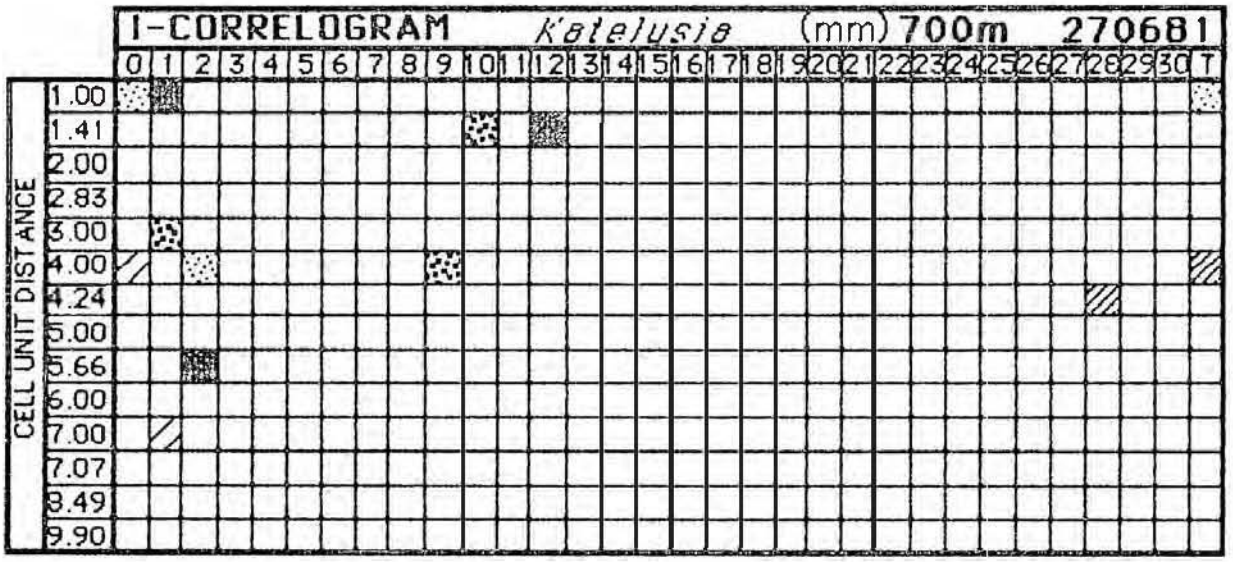
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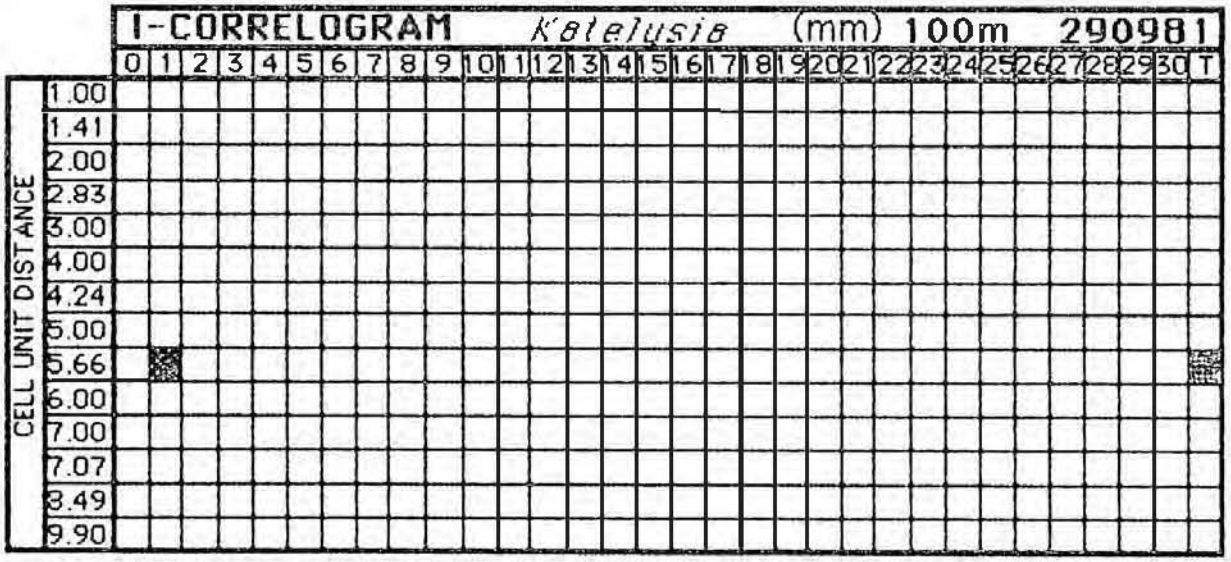
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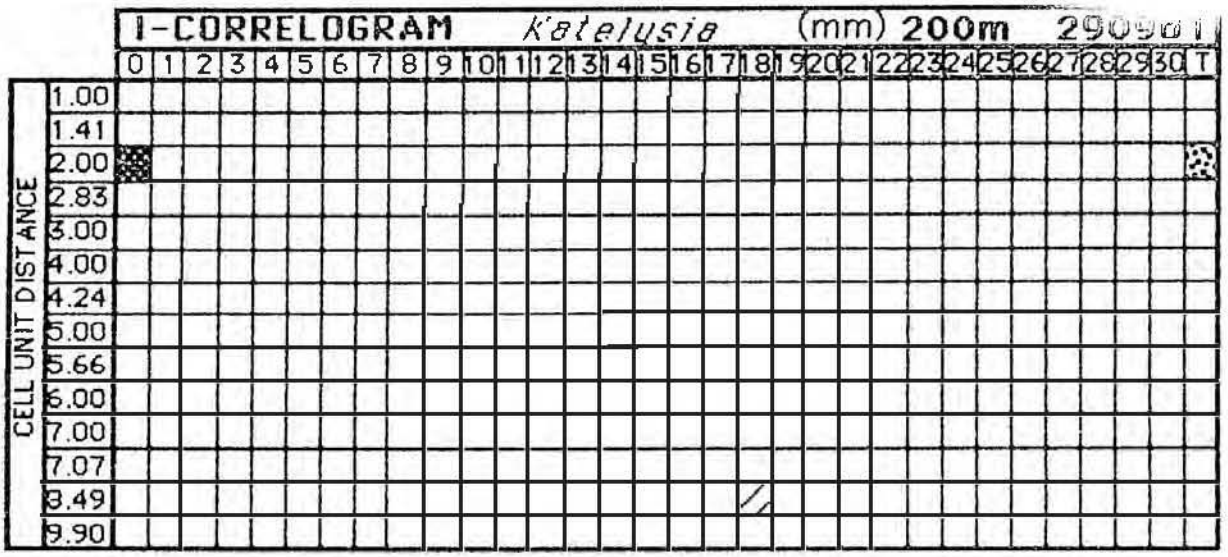
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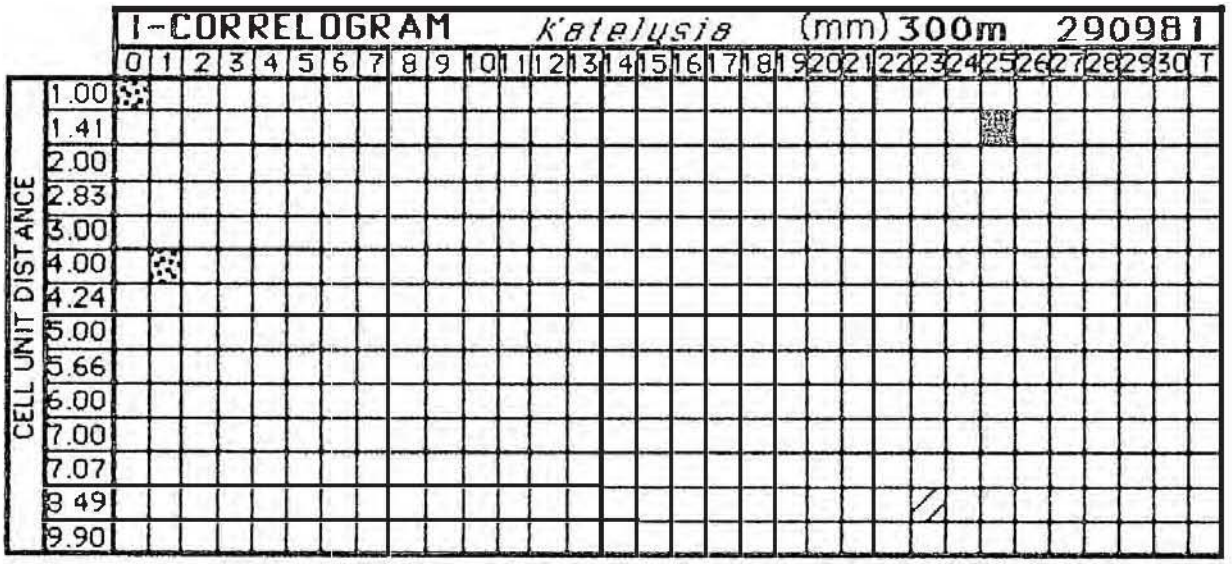
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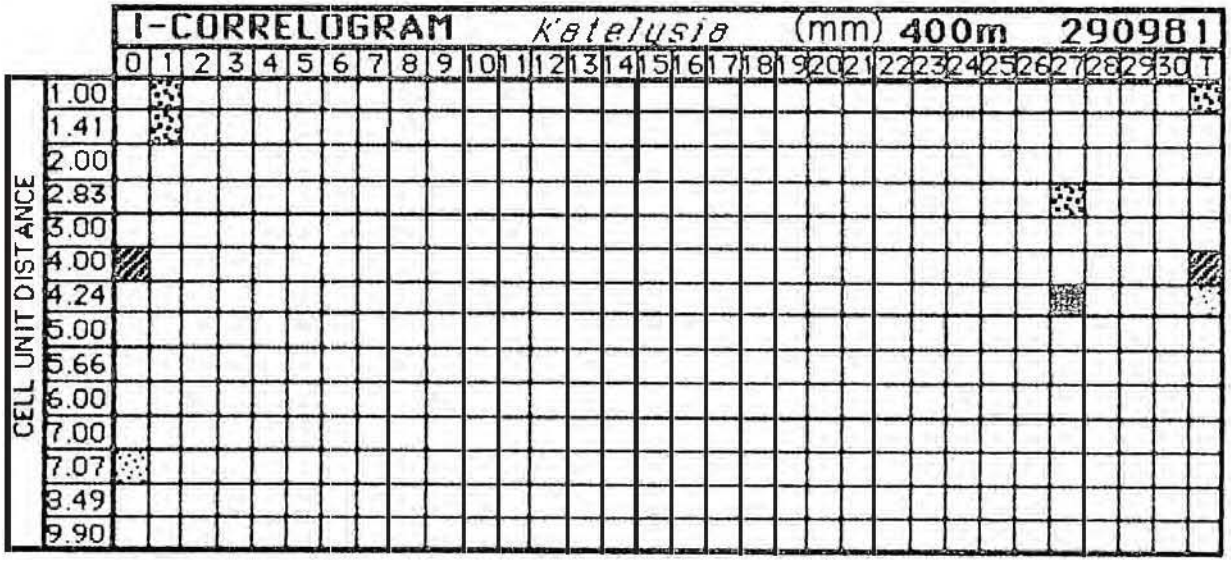
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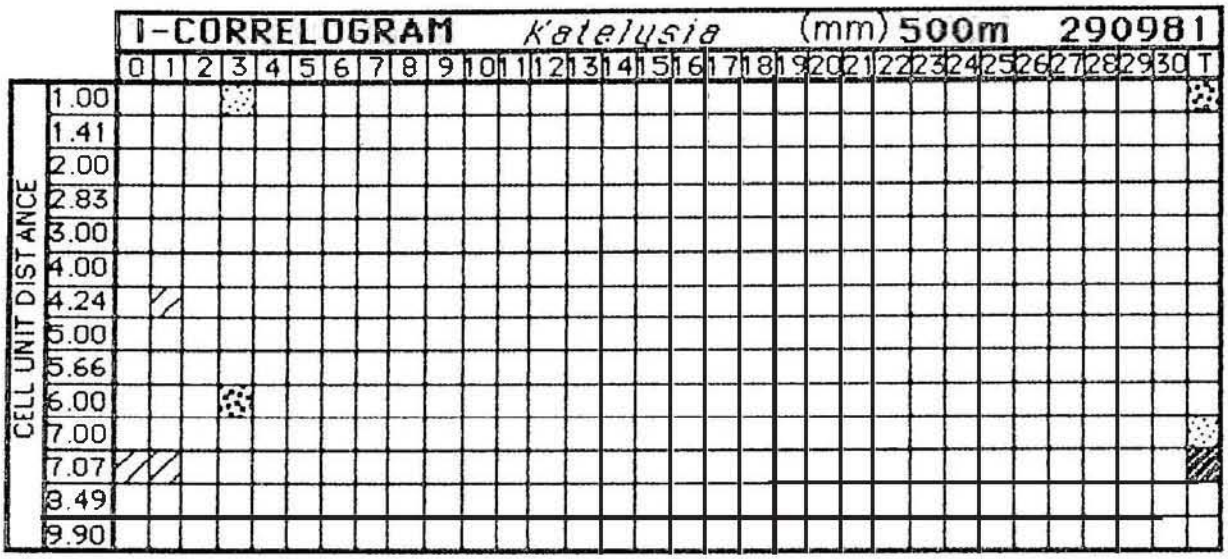
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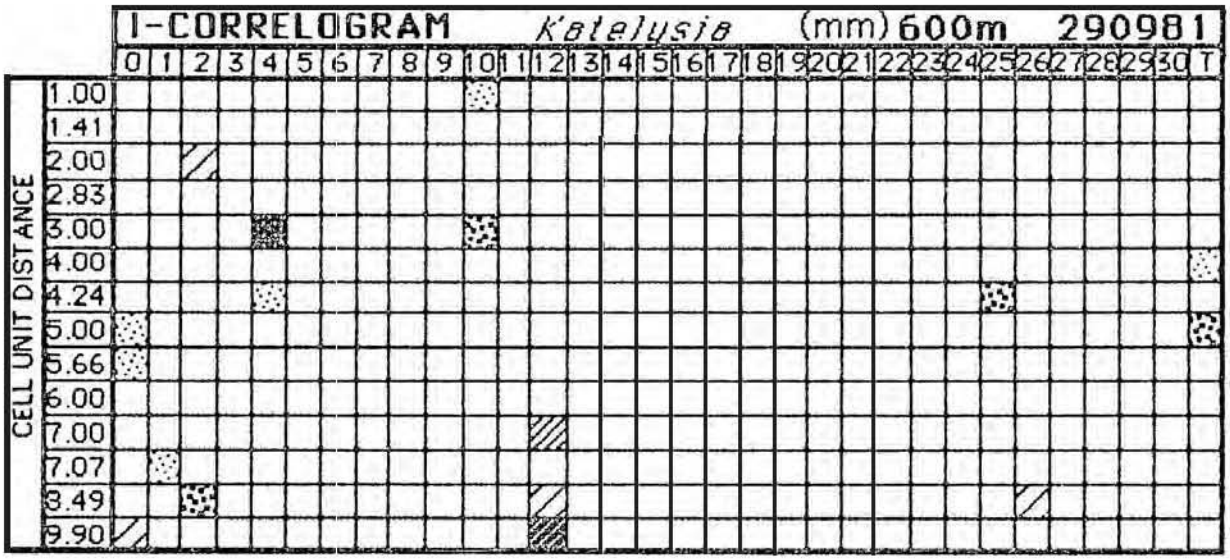
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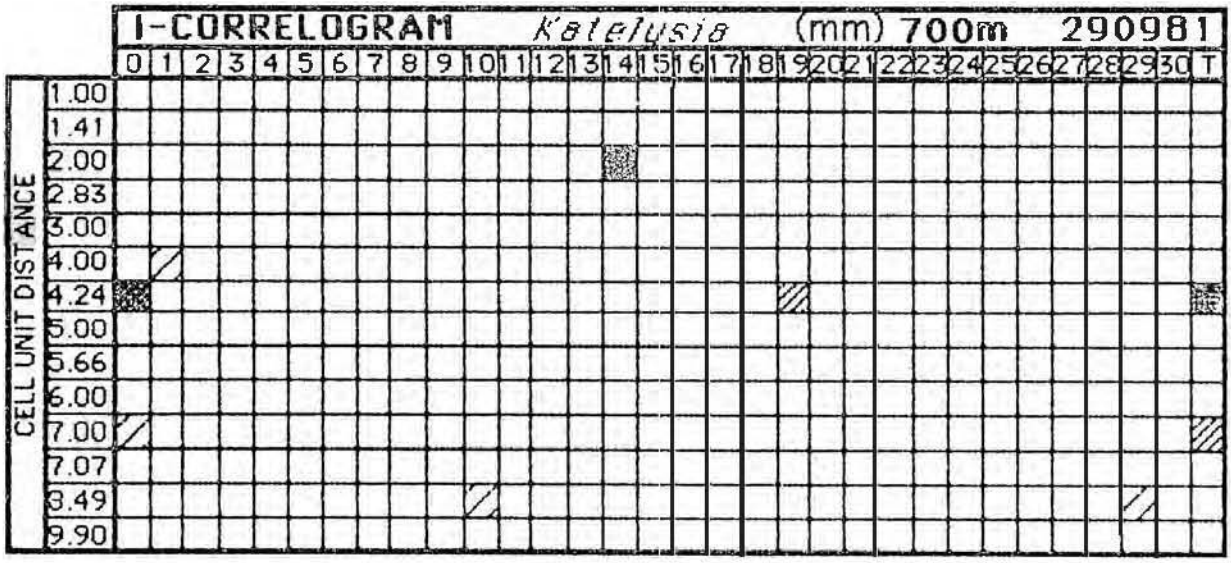
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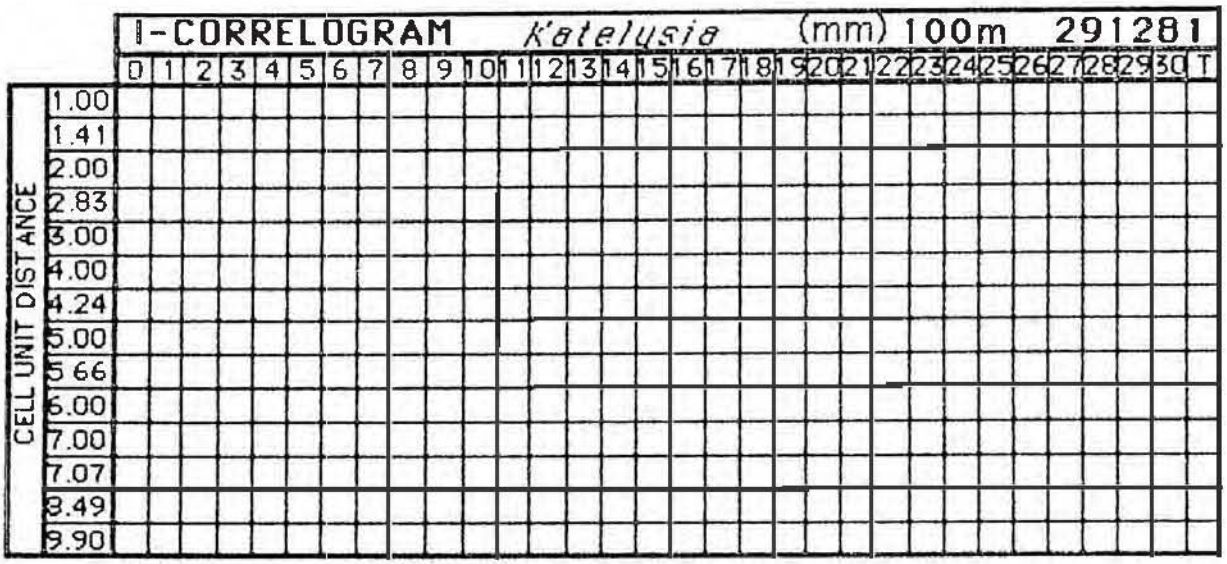
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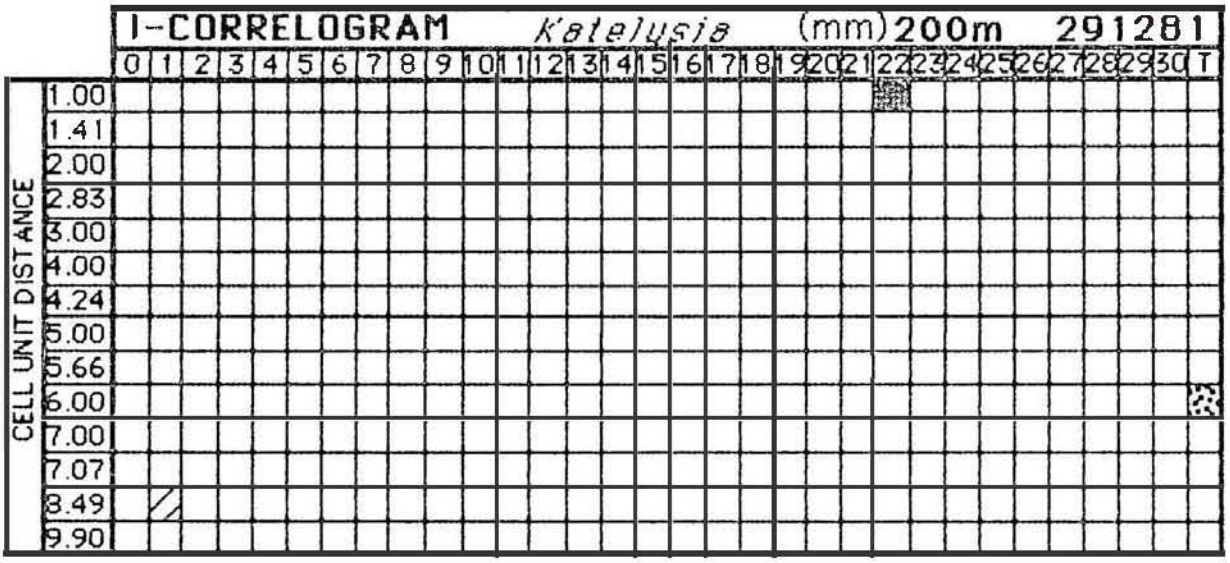
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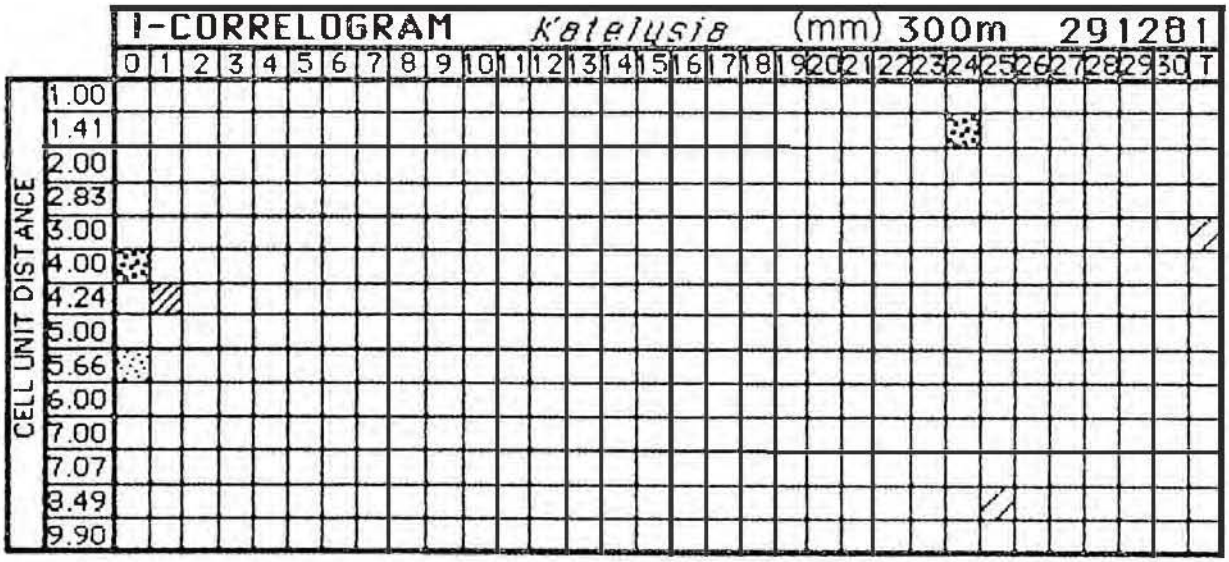
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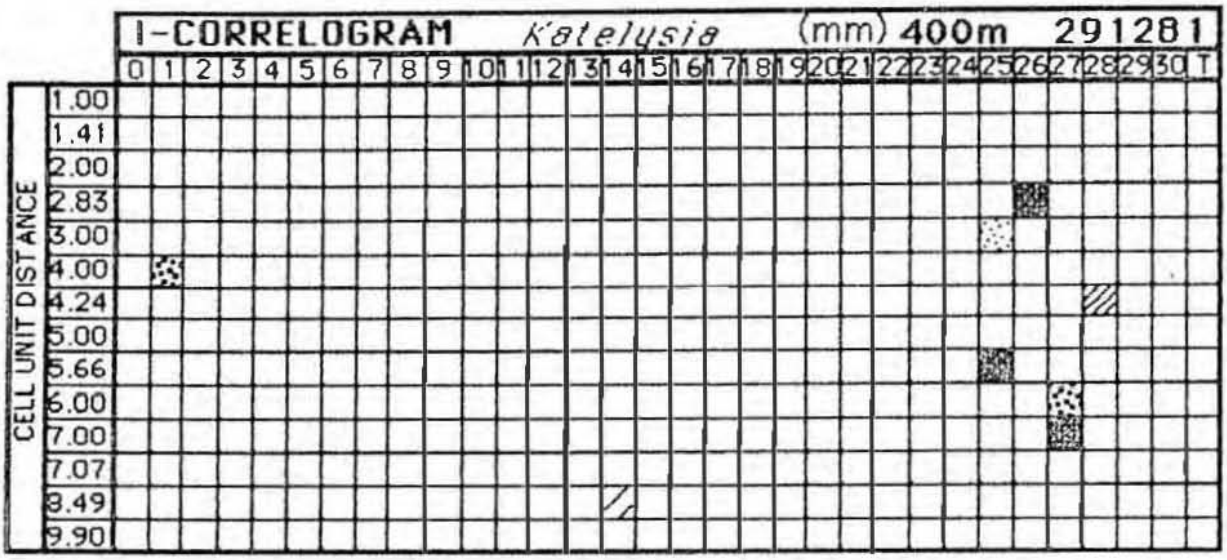
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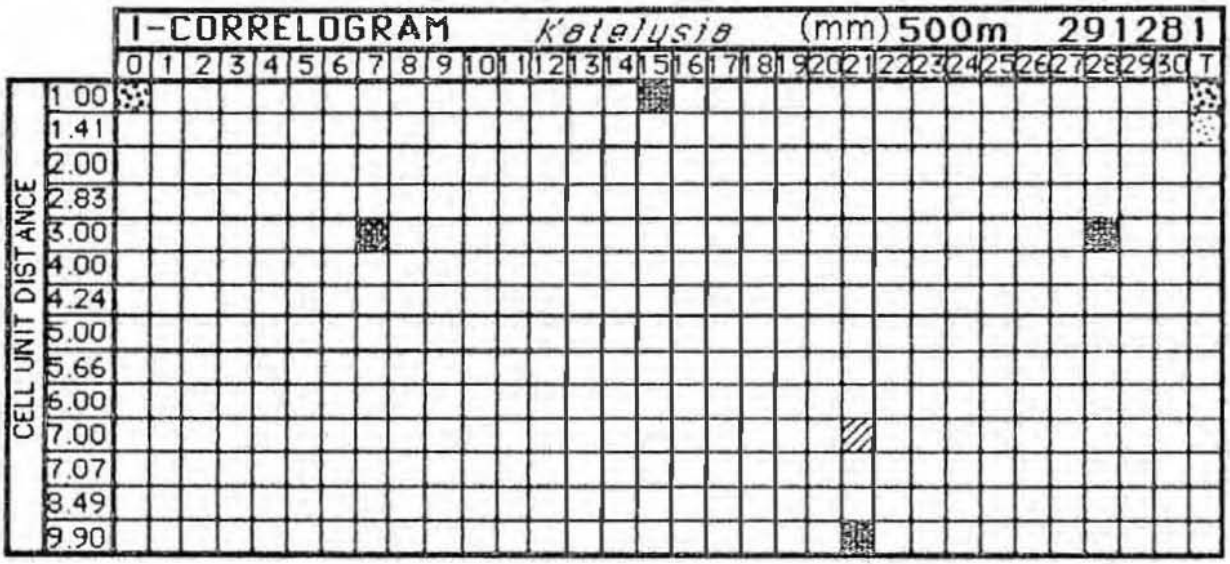
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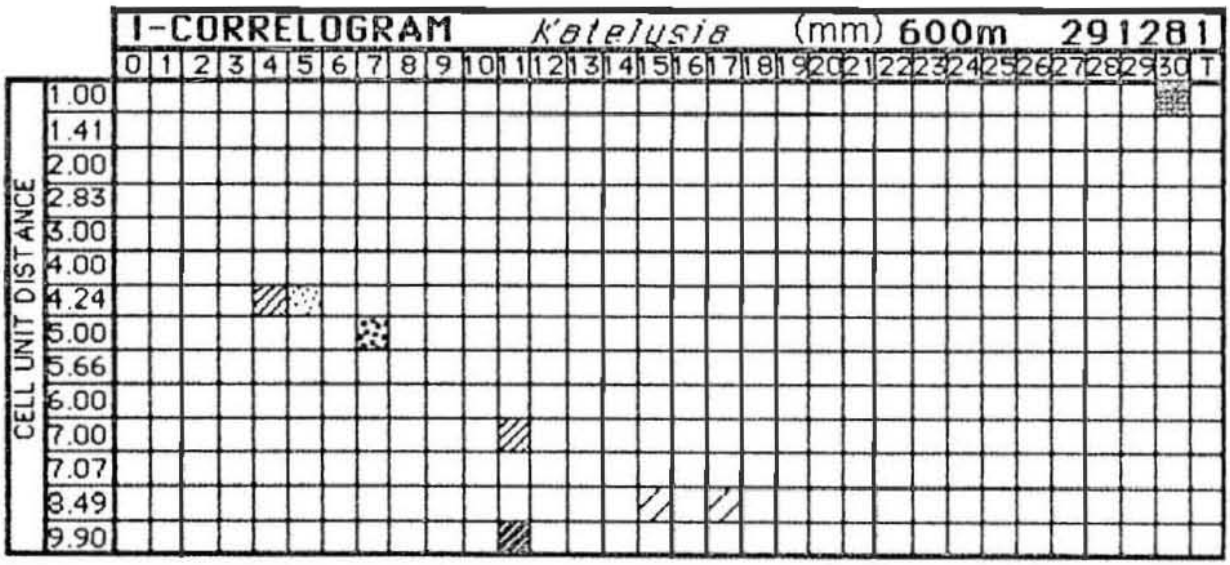
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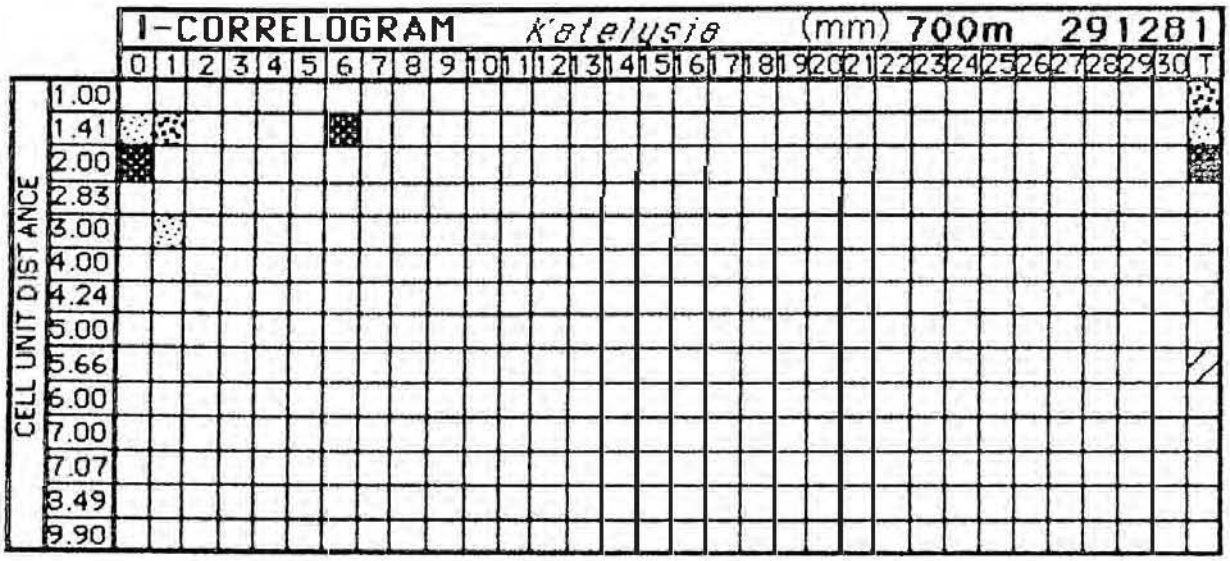
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Katelysie
(mm) 700m
291281
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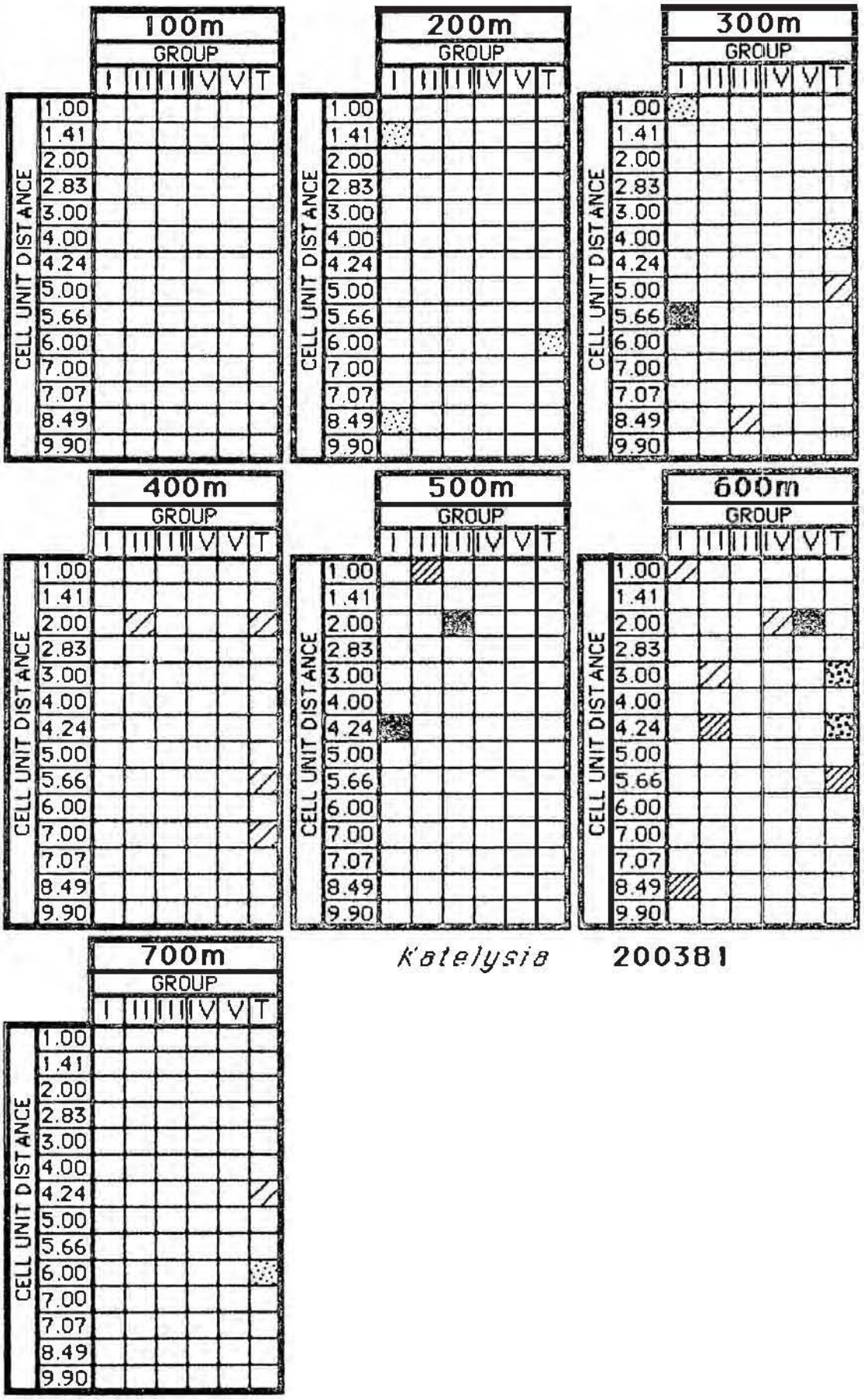
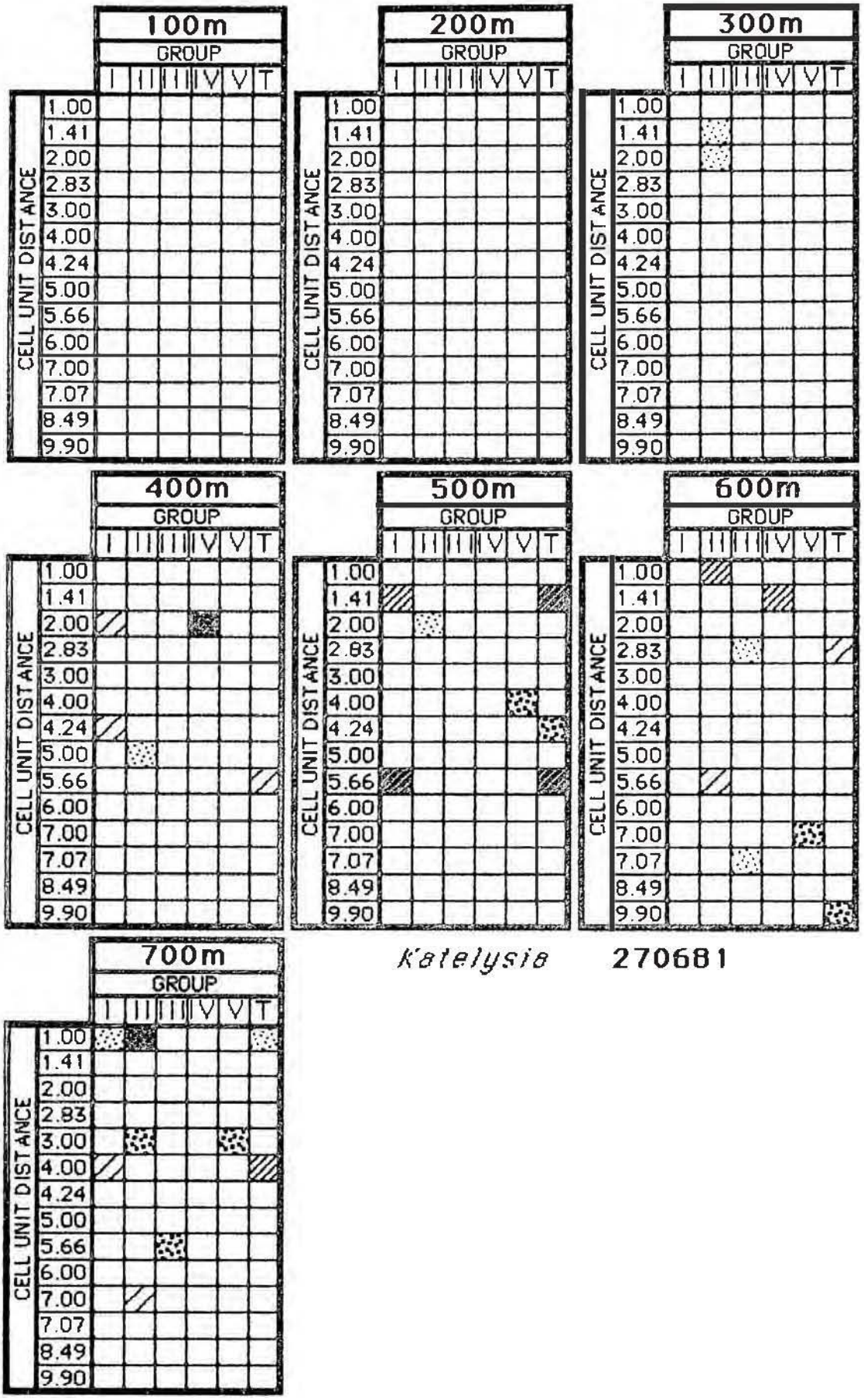
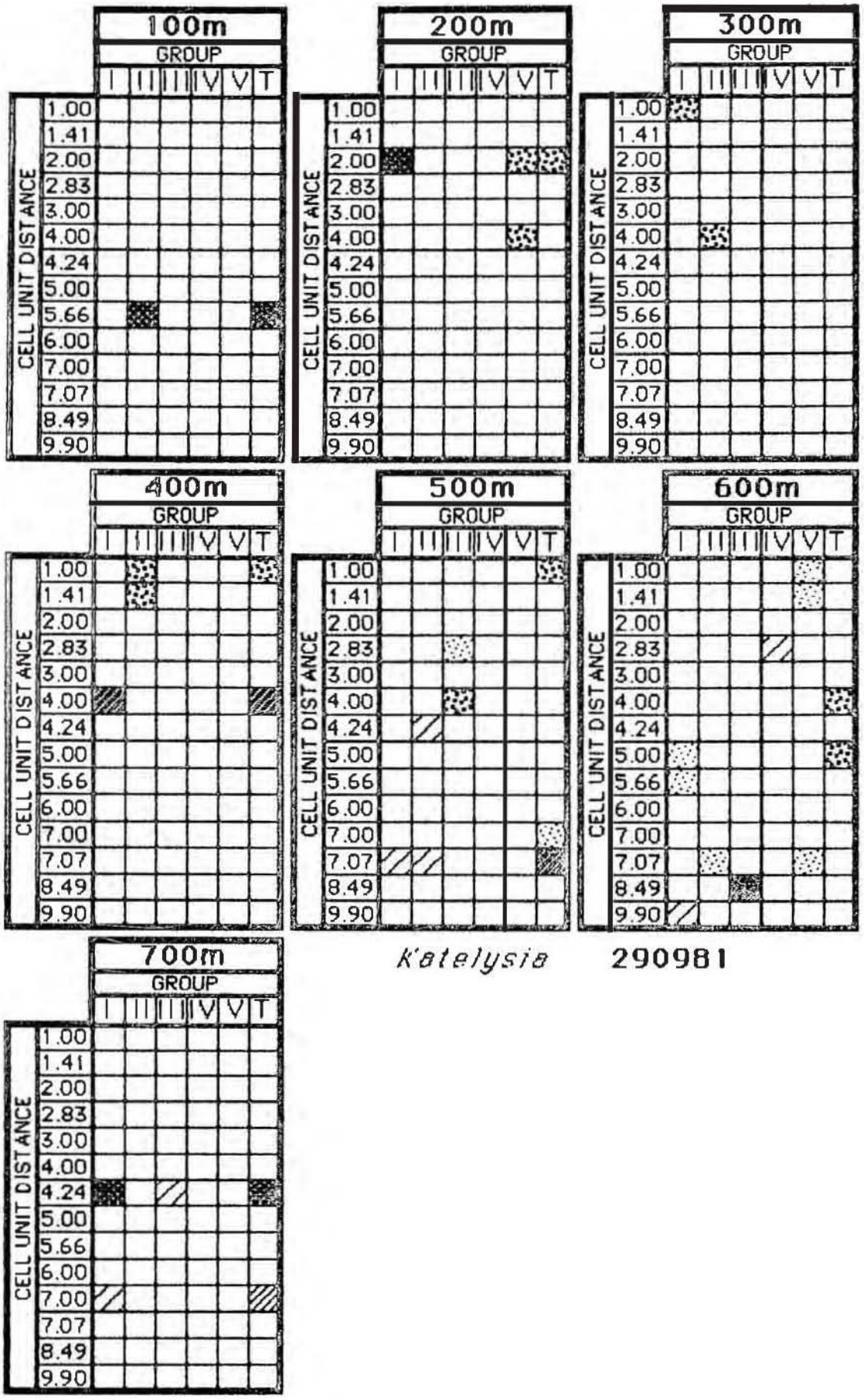


Katelysia **200381**



Katelysie **270681**



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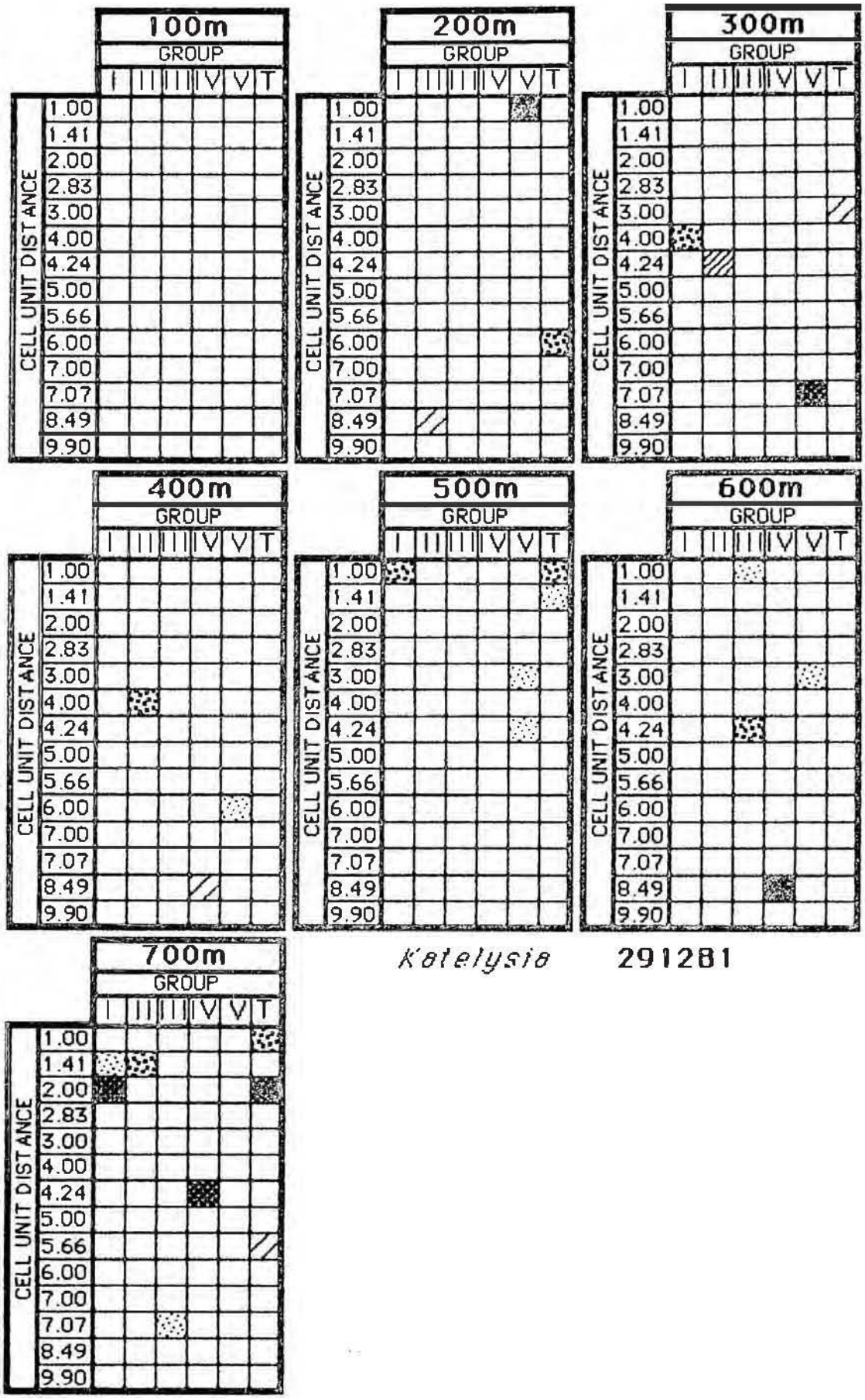

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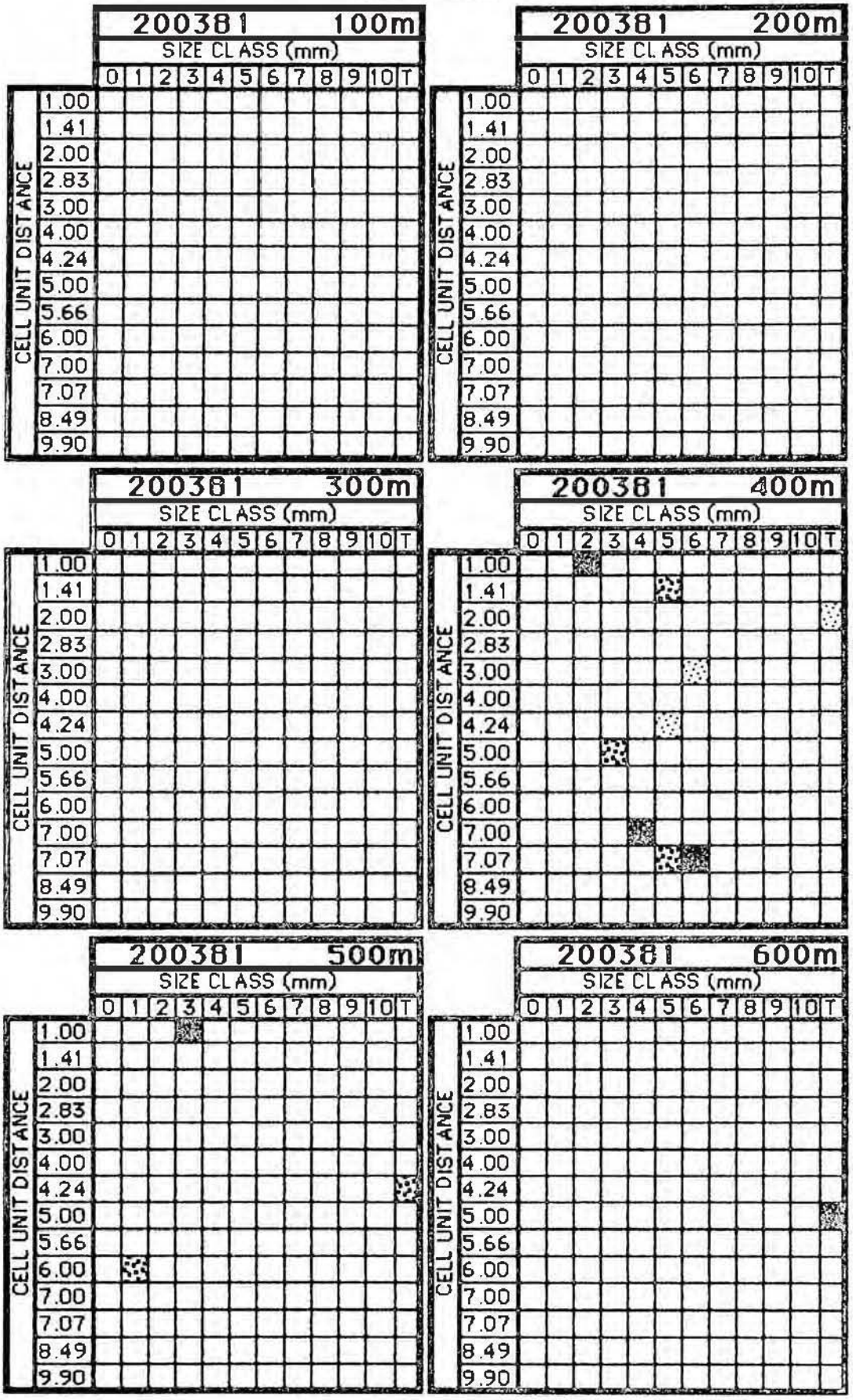
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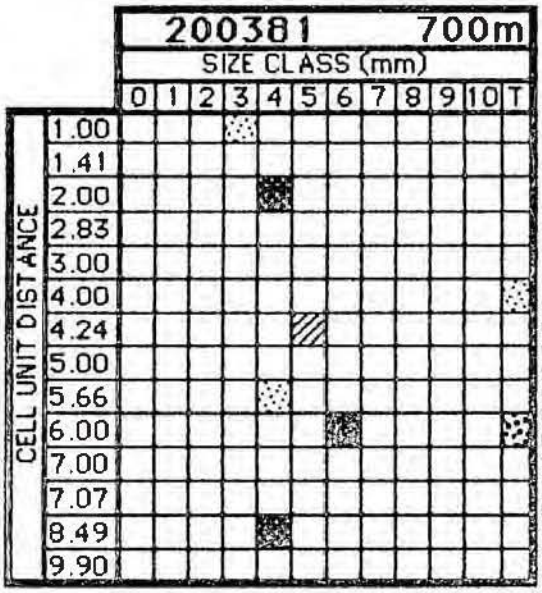
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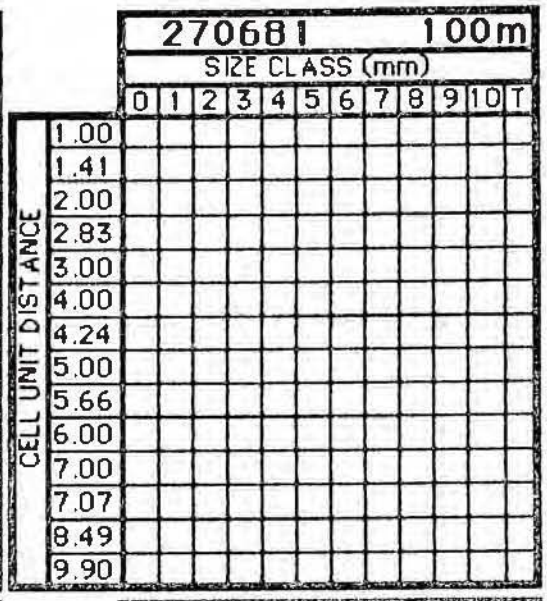
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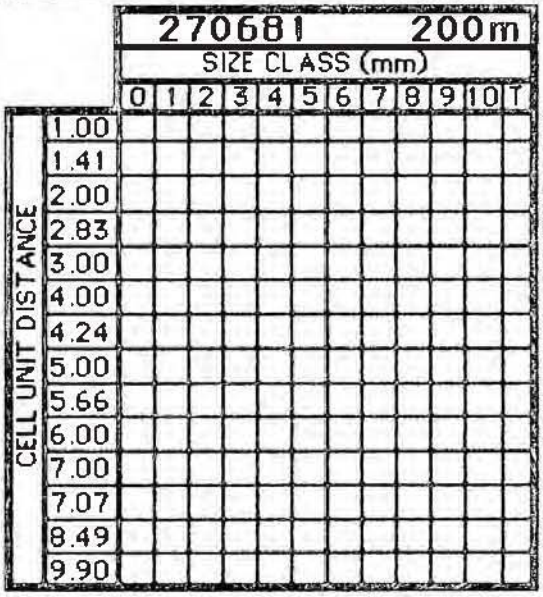
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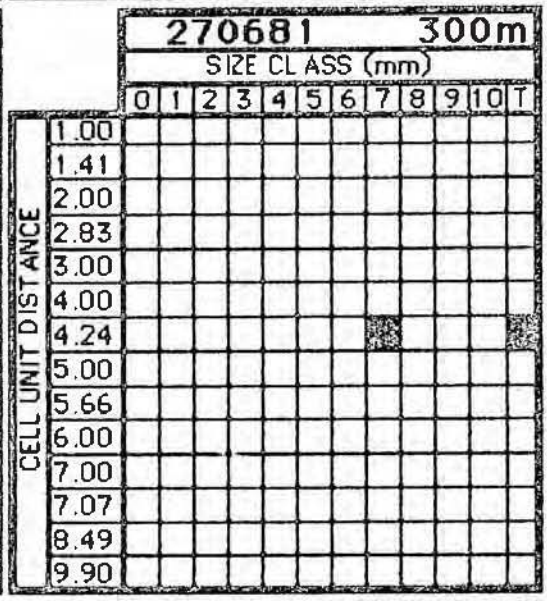
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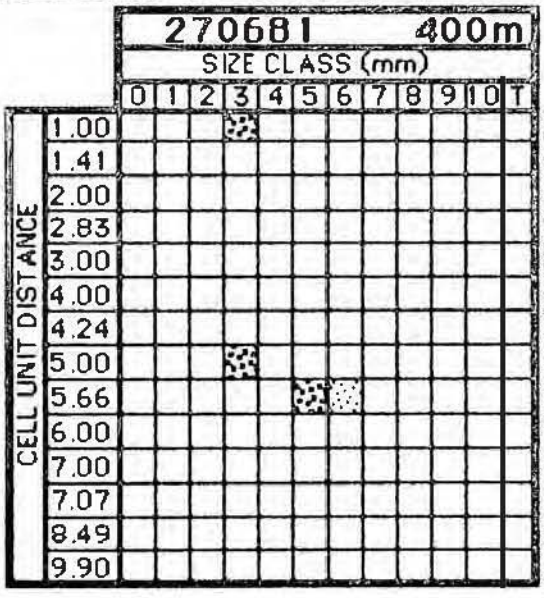
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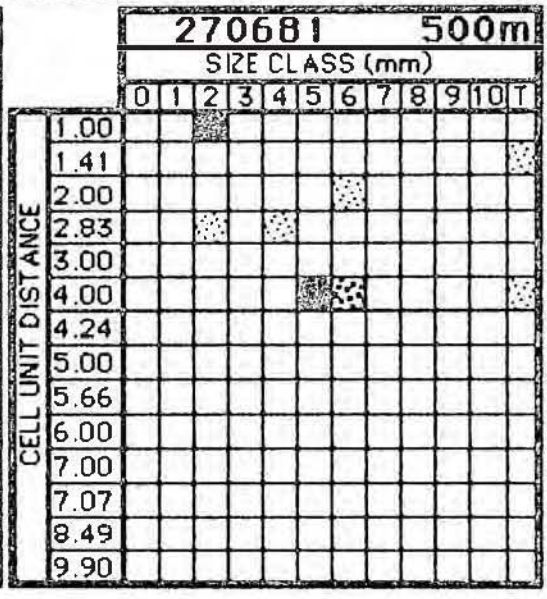
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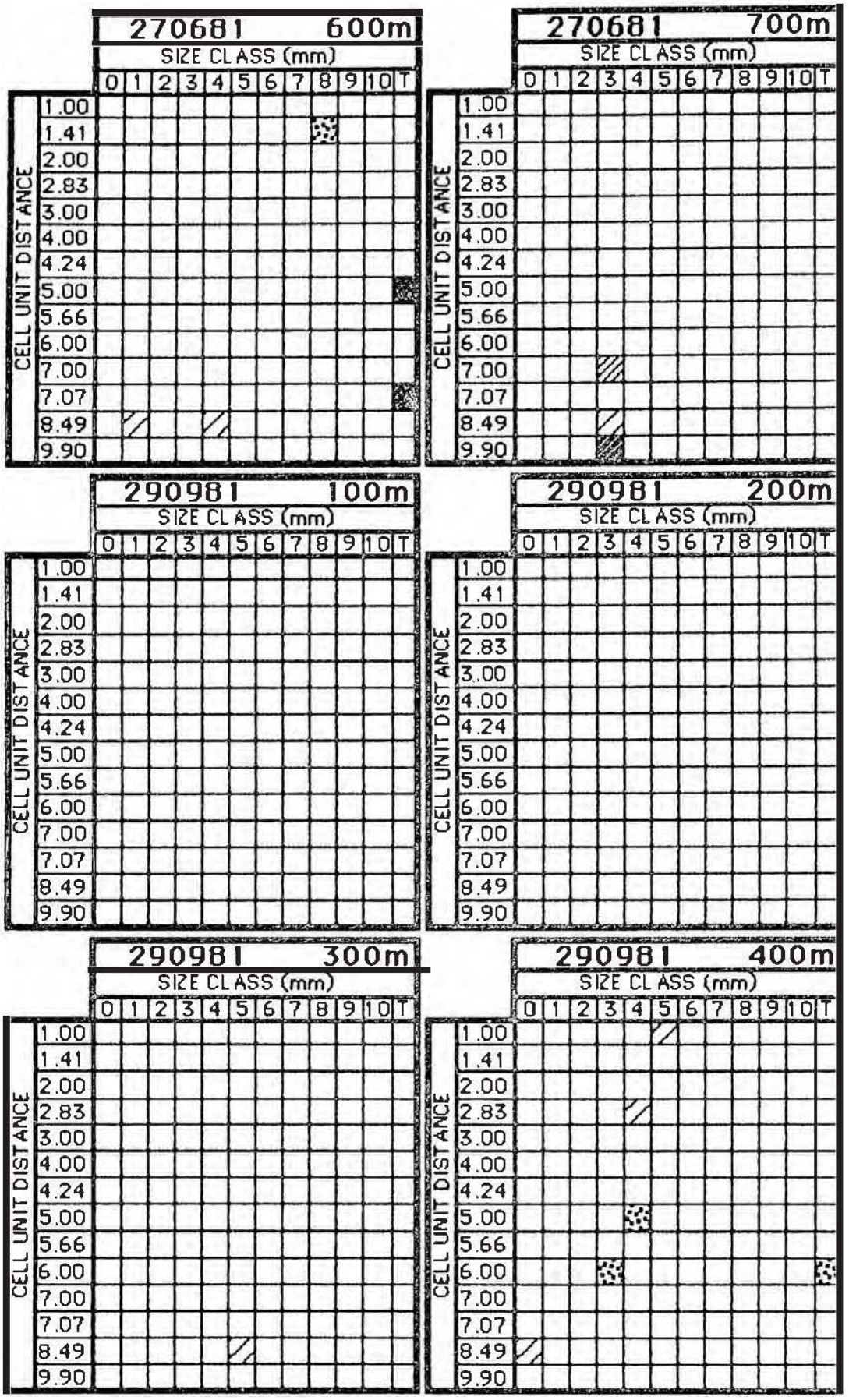
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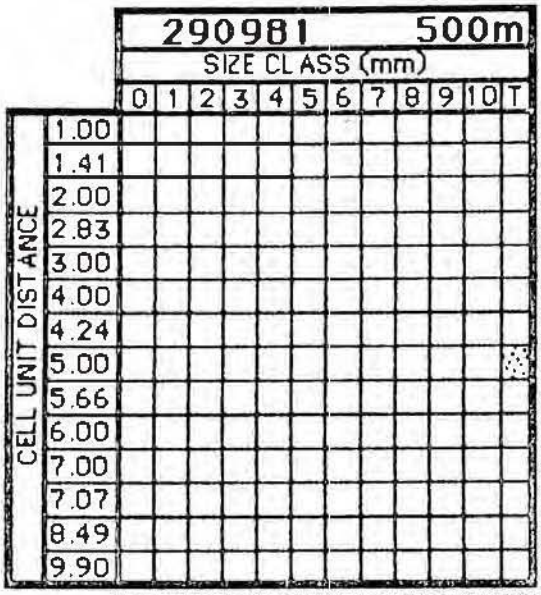
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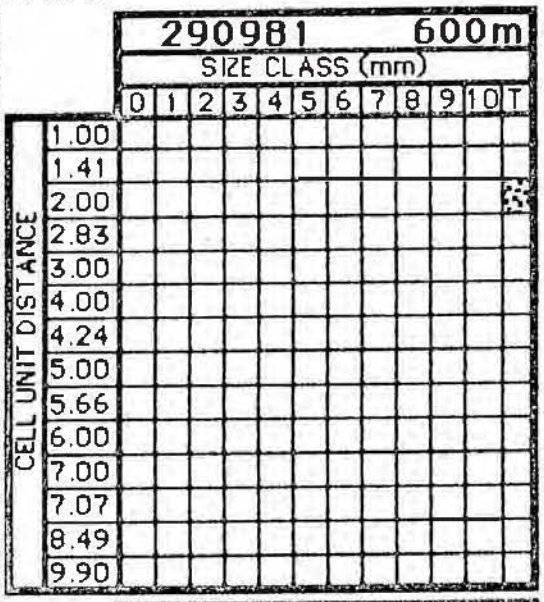
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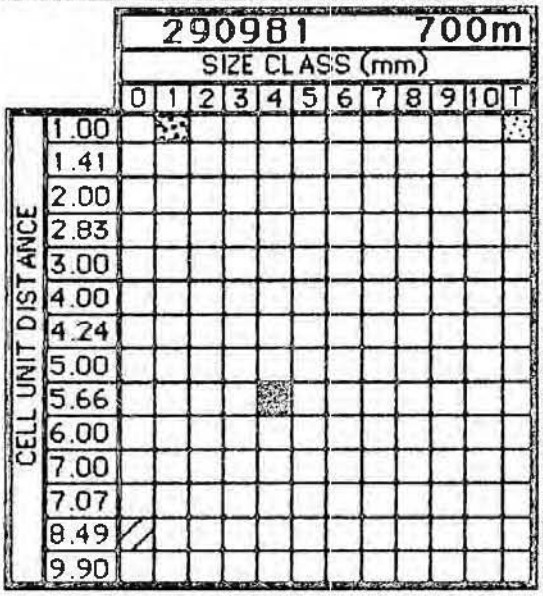
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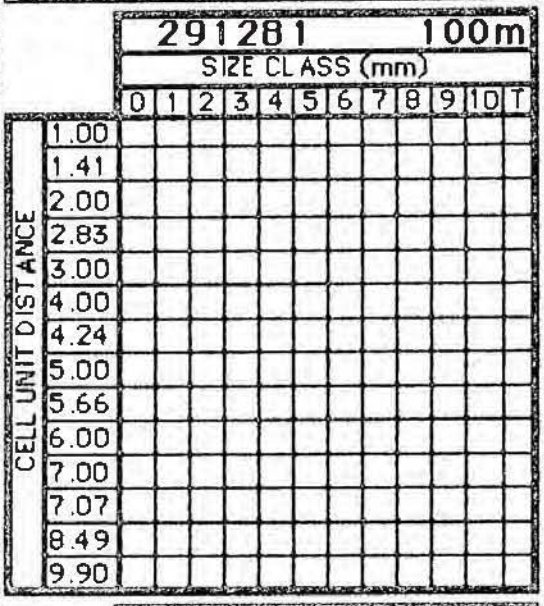
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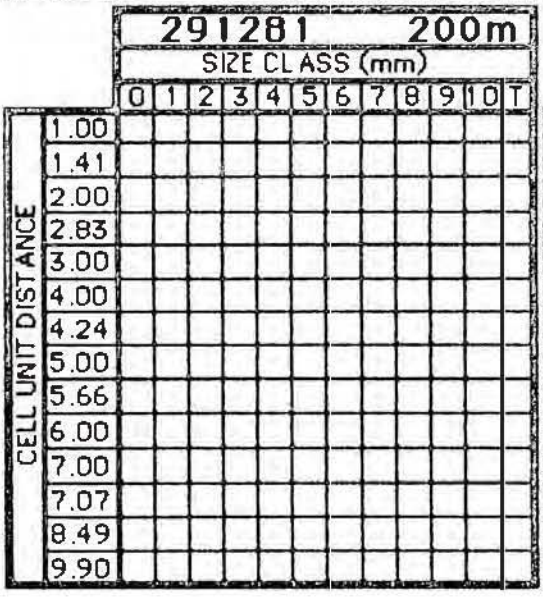
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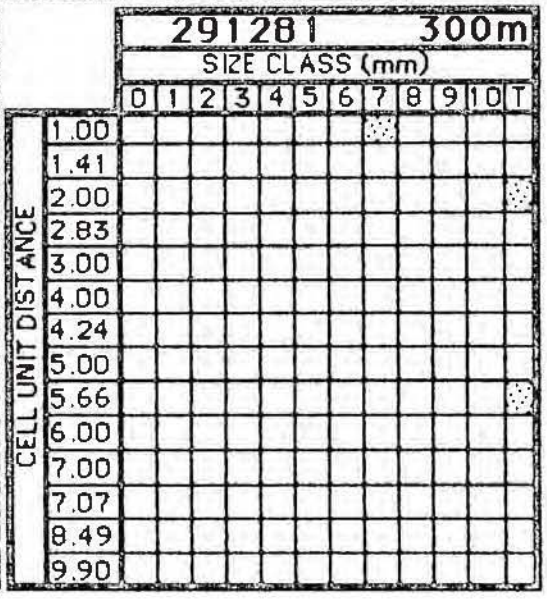
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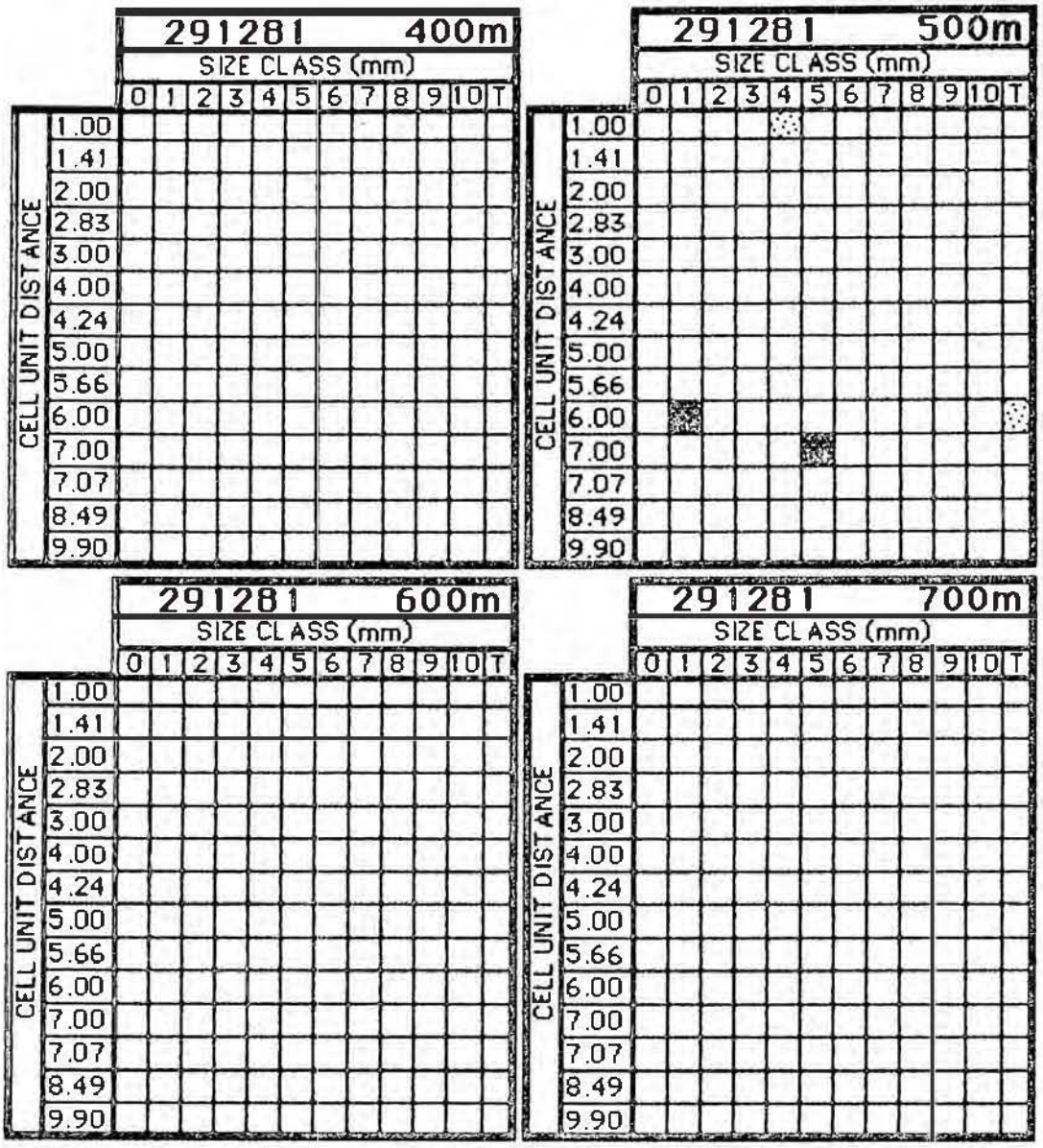
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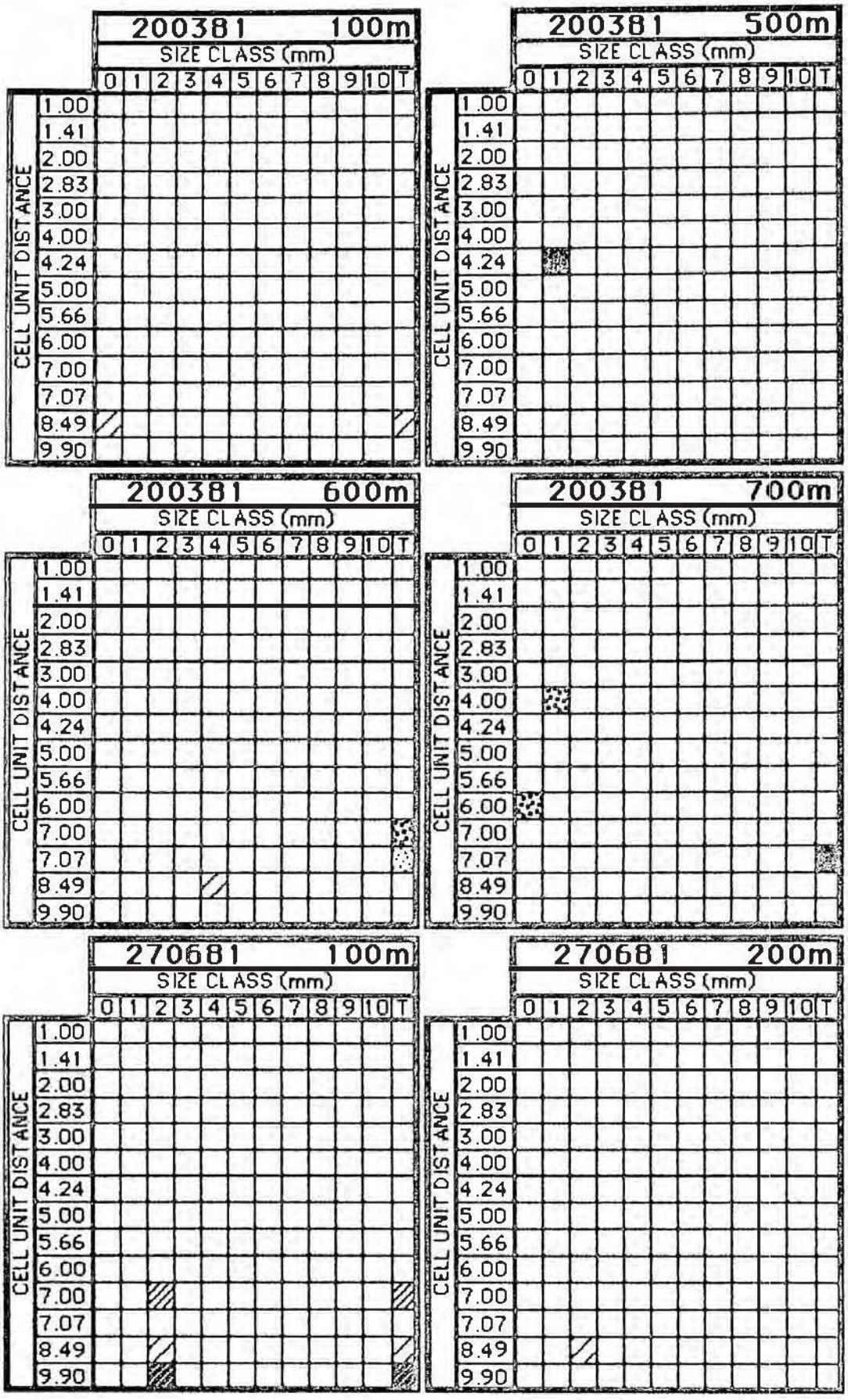
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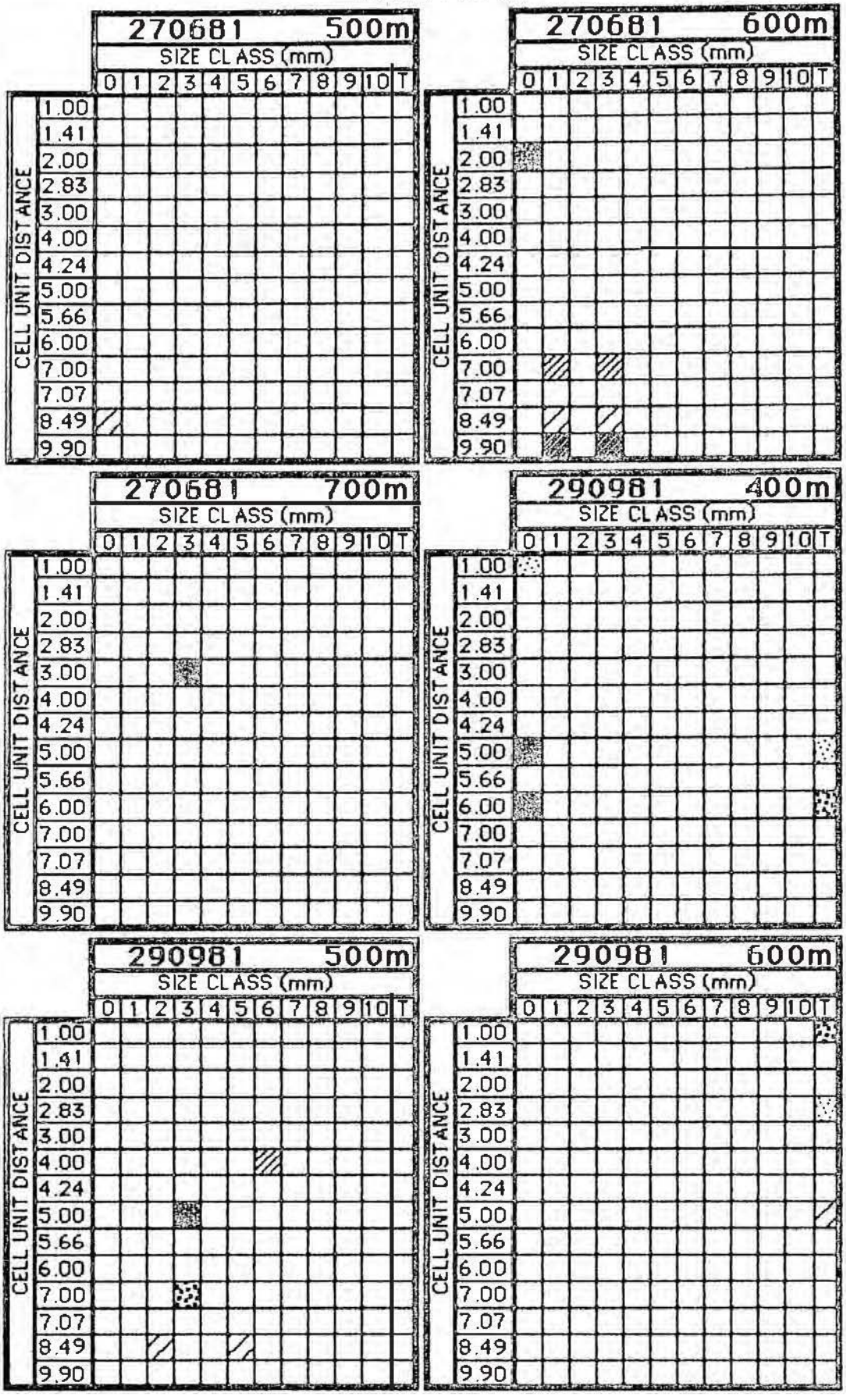
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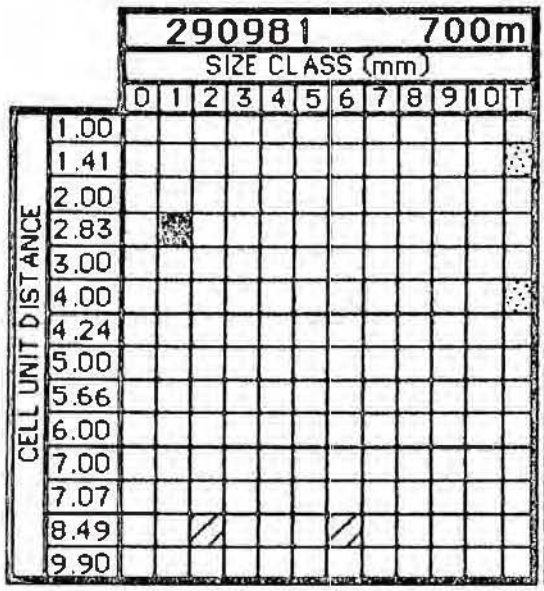
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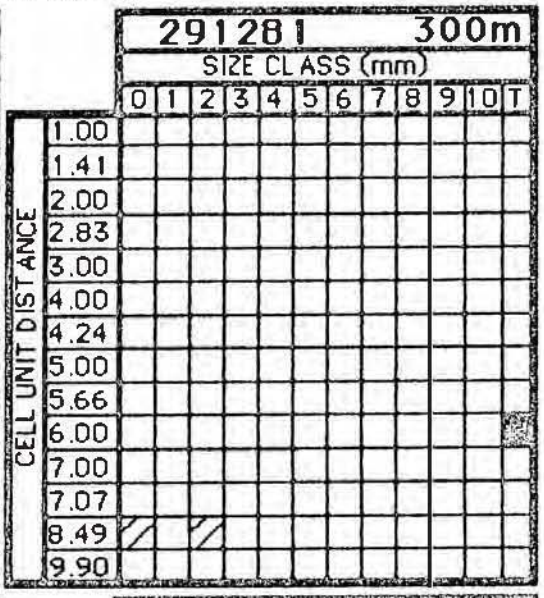
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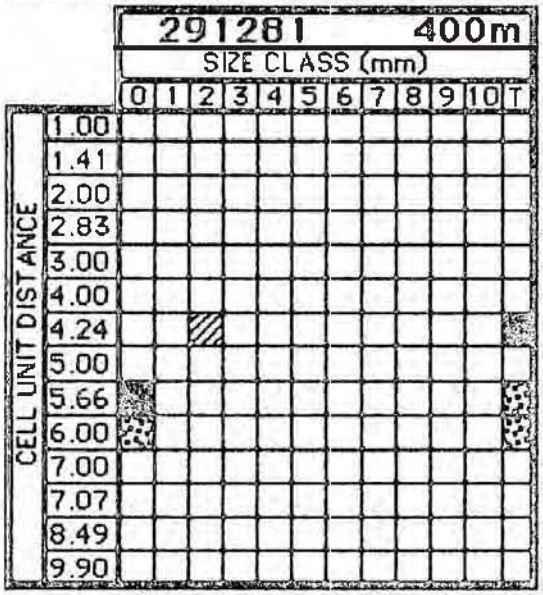
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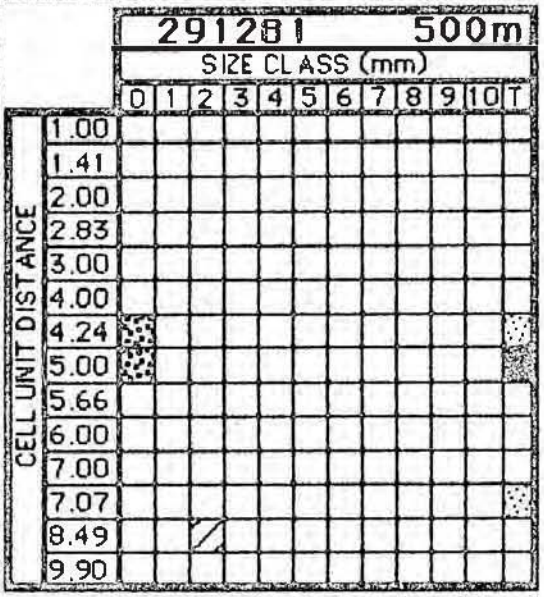
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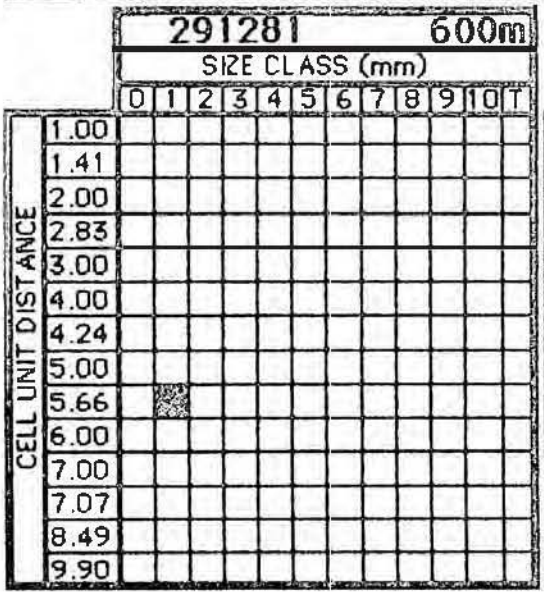
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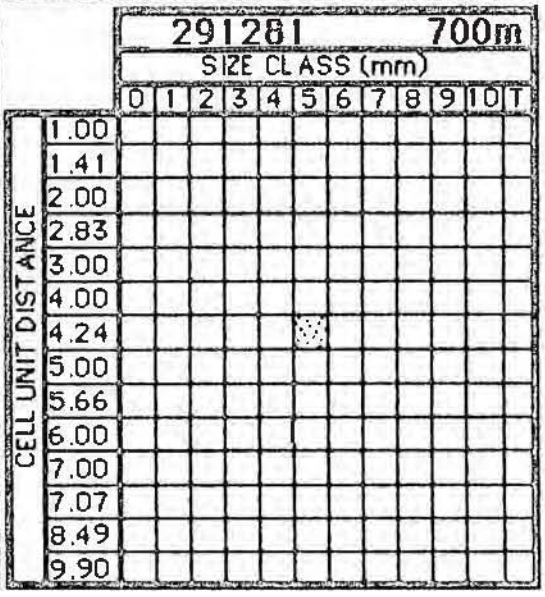
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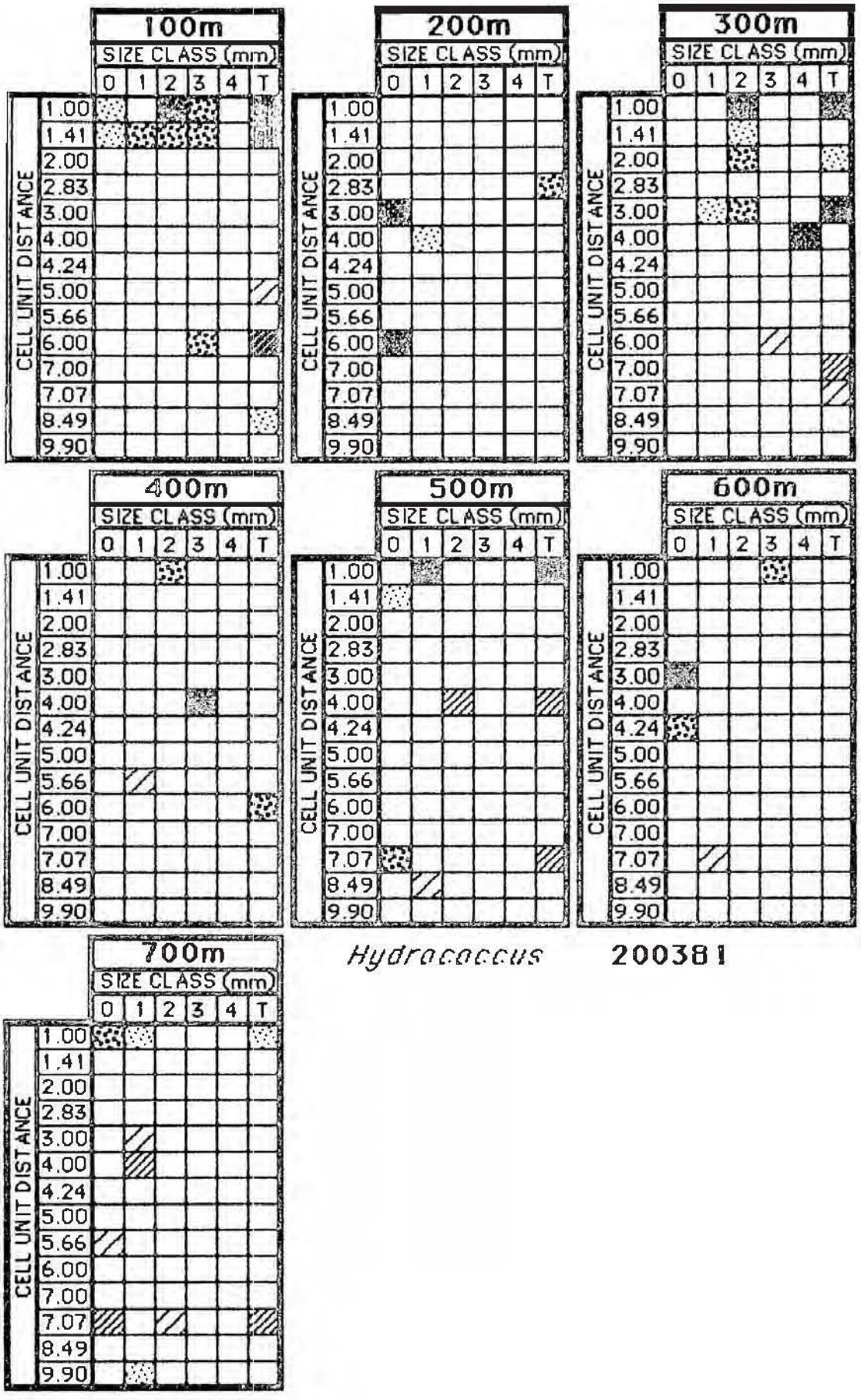
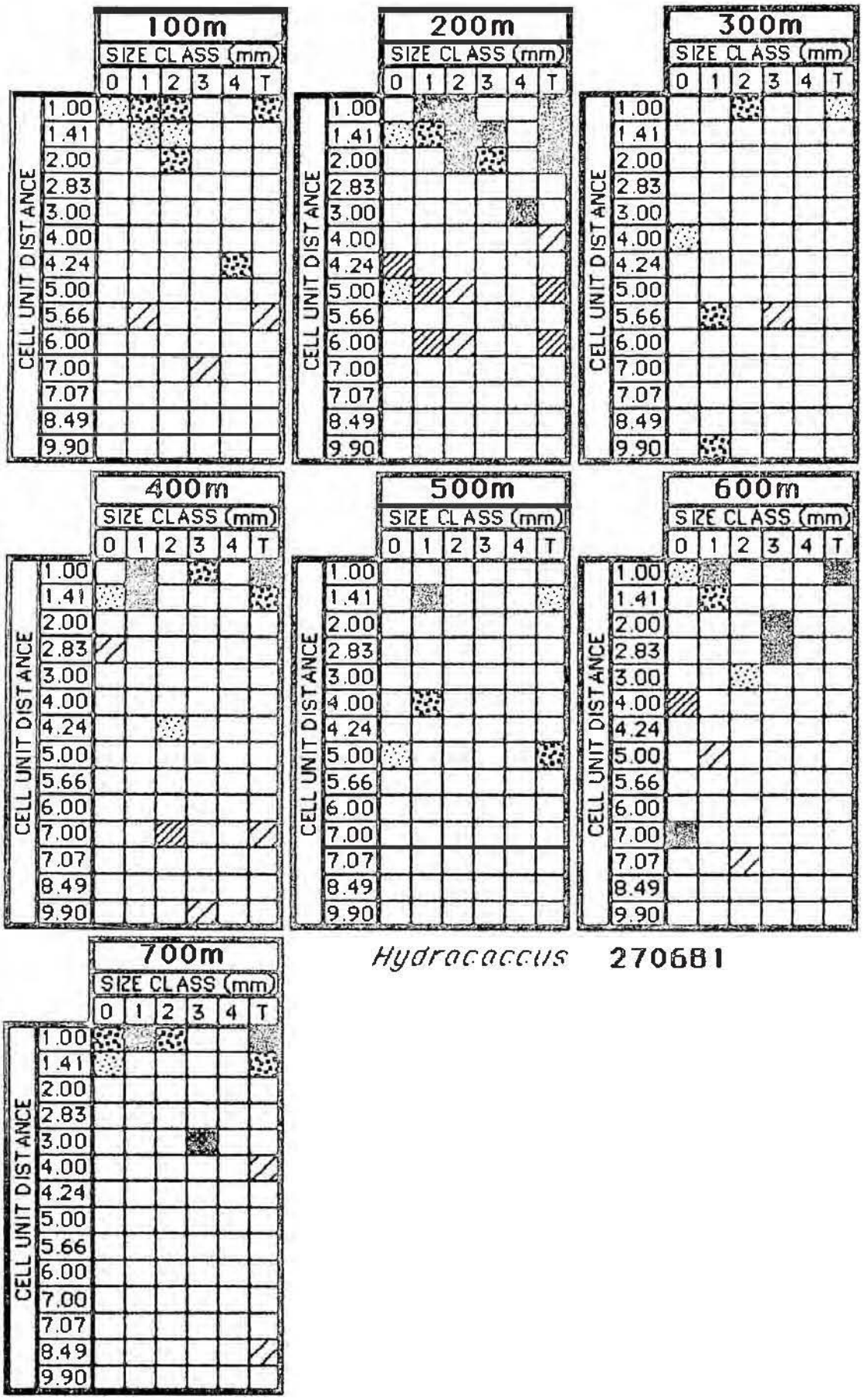
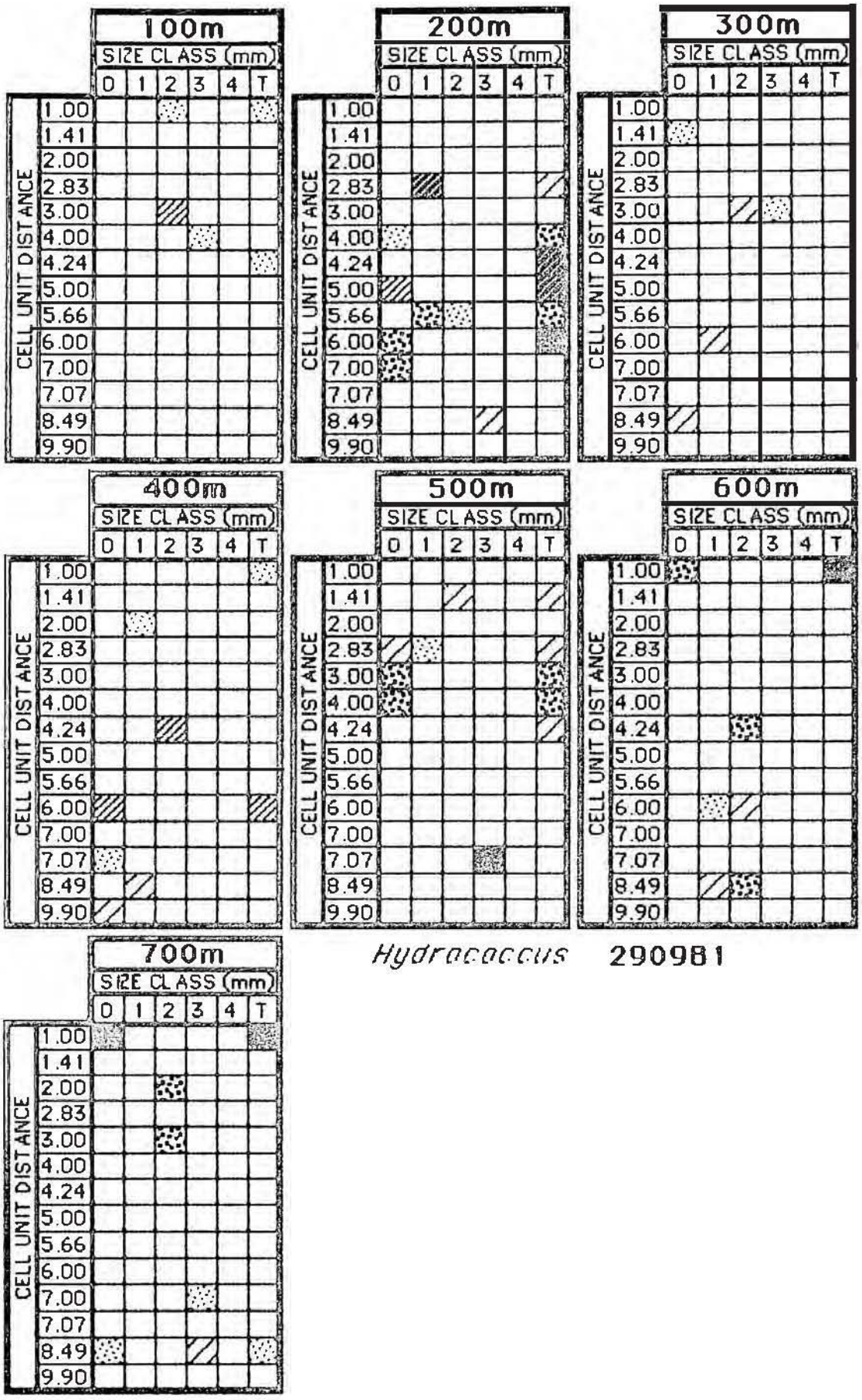


Hydrococcus 200381



Hydrococcus **270681**



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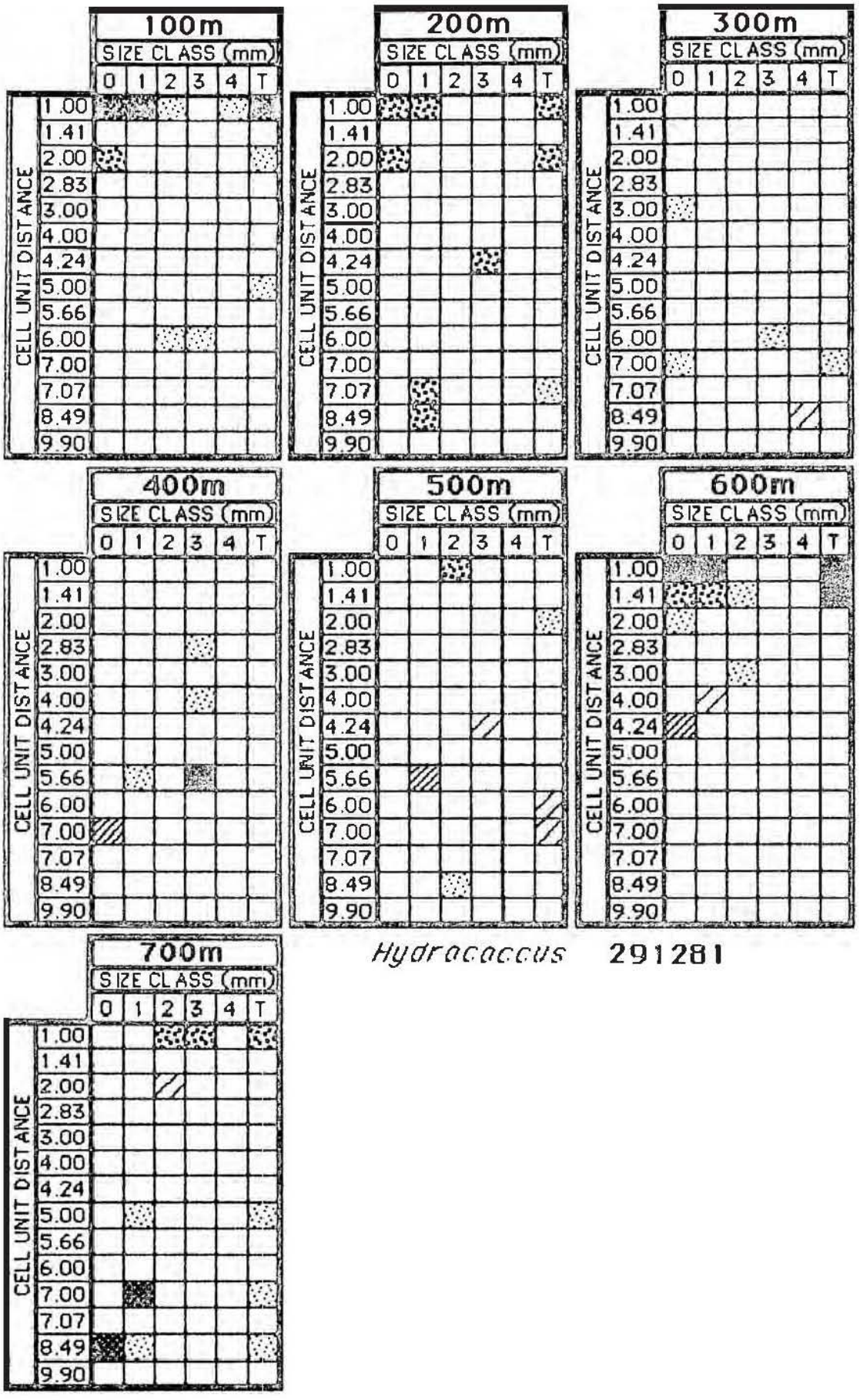

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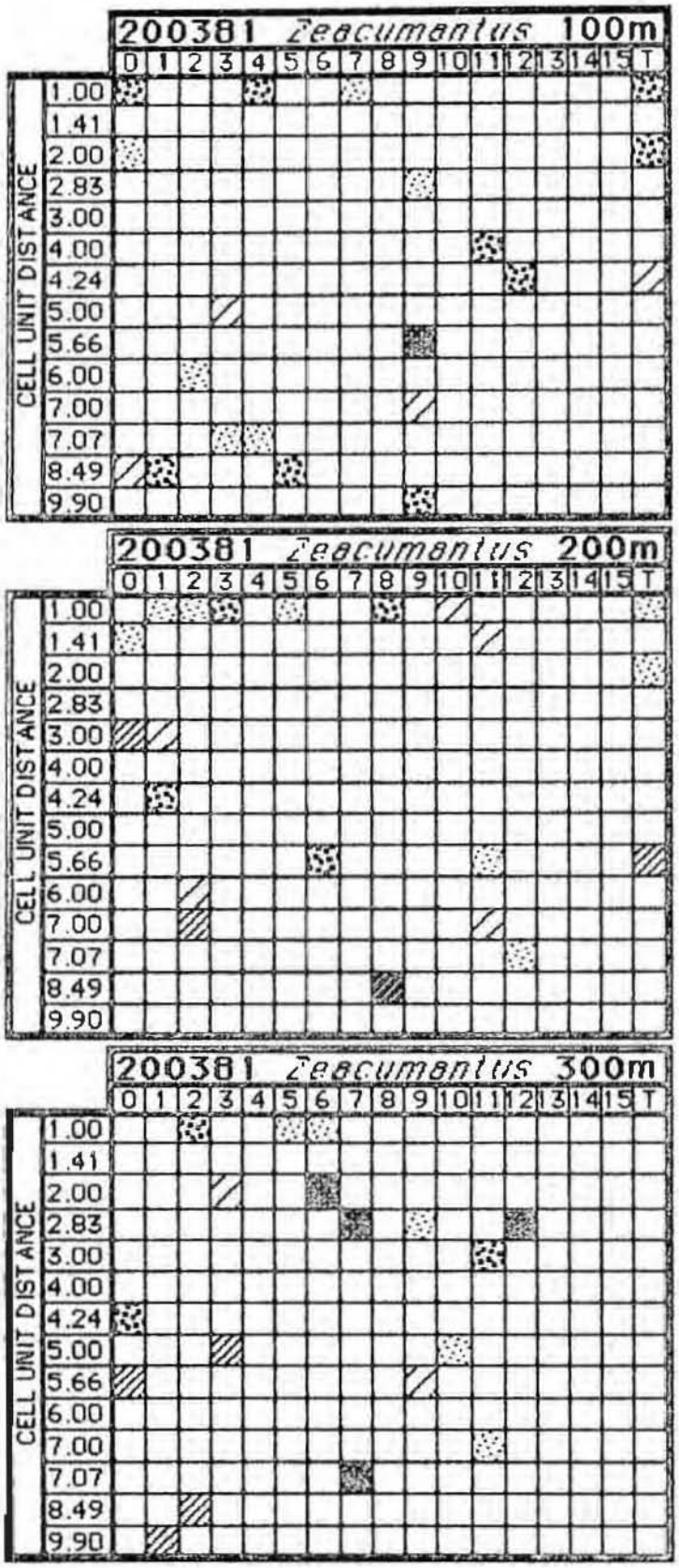
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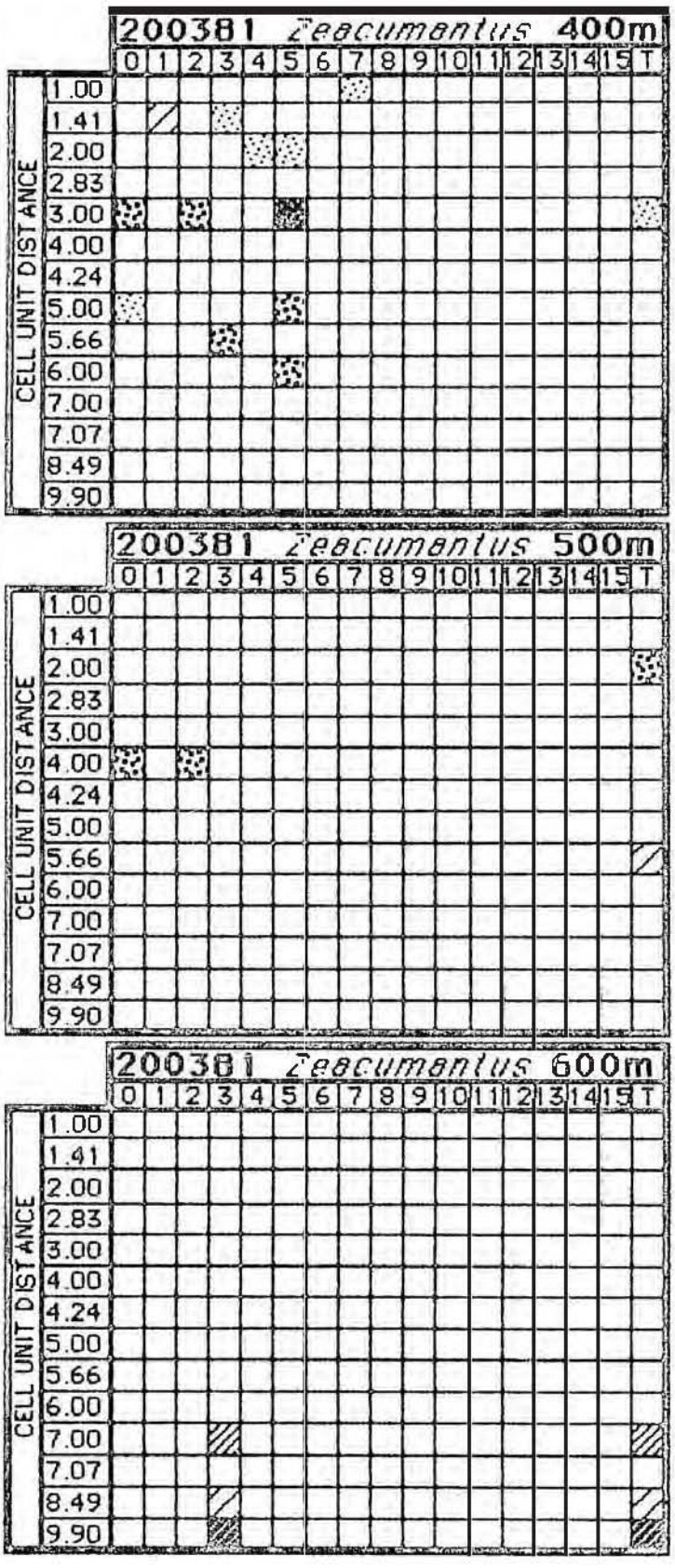
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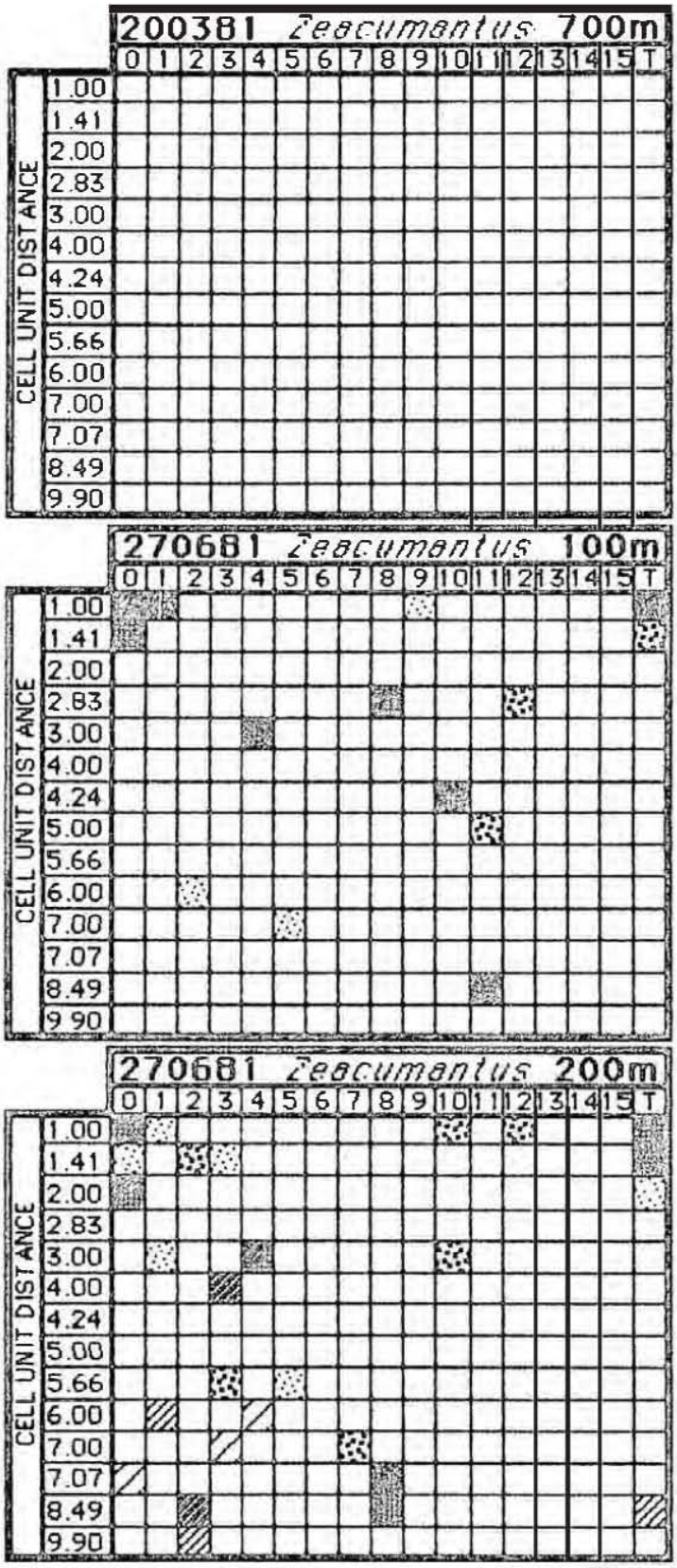
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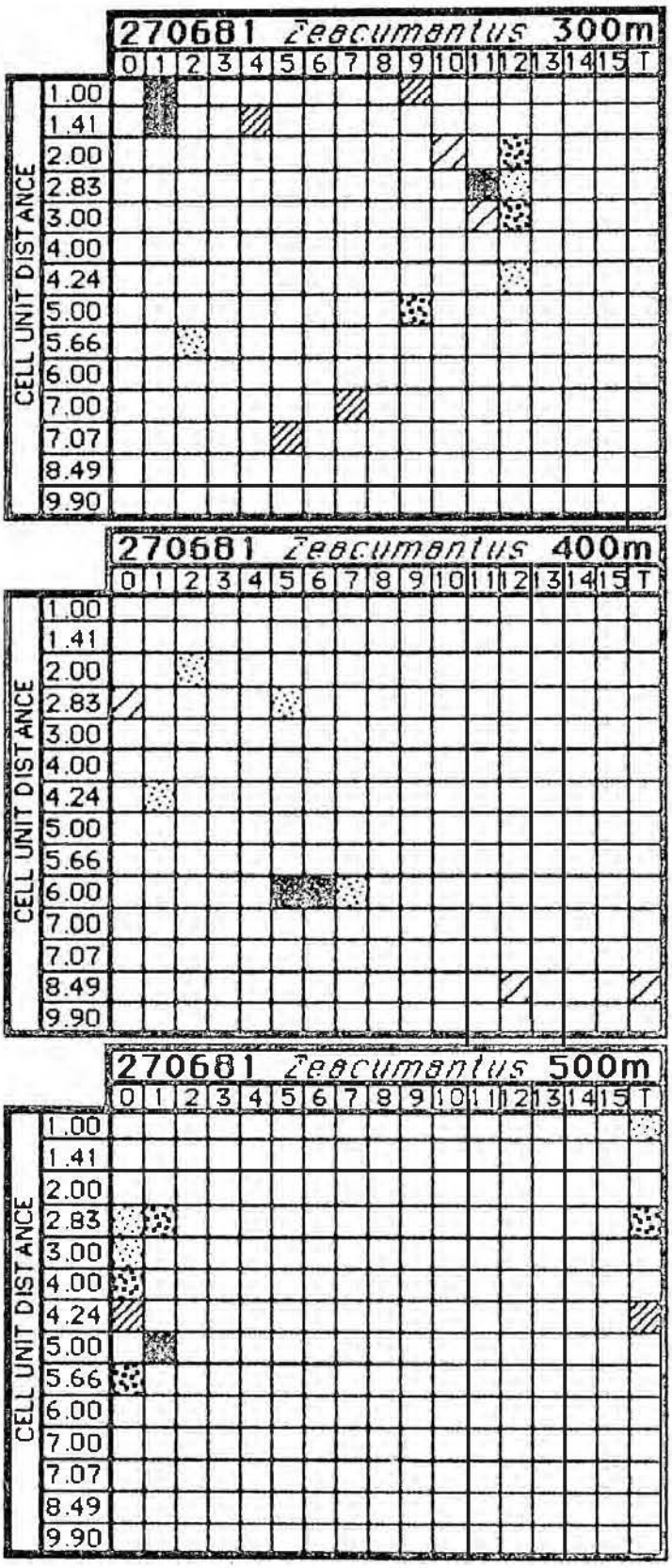
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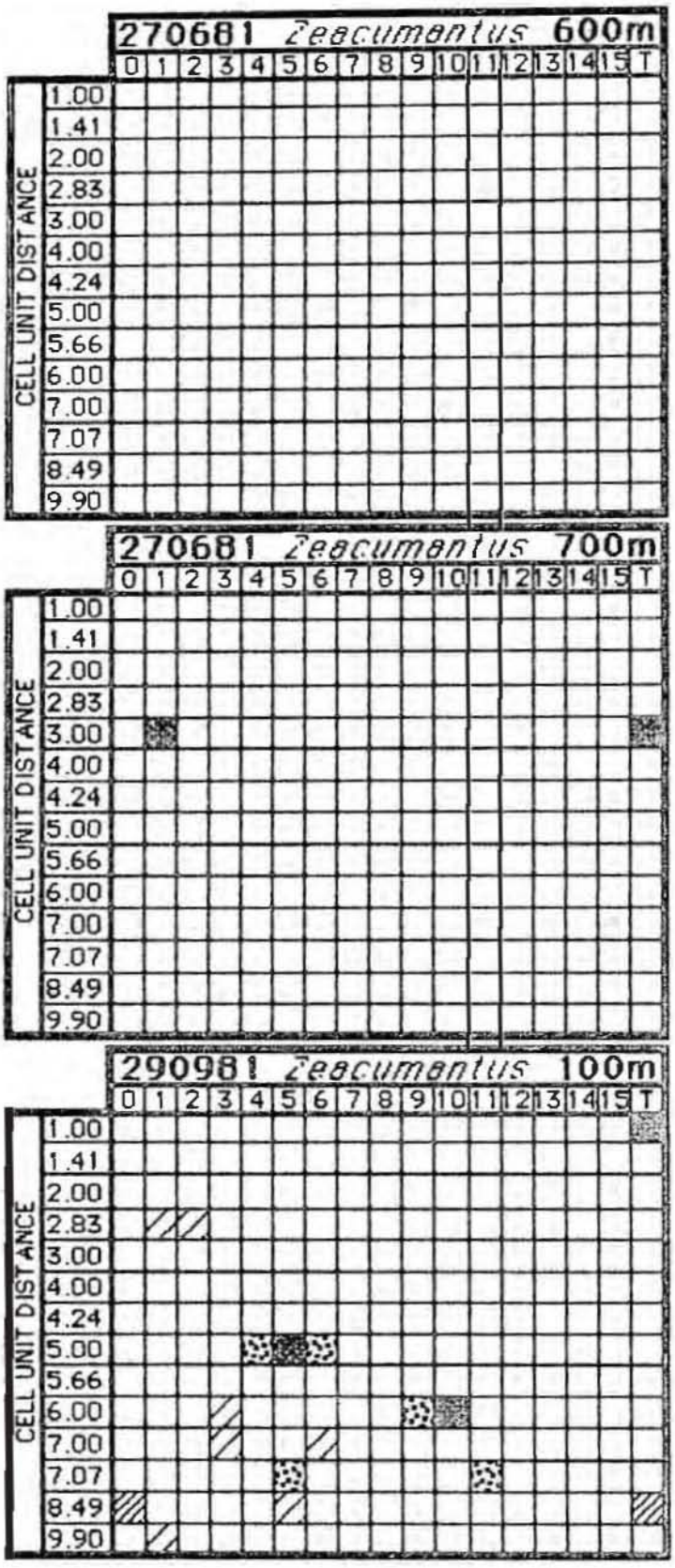
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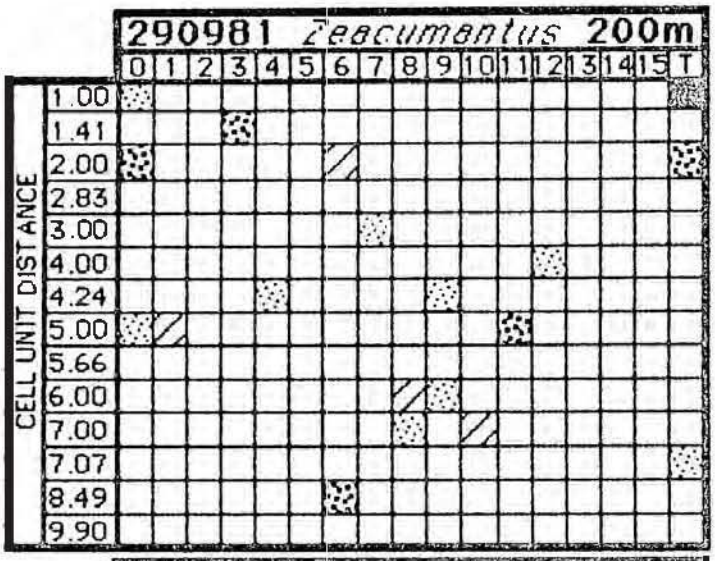
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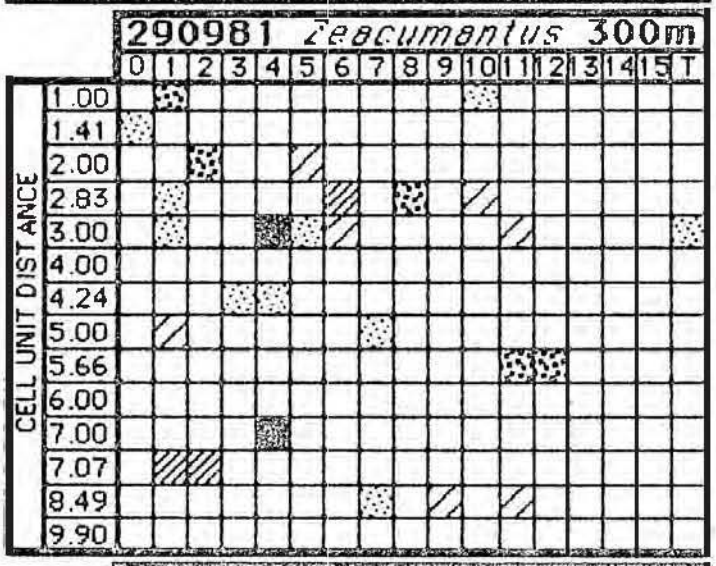
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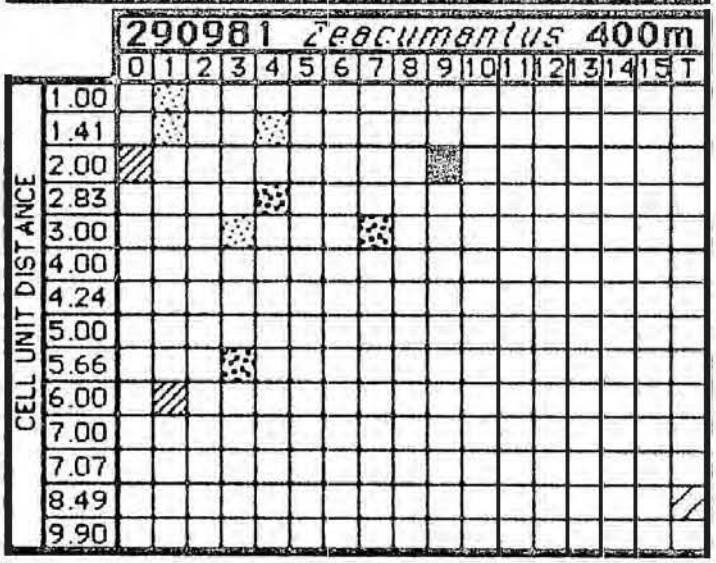
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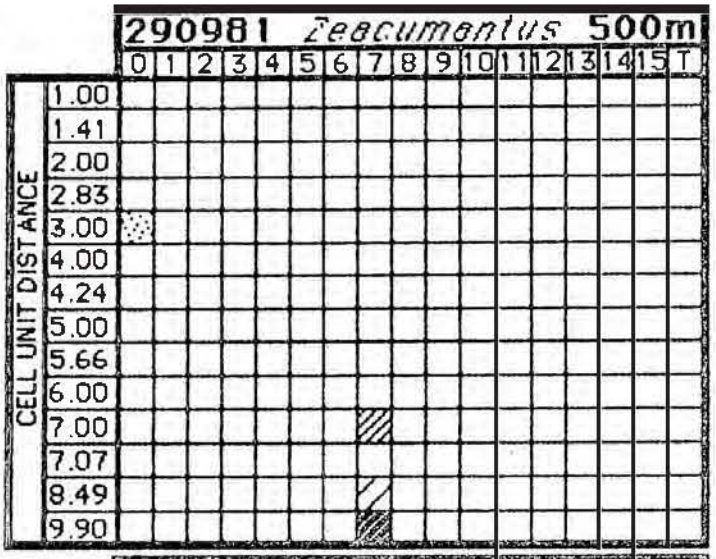
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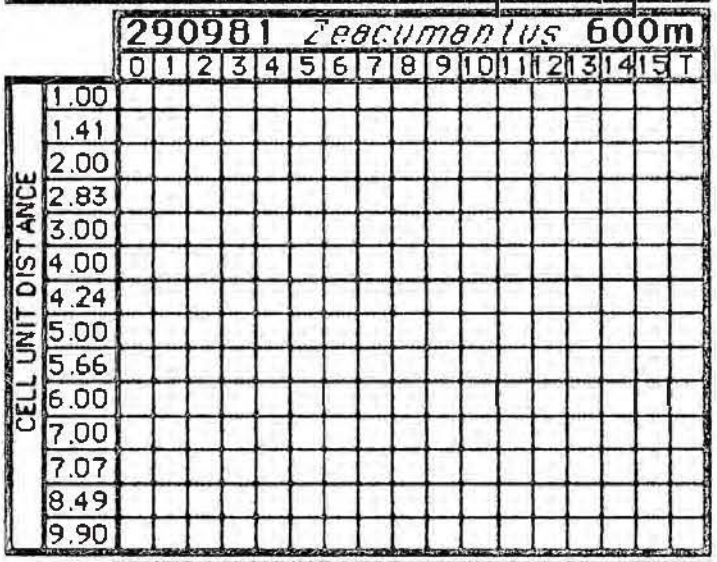
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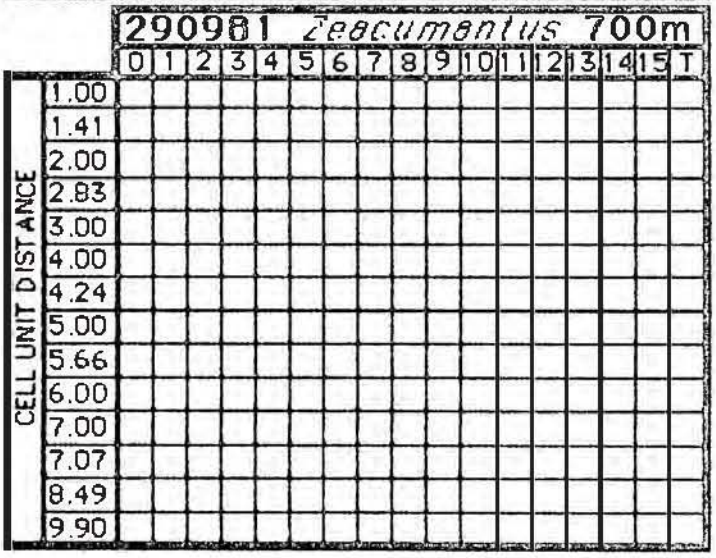
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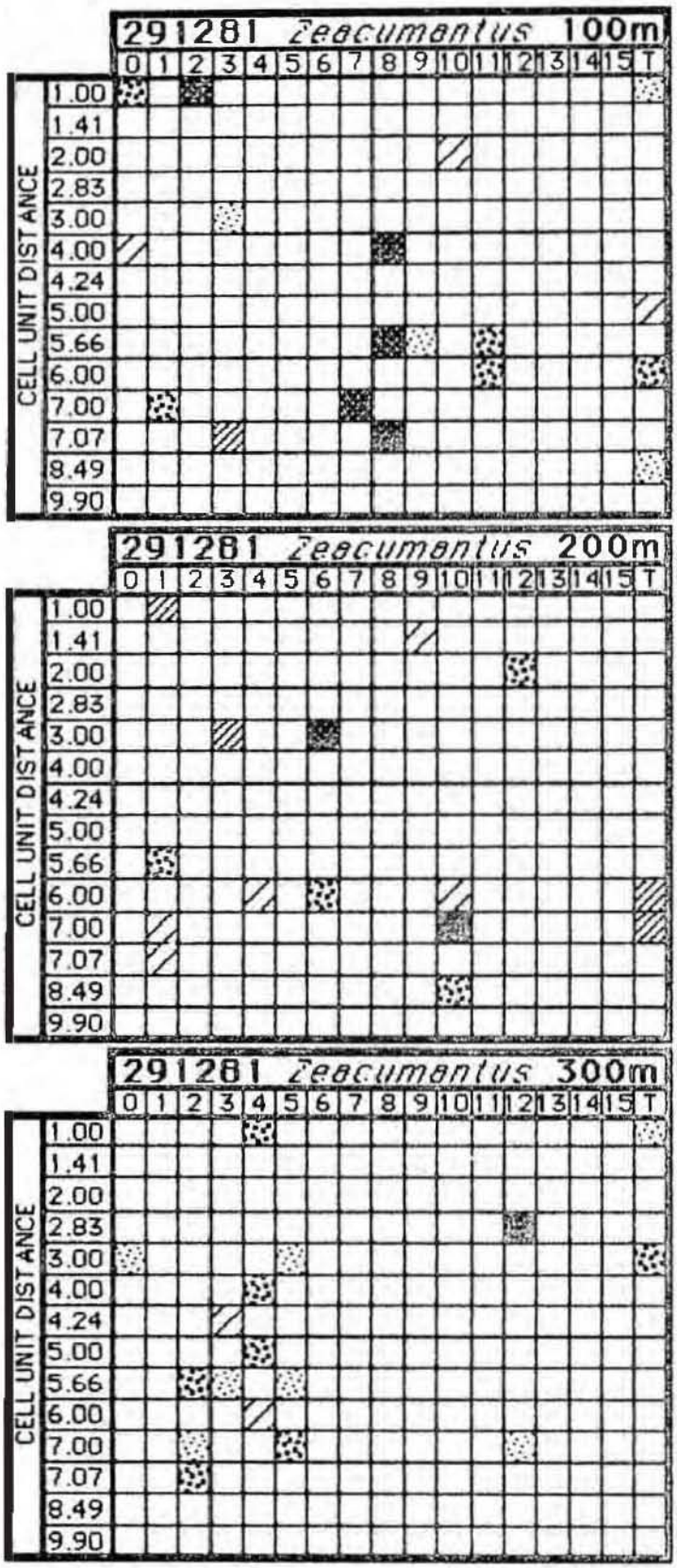
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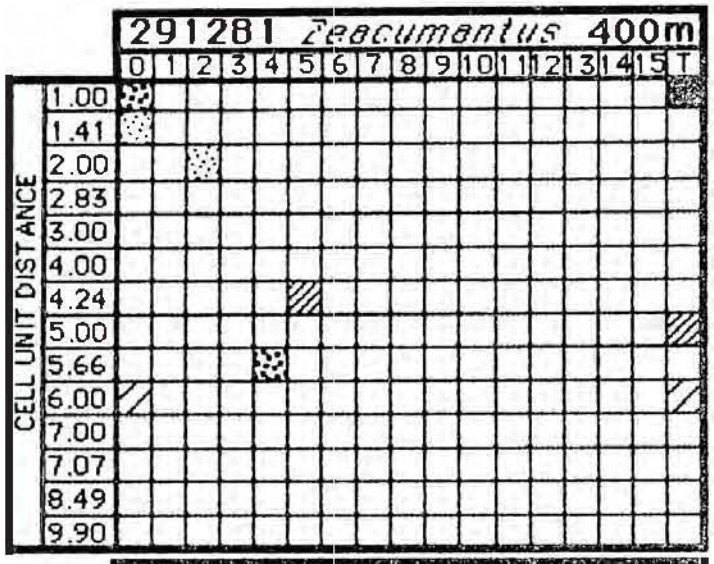
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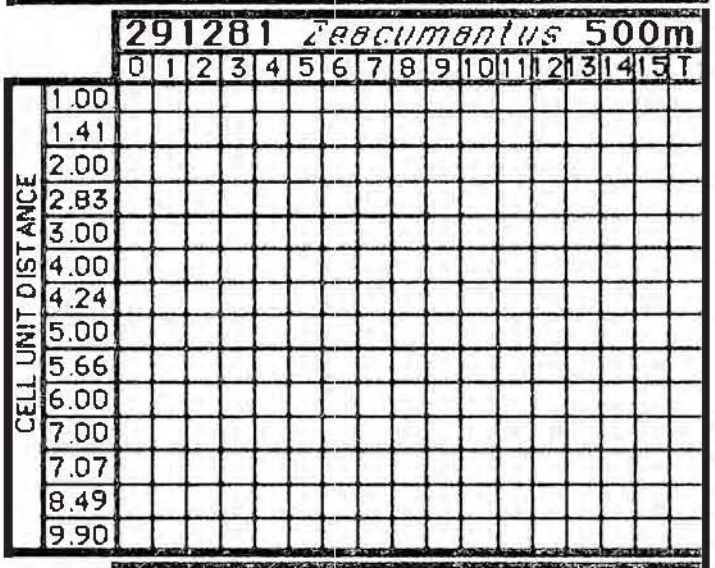
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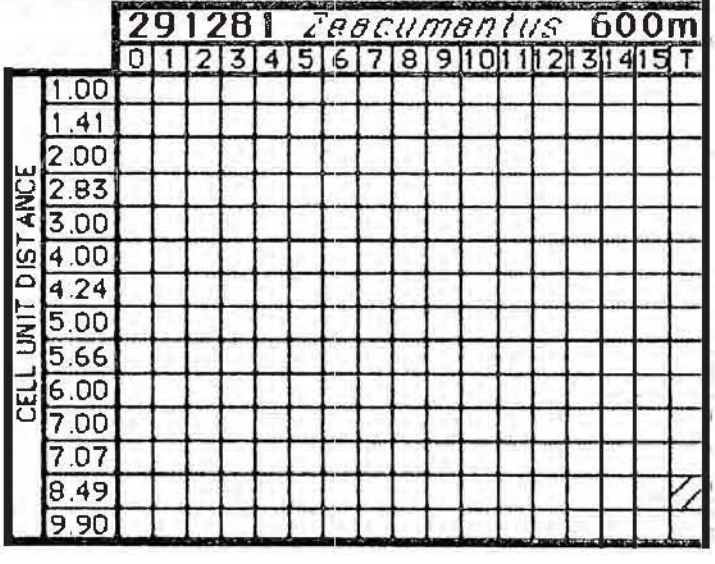
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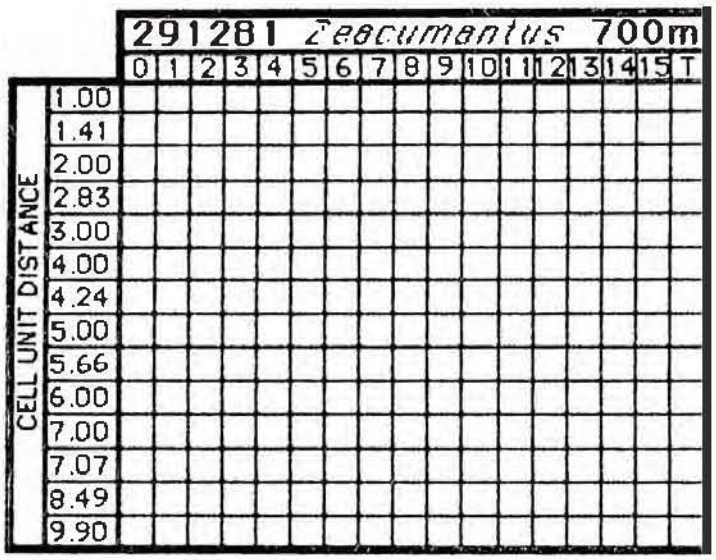
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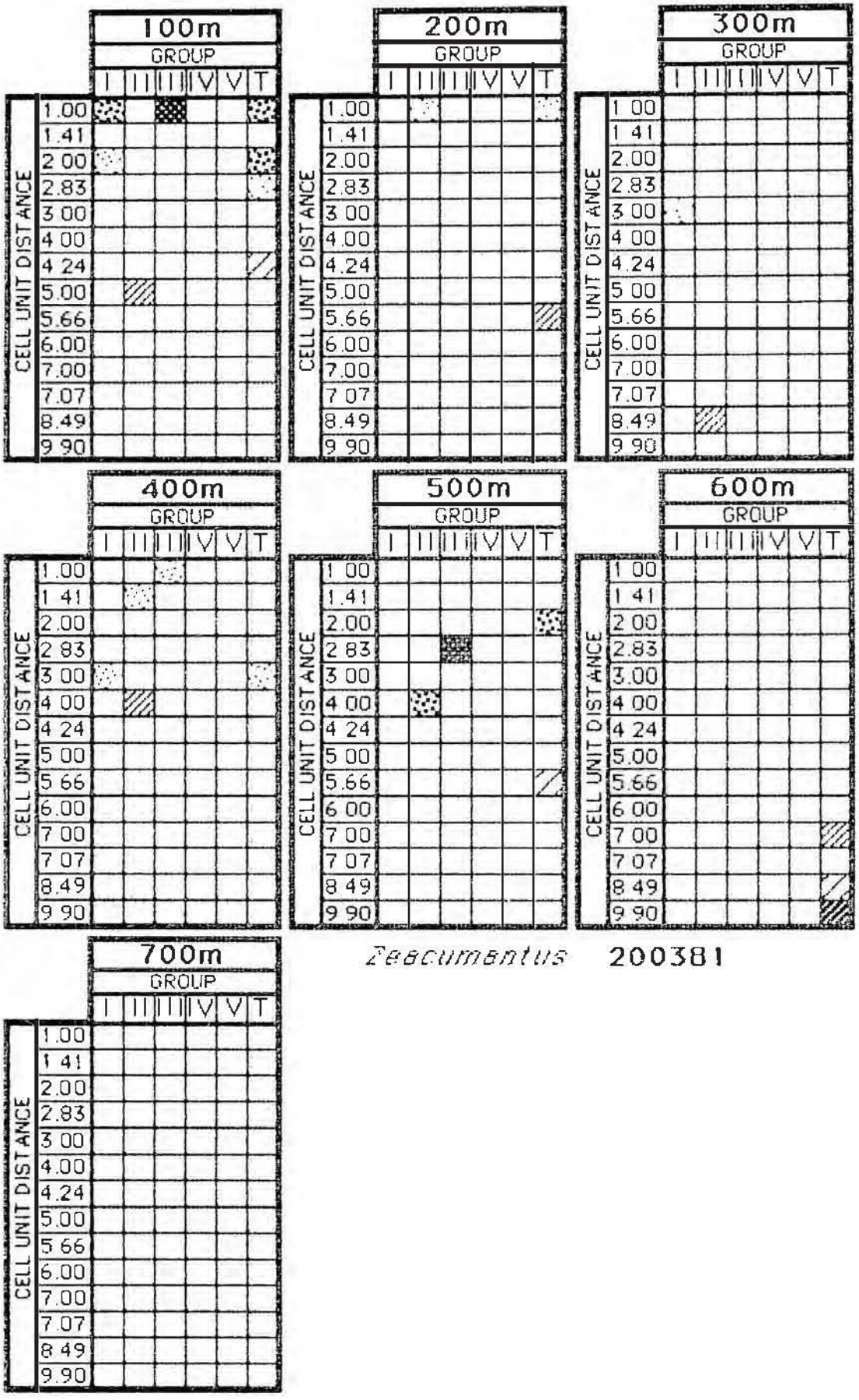

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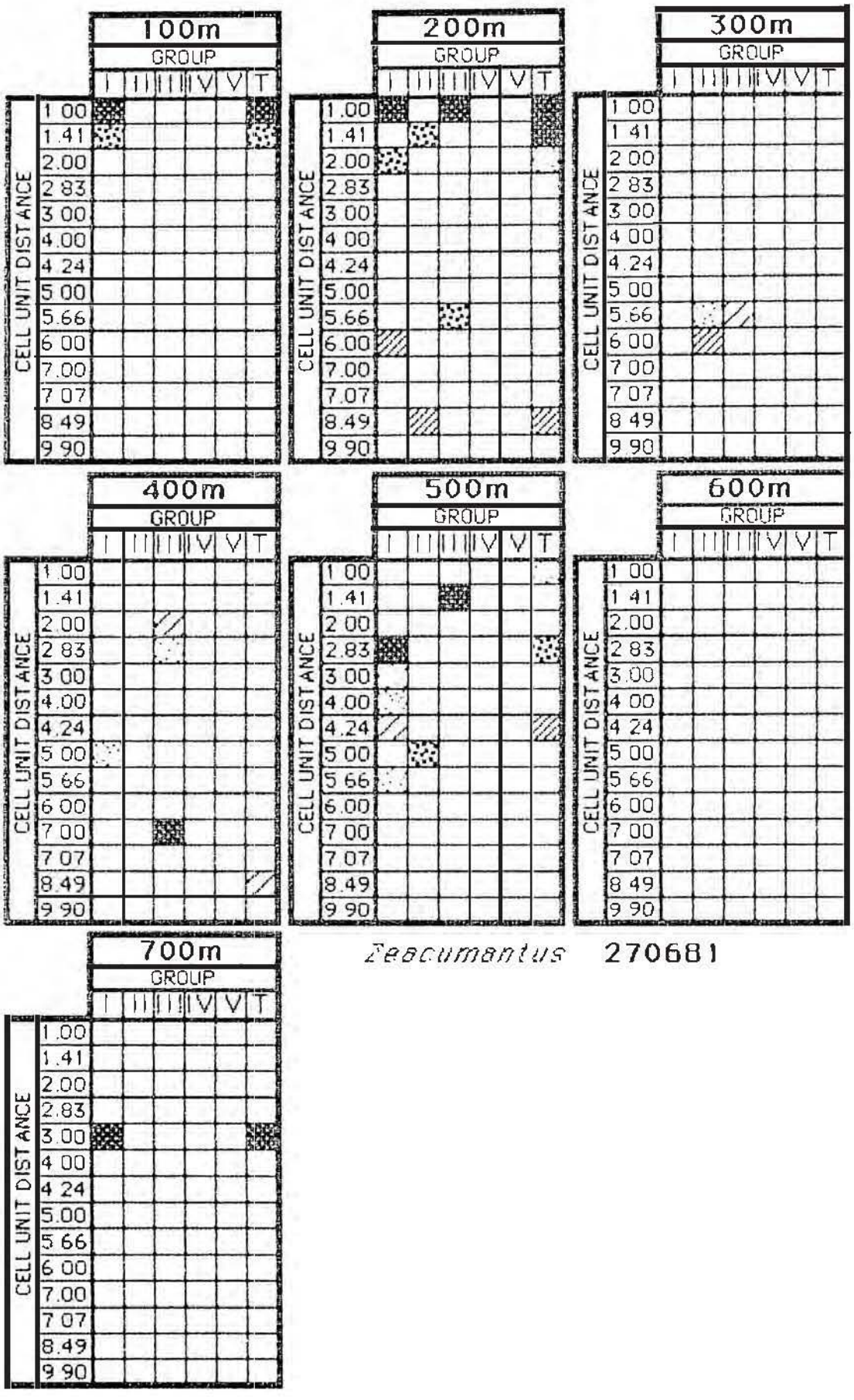

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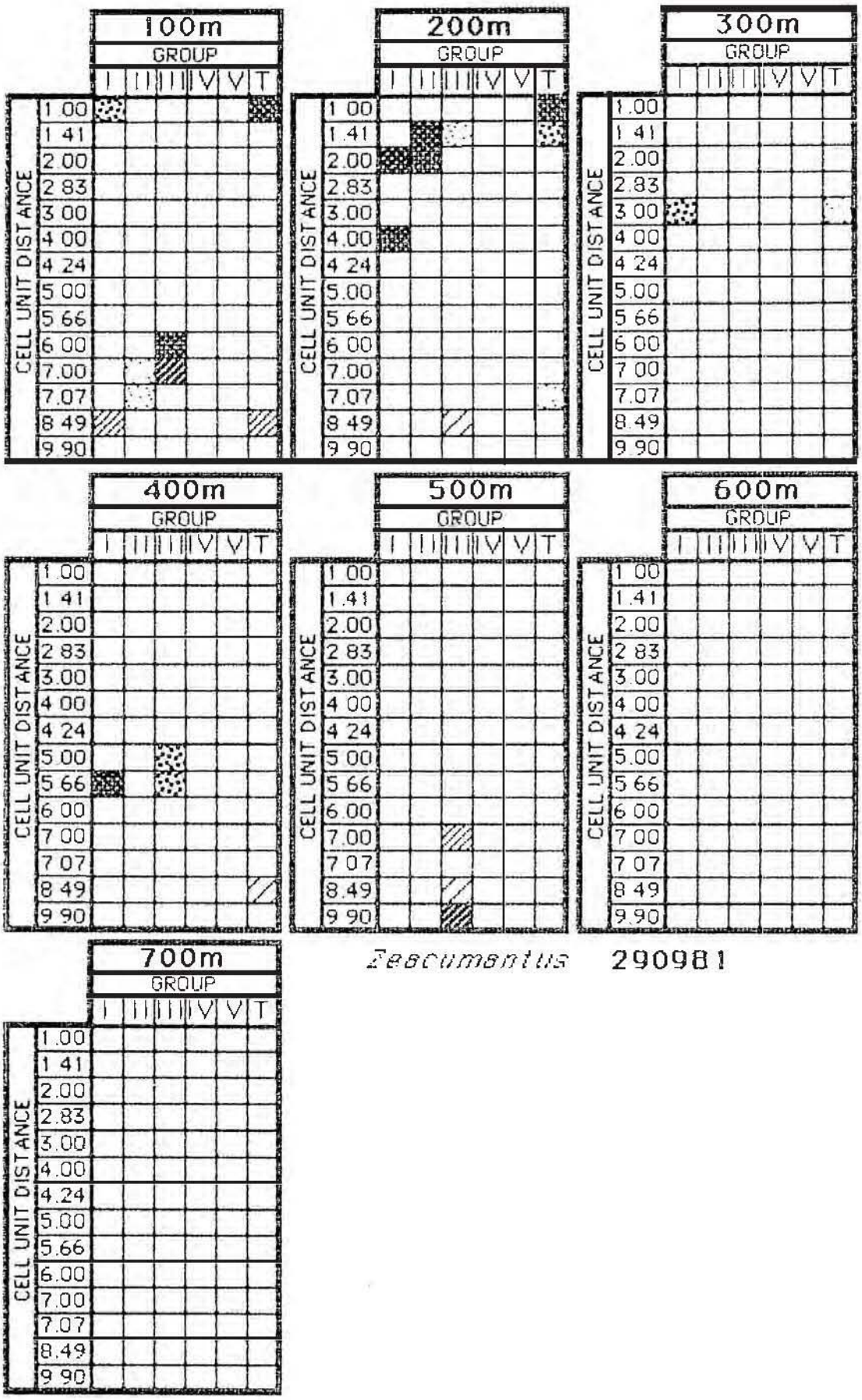
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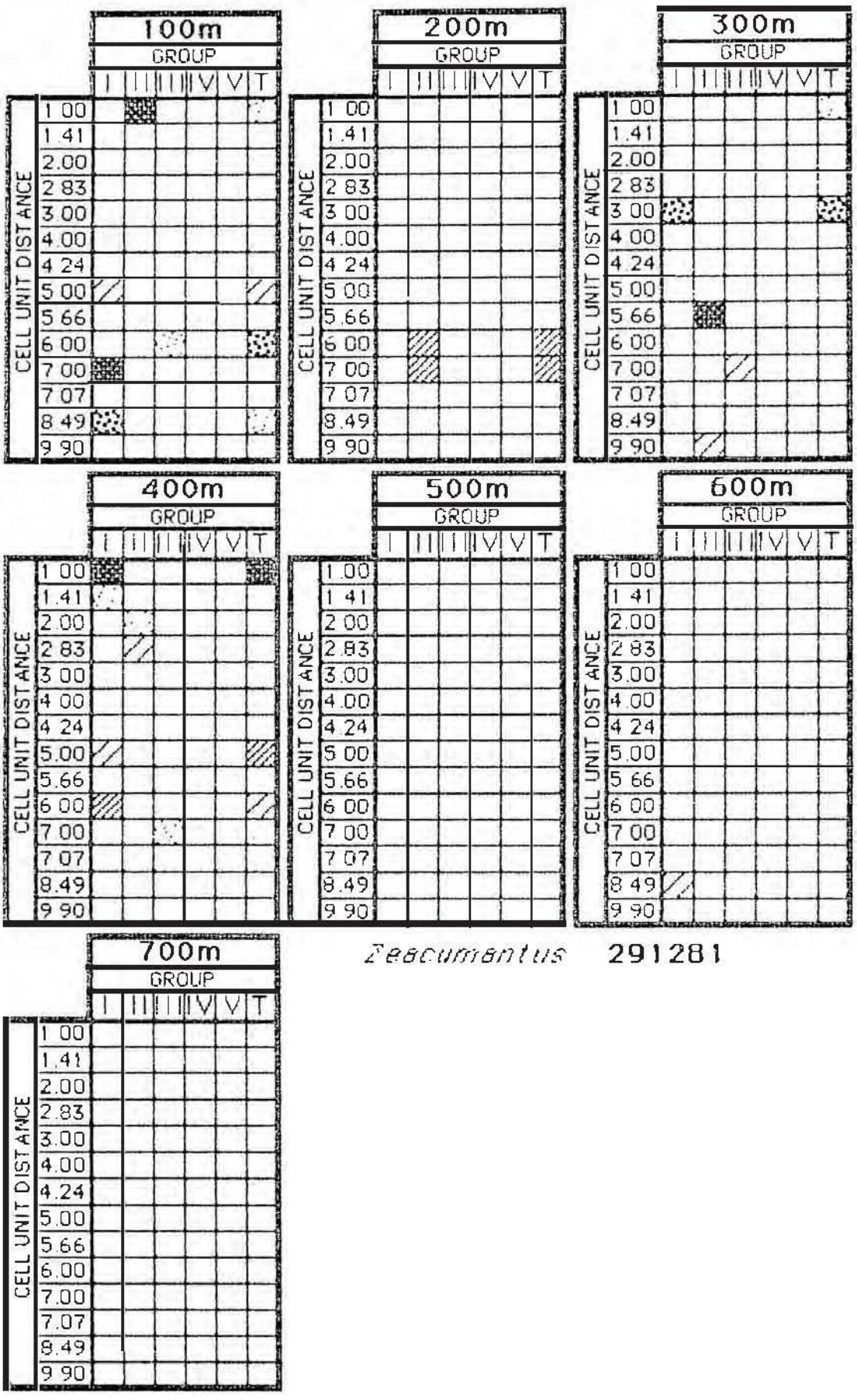

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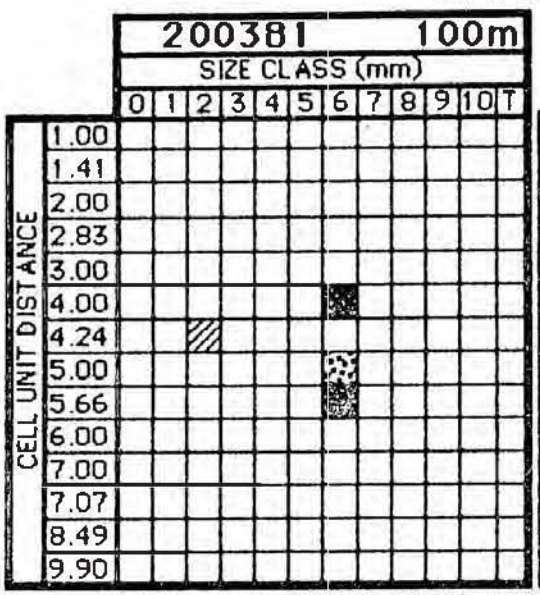
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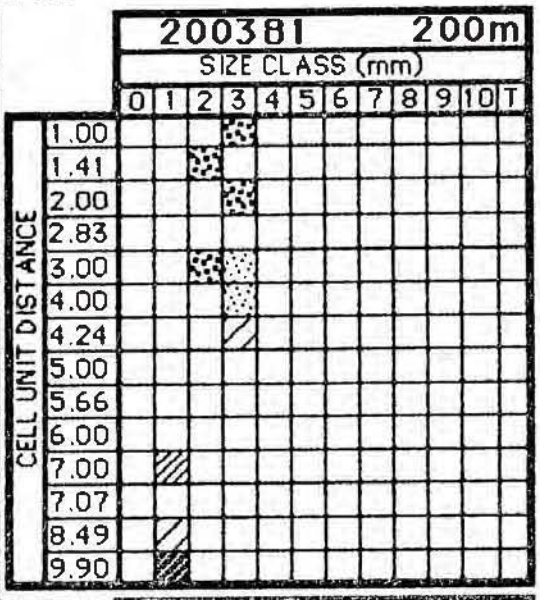
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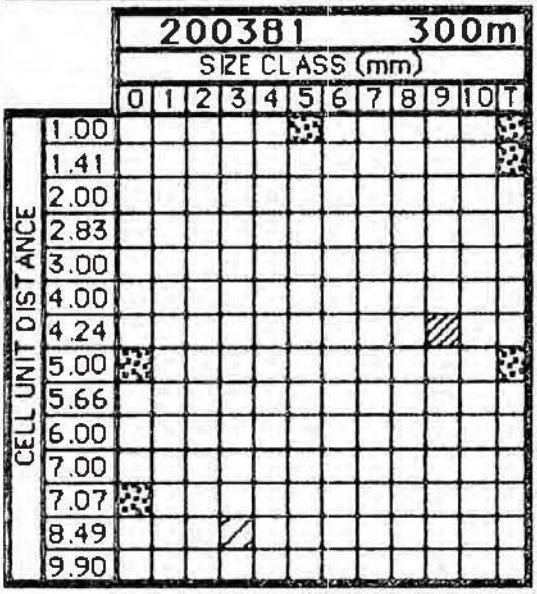
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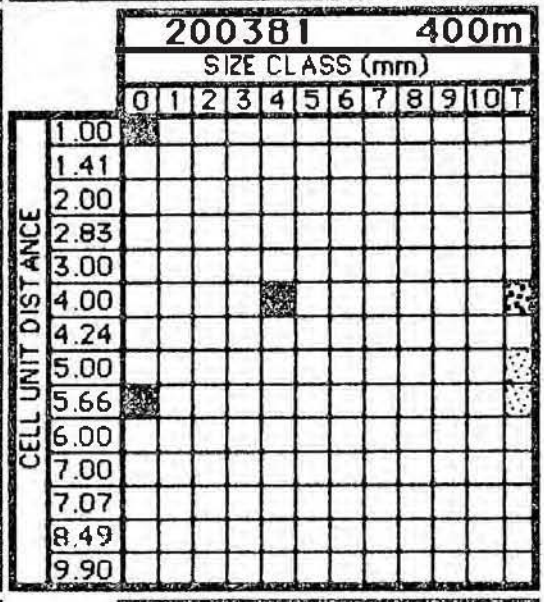
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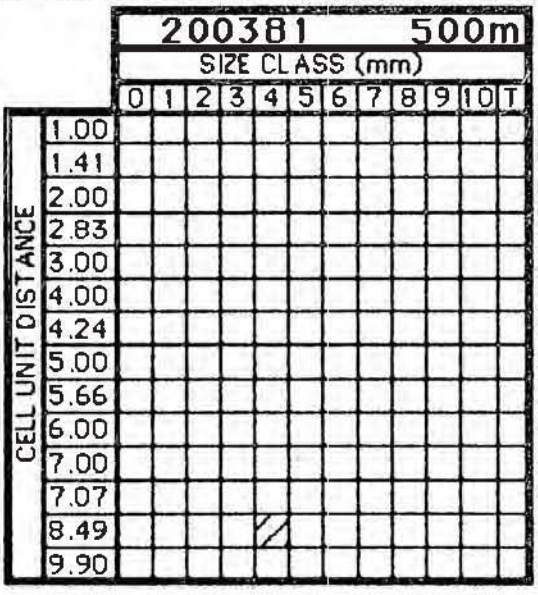
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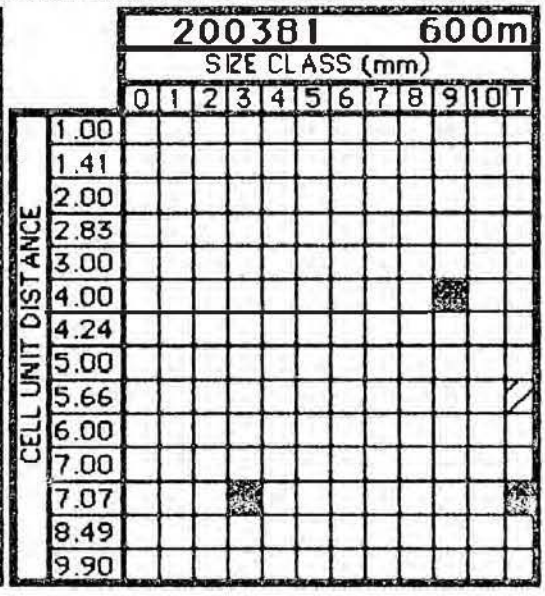
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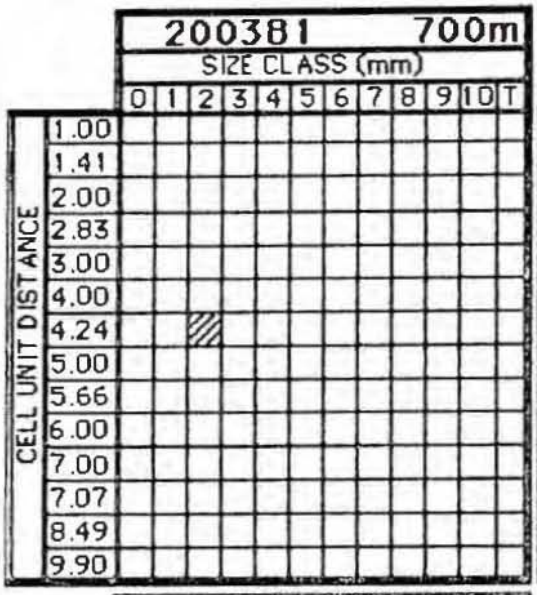
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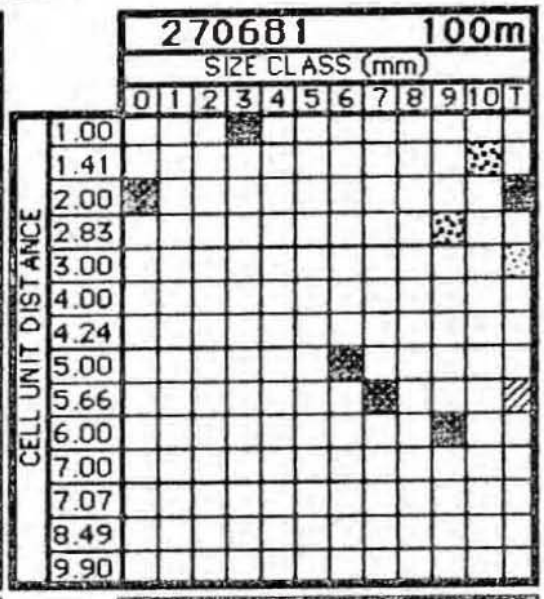
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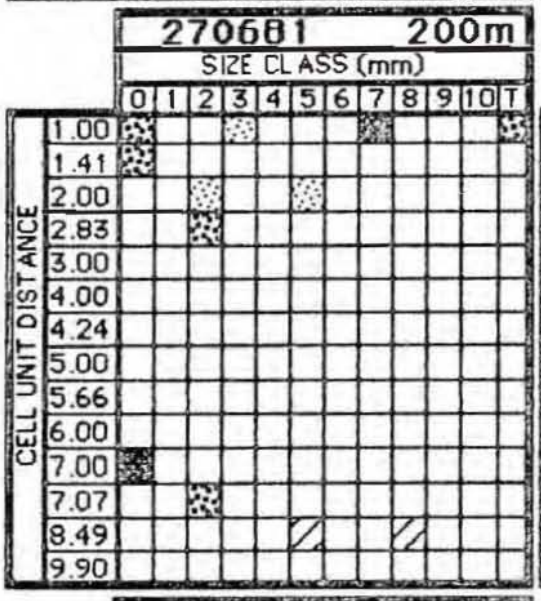
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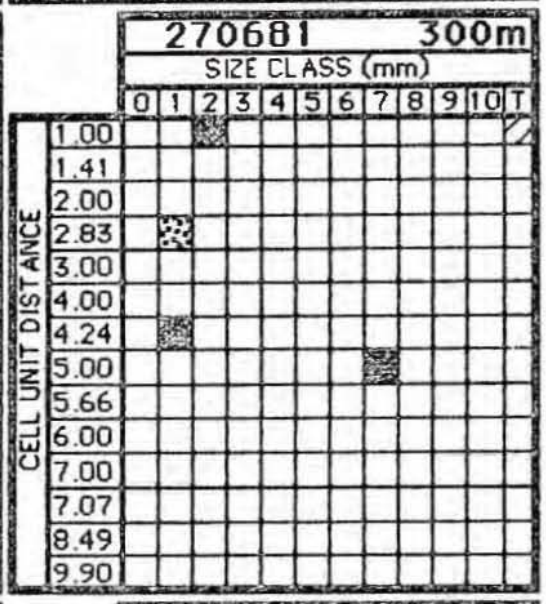
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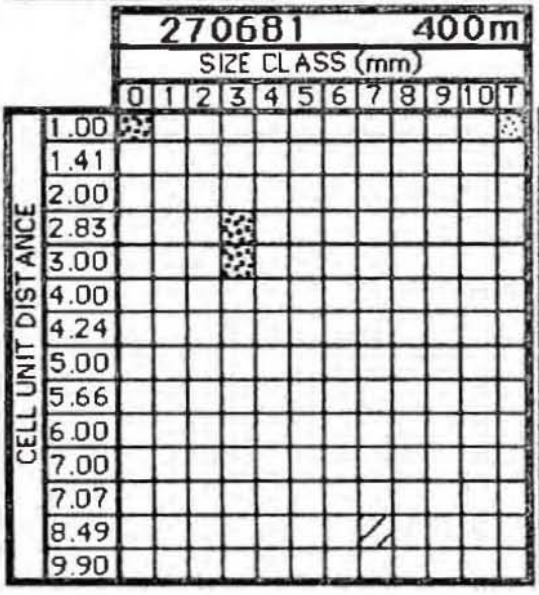
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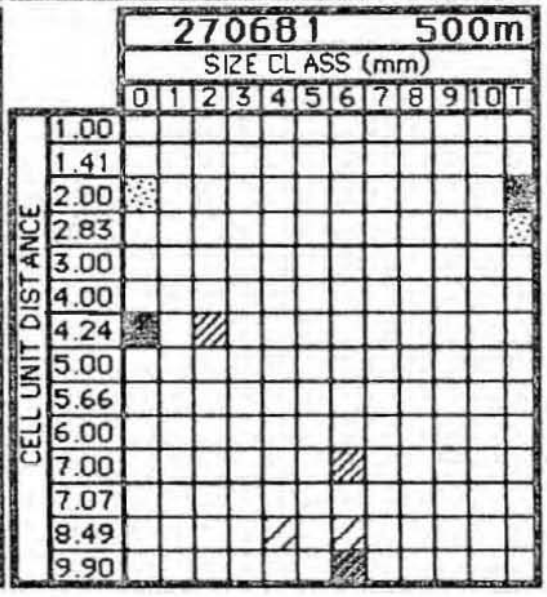
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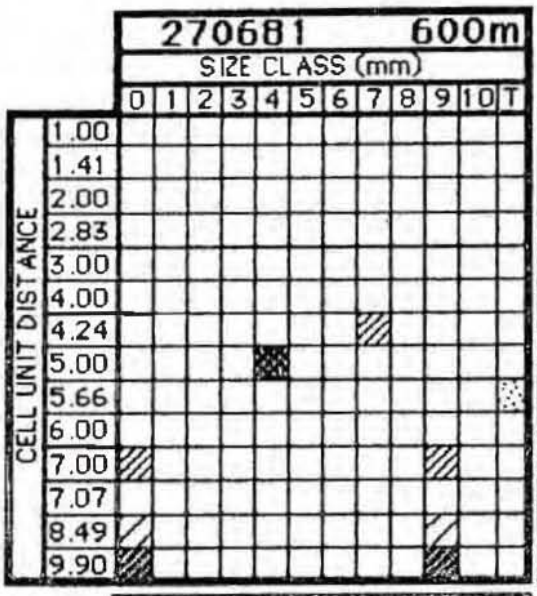
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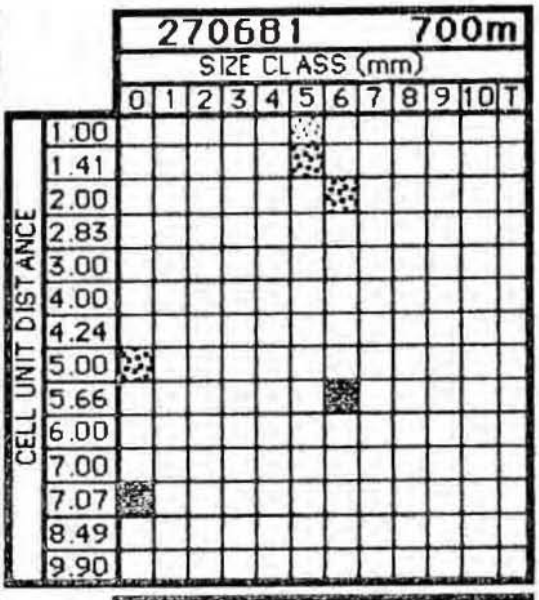
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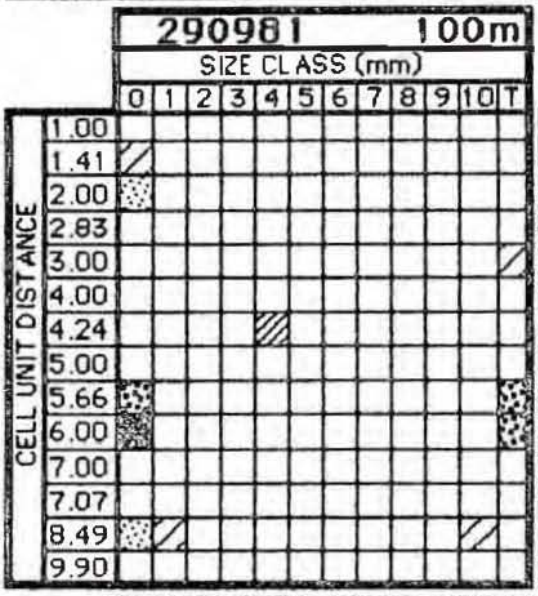
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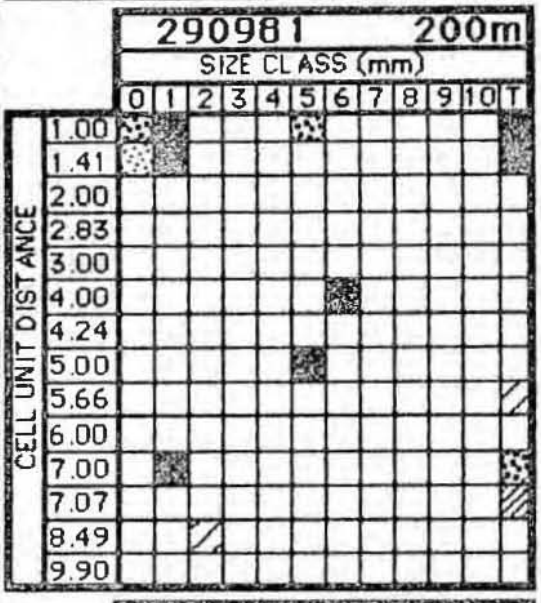
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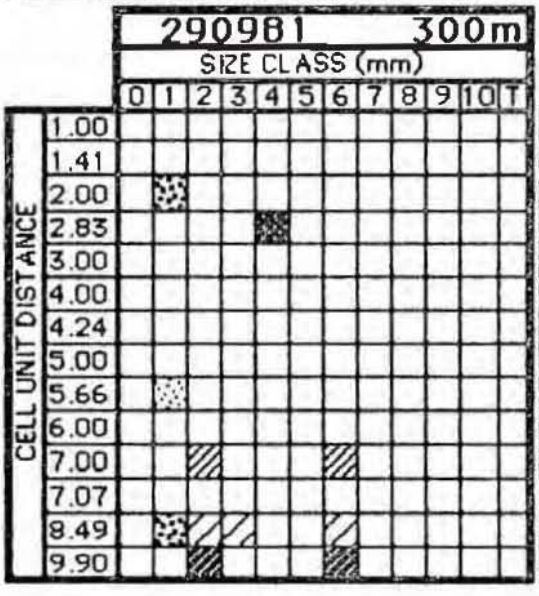
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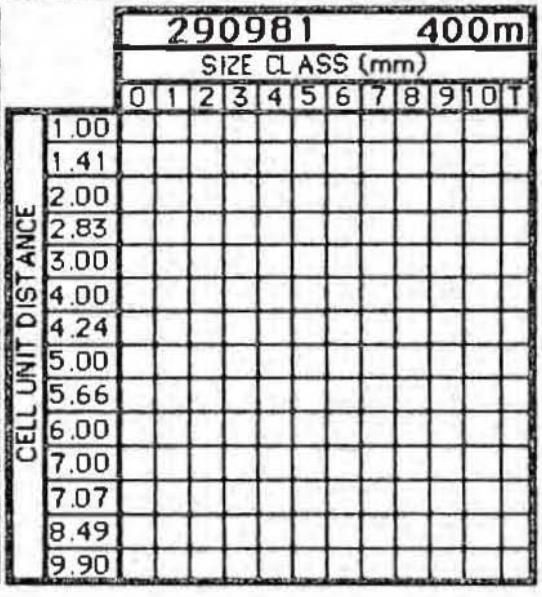
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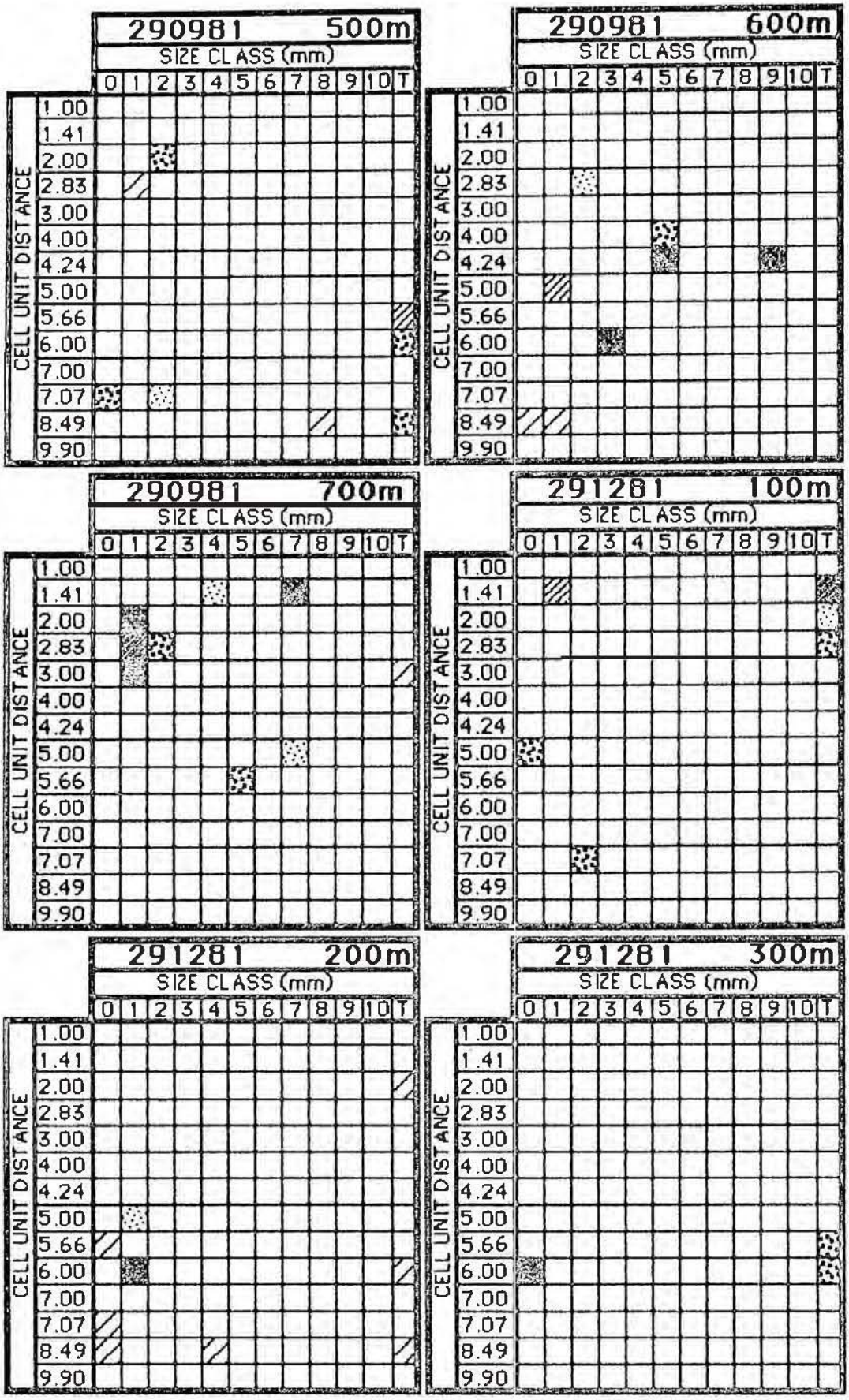
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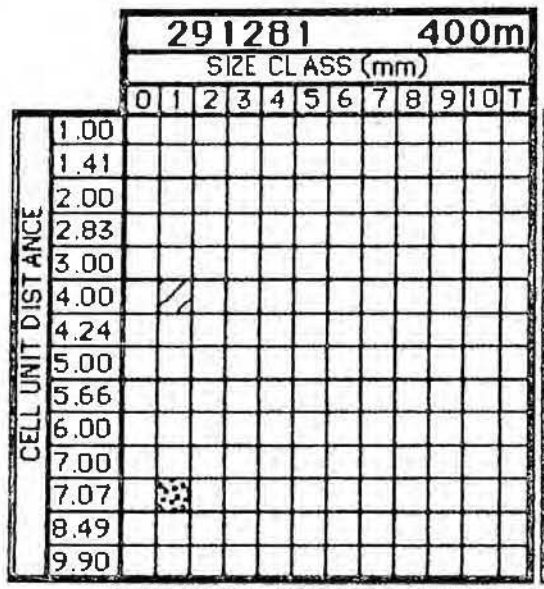
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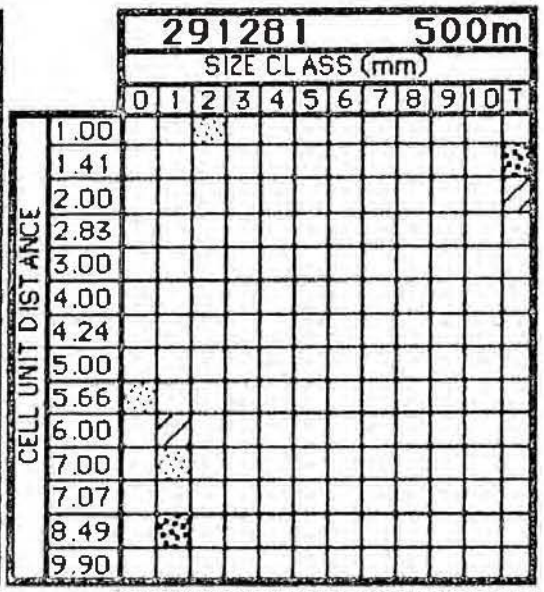
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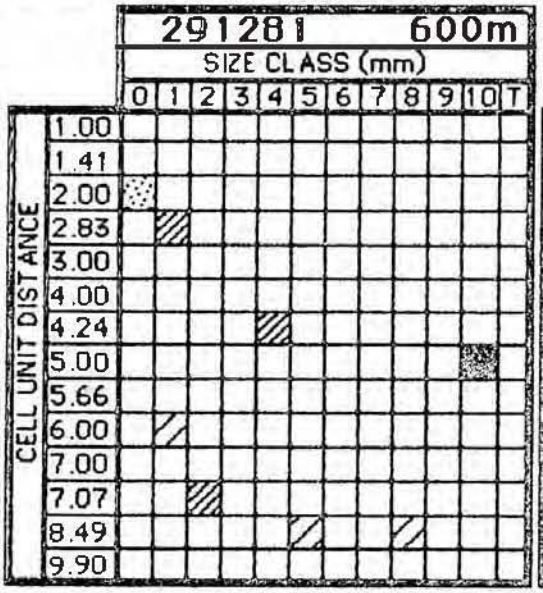
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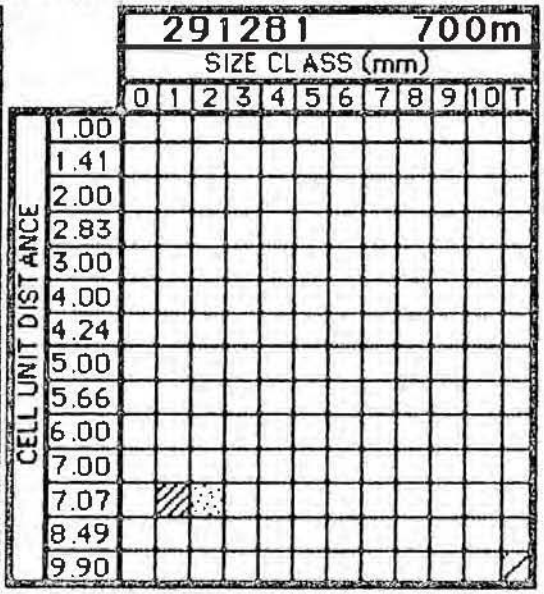
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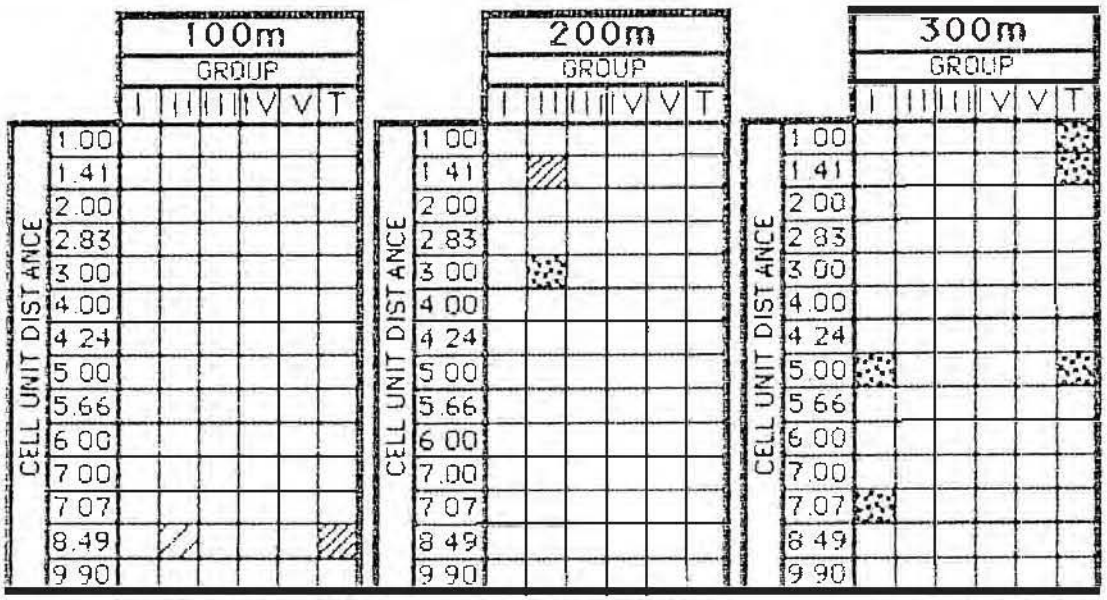

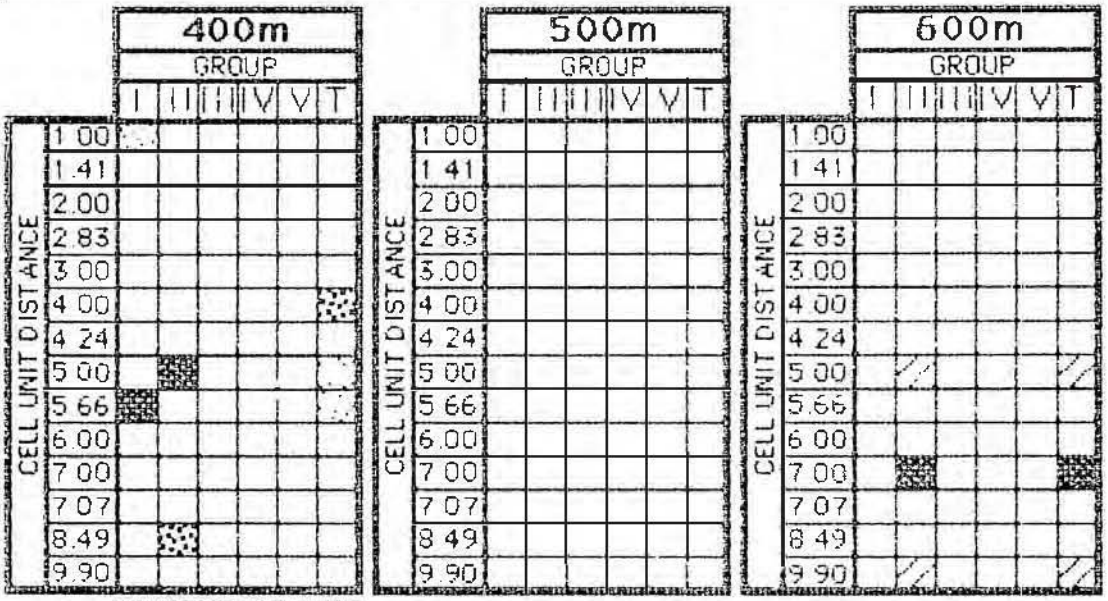

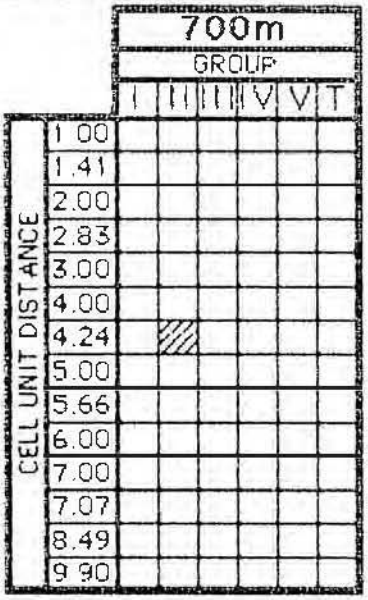

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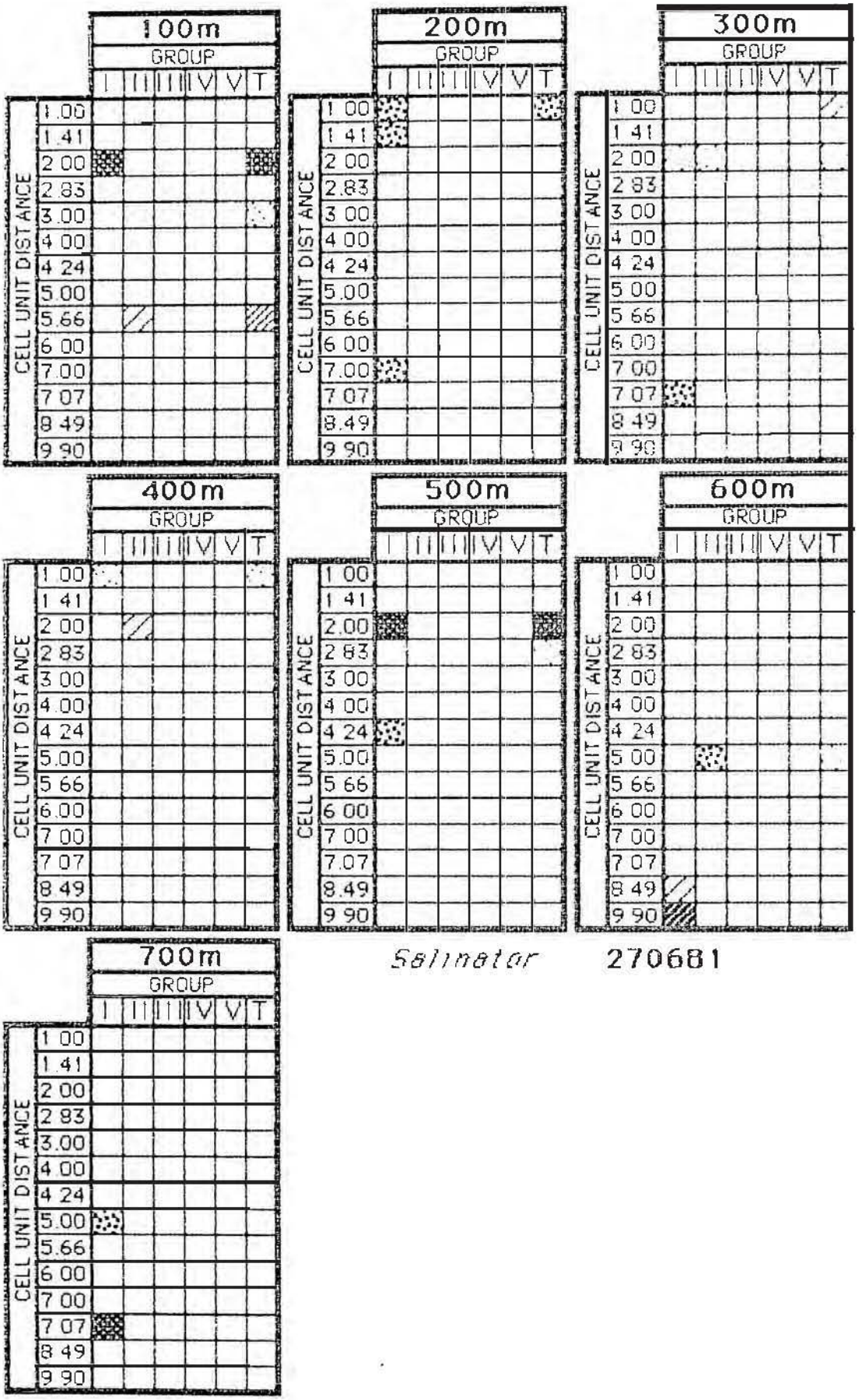
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CELL UNIT DISTANCE
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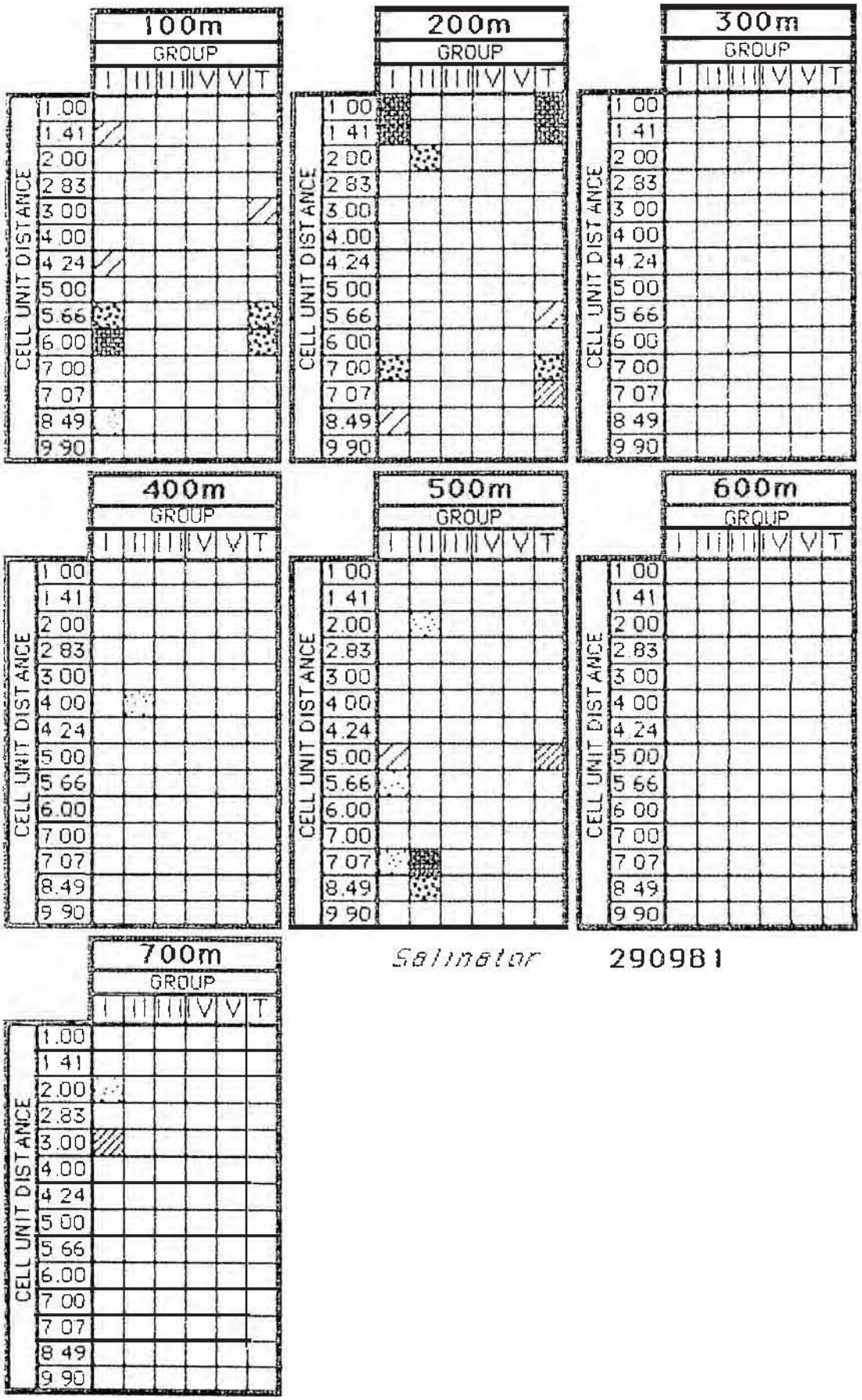
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GROUP
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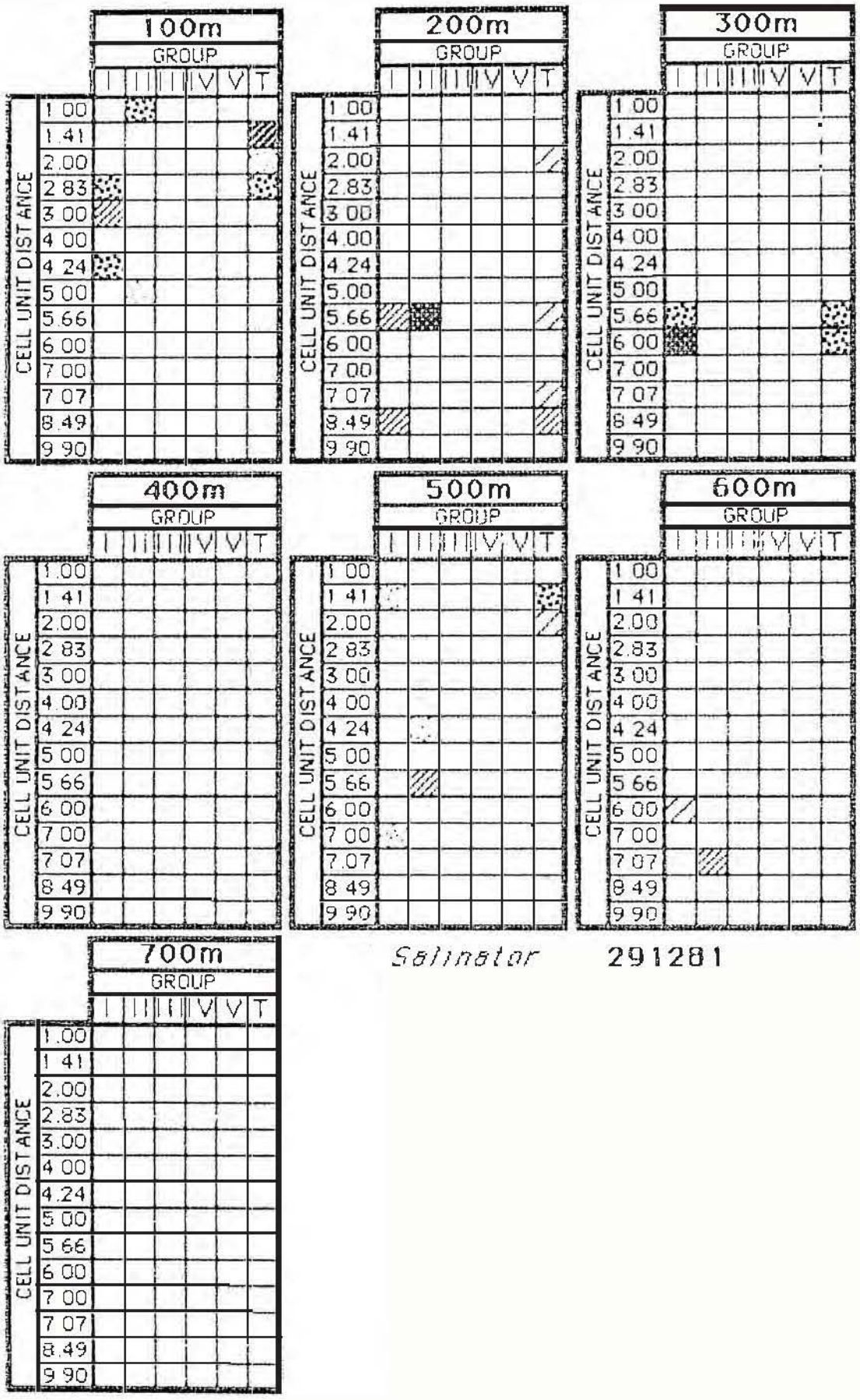
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GROUP
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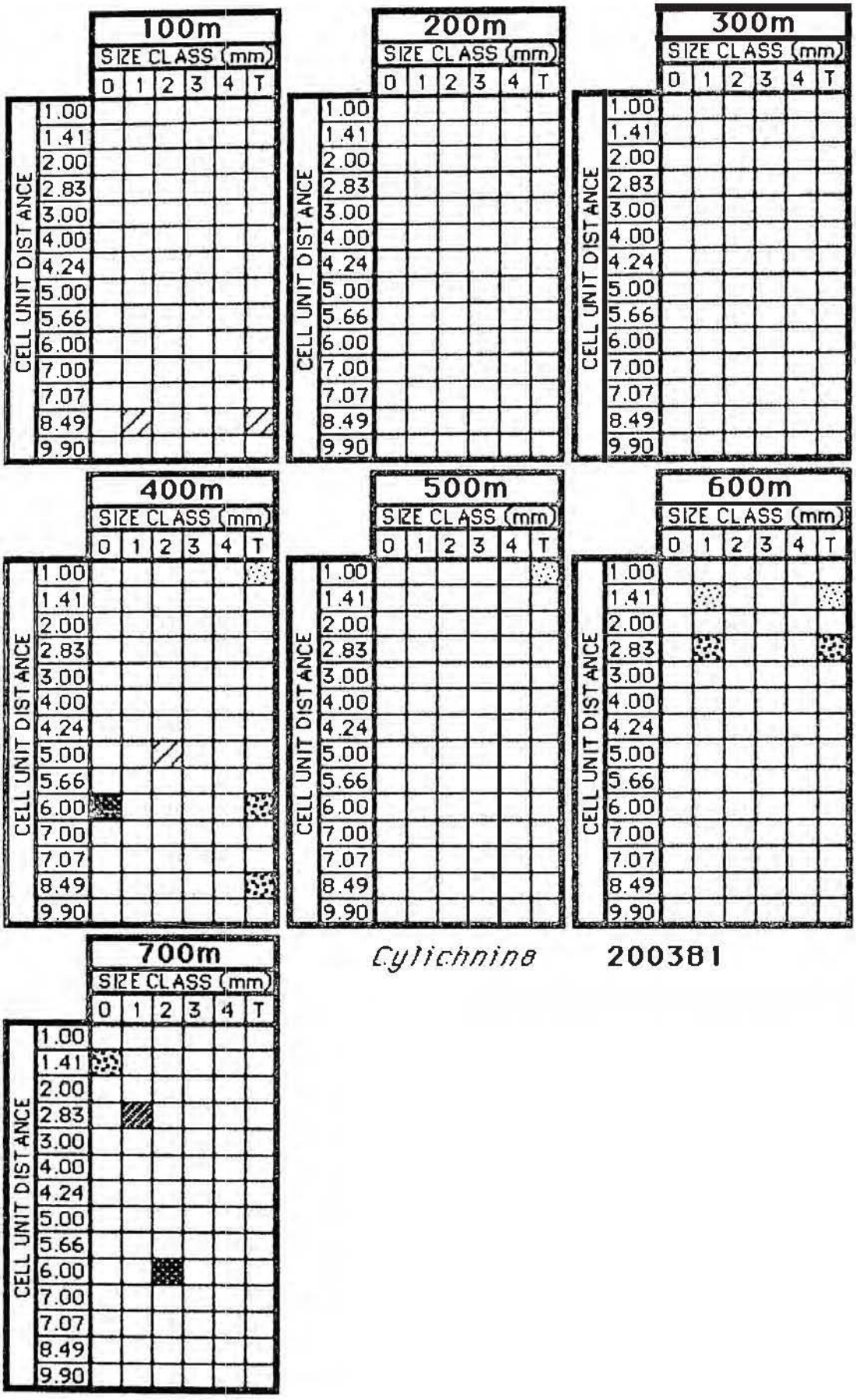

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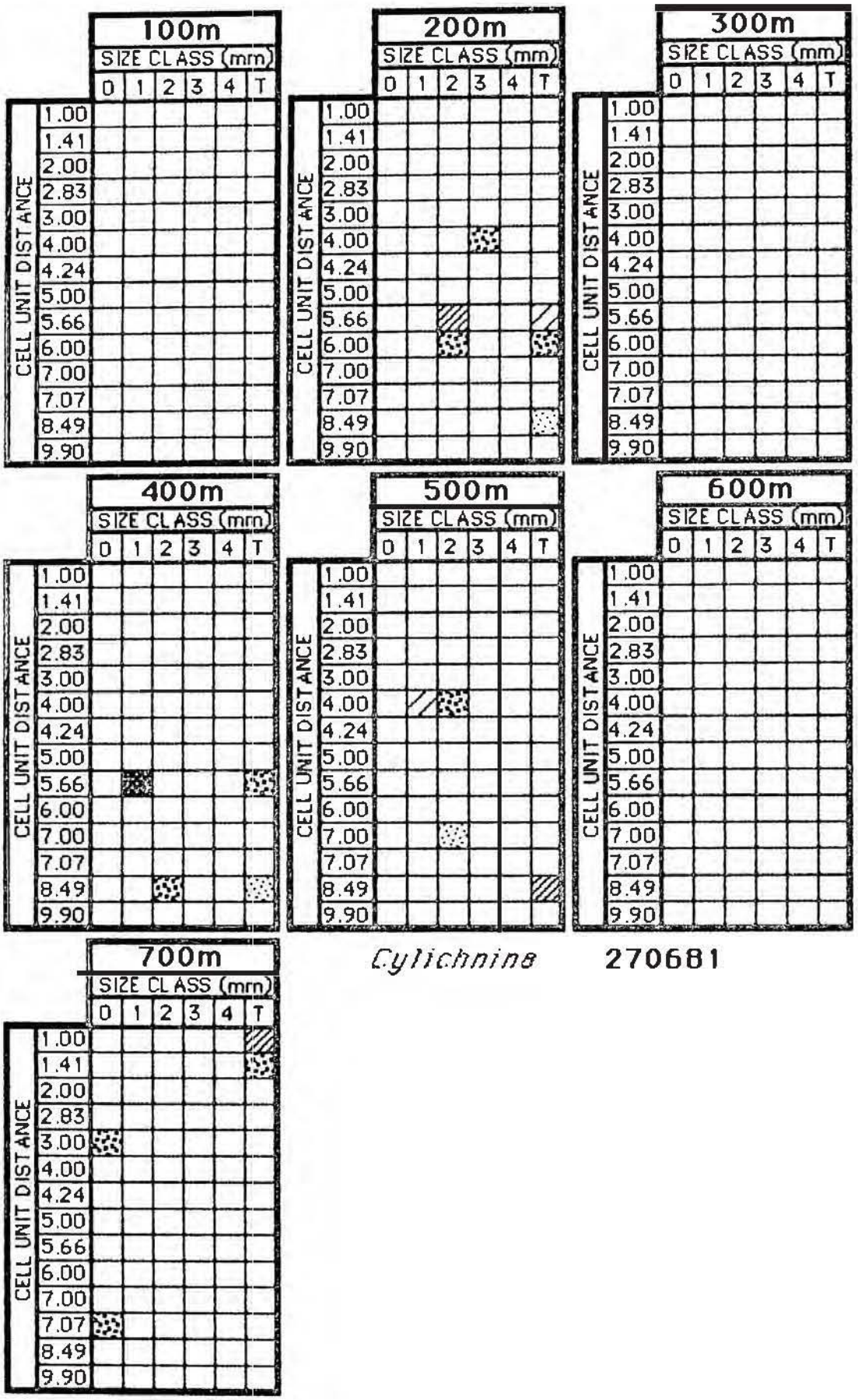

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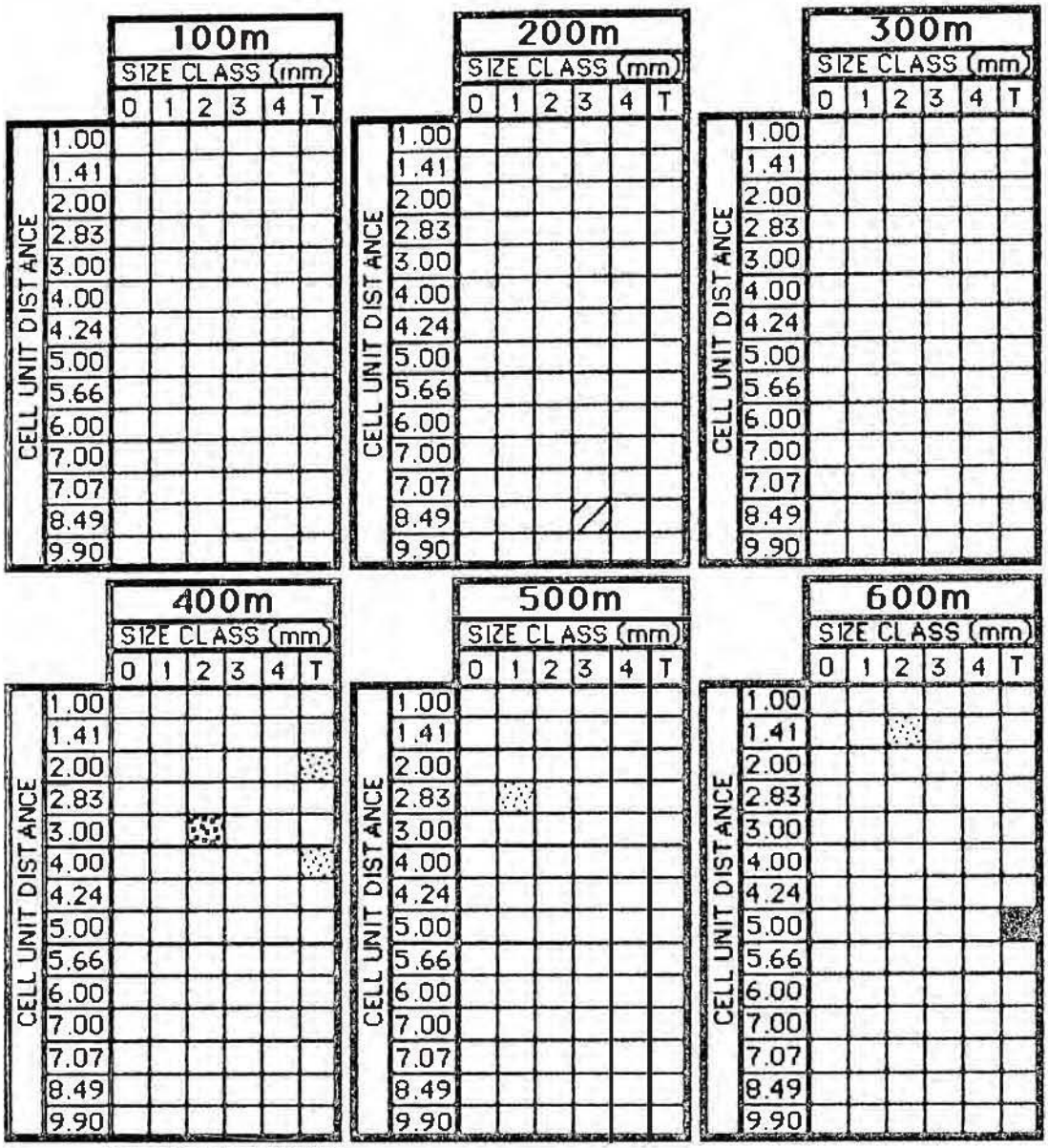

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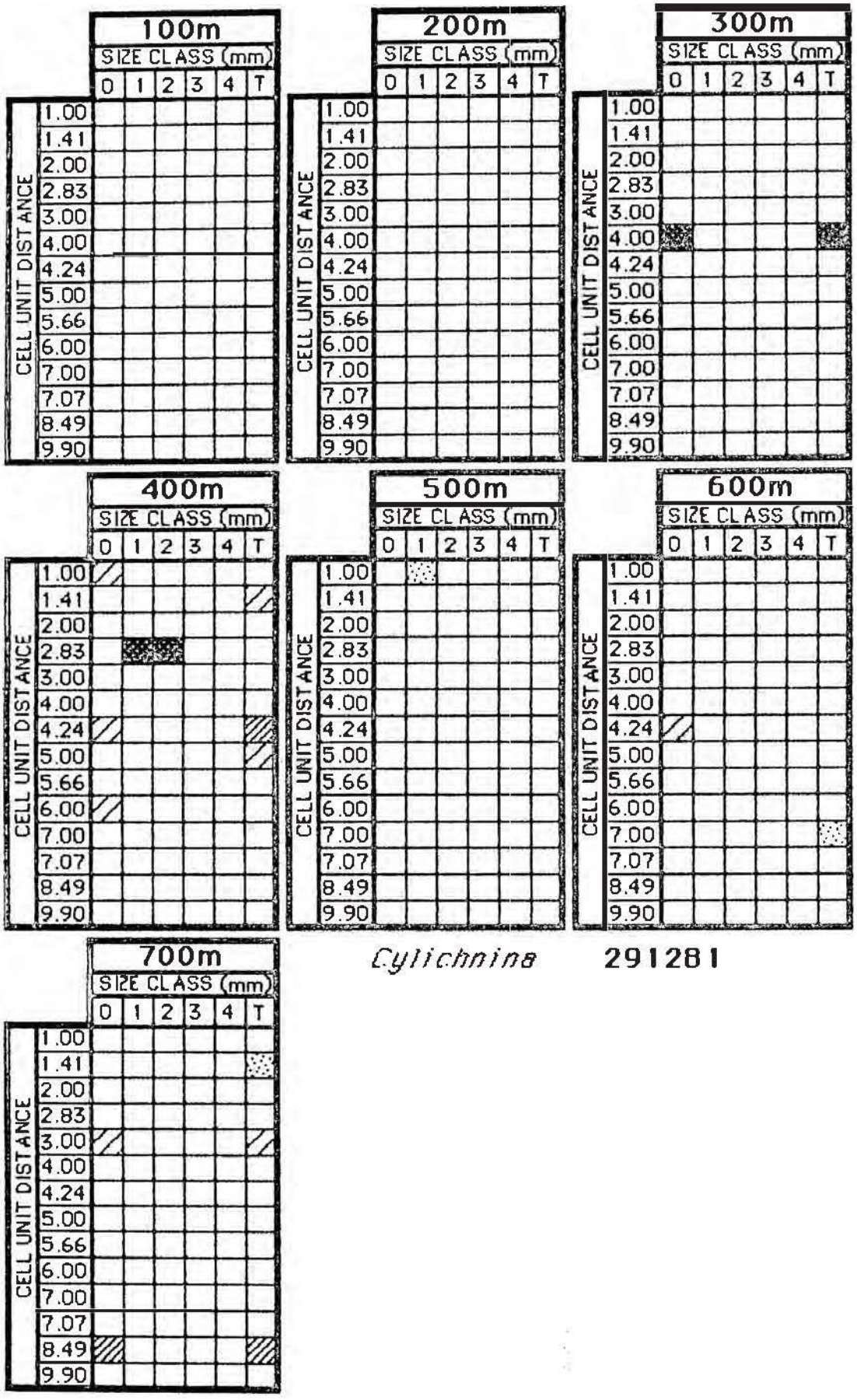

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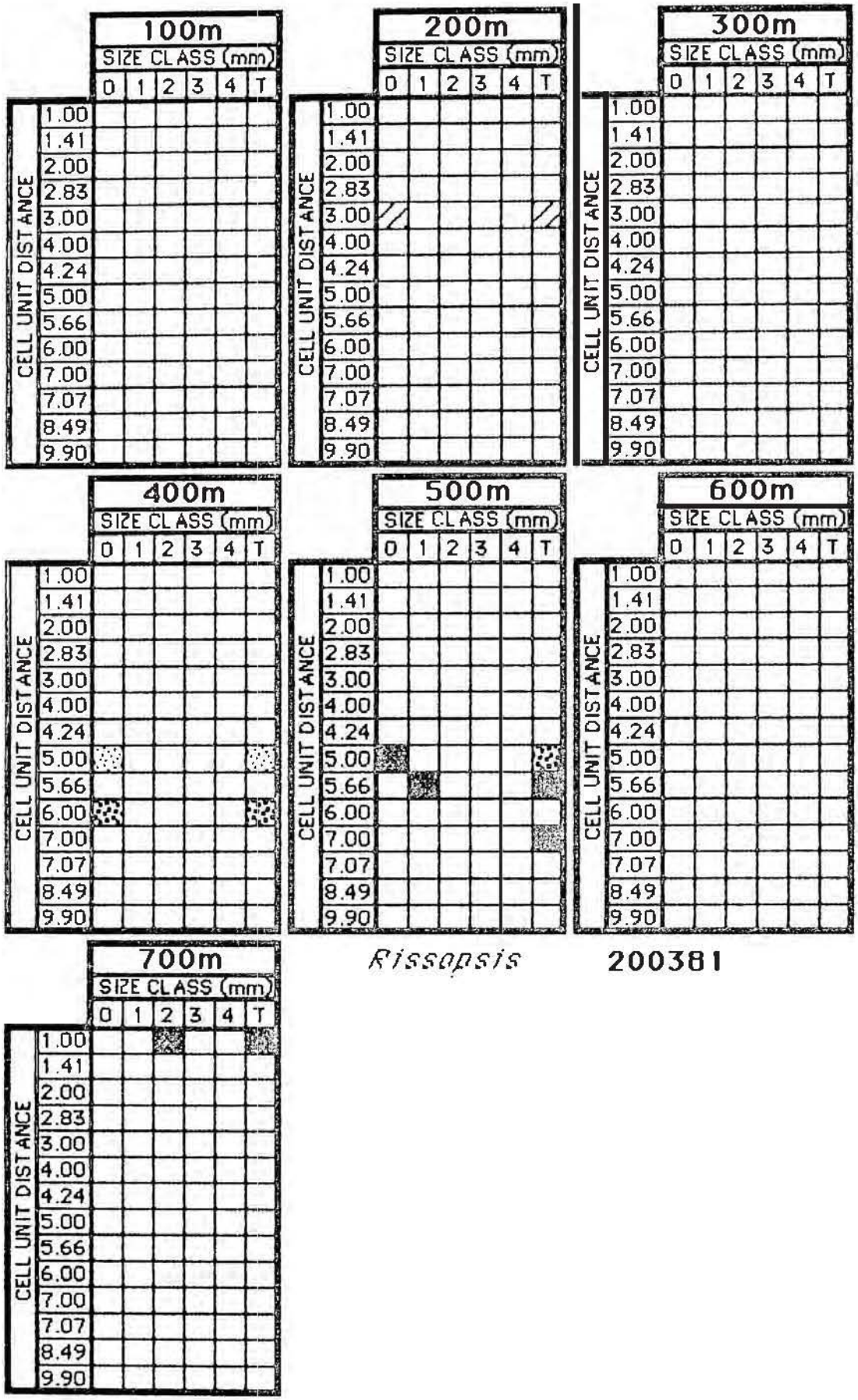

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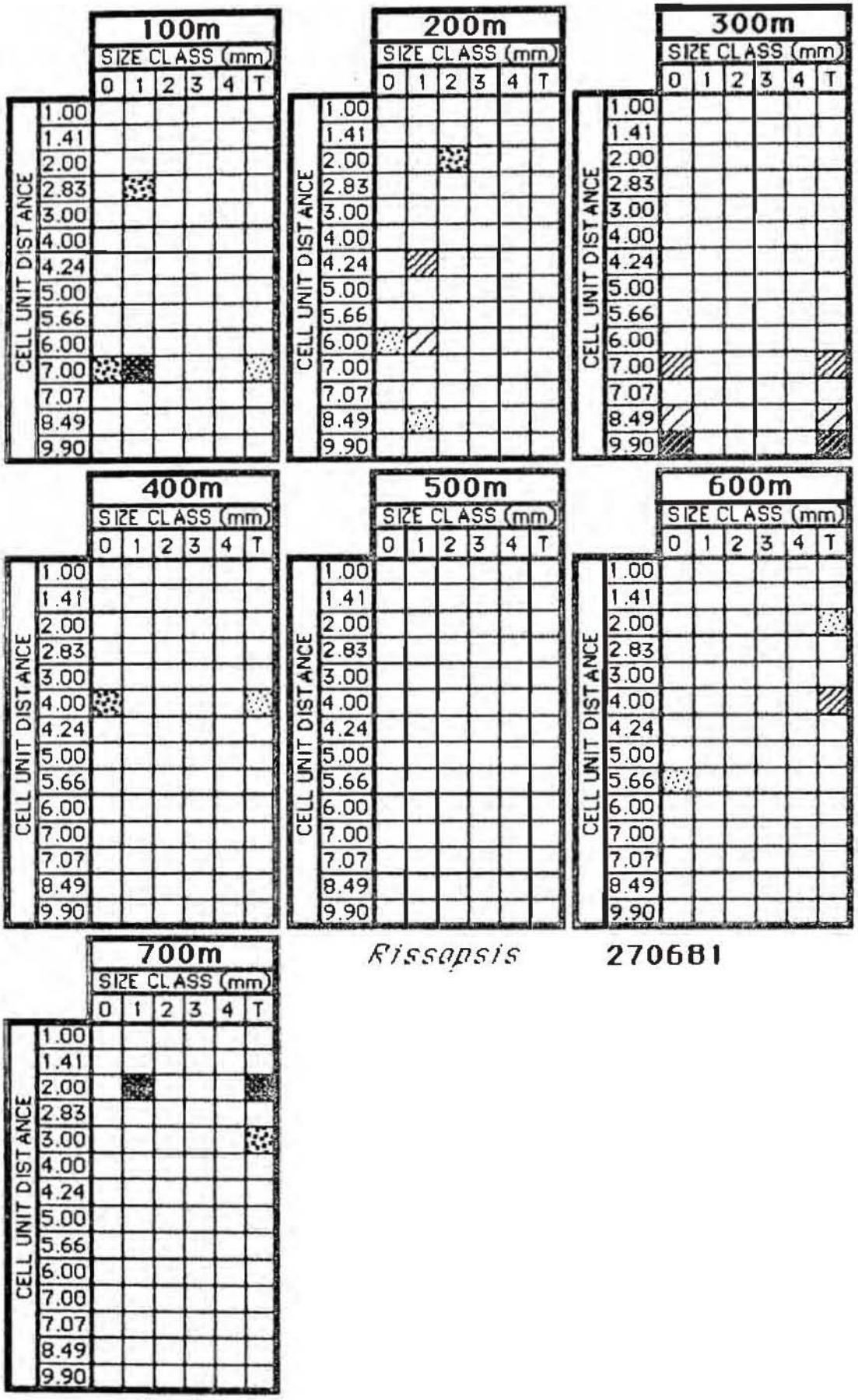

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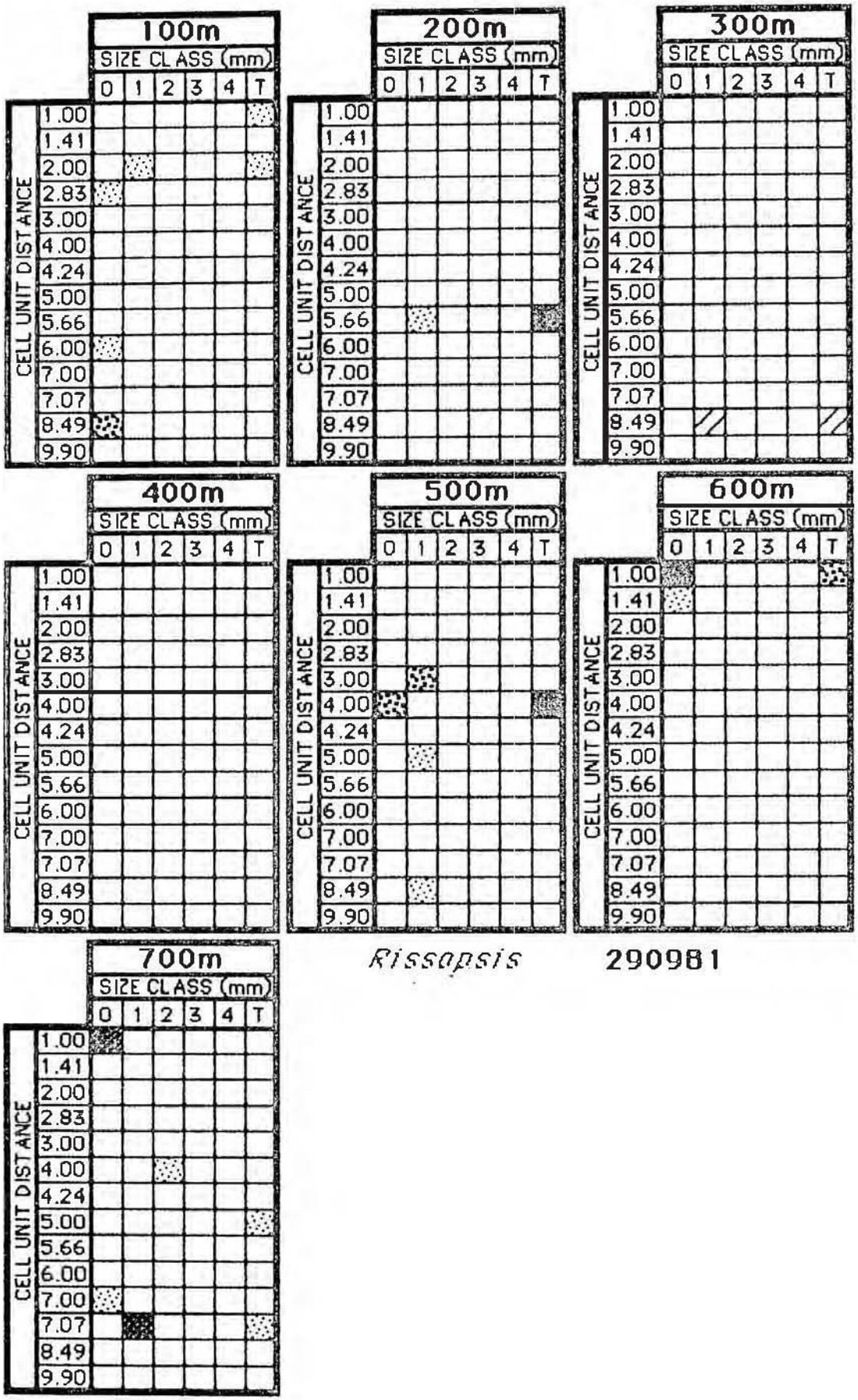

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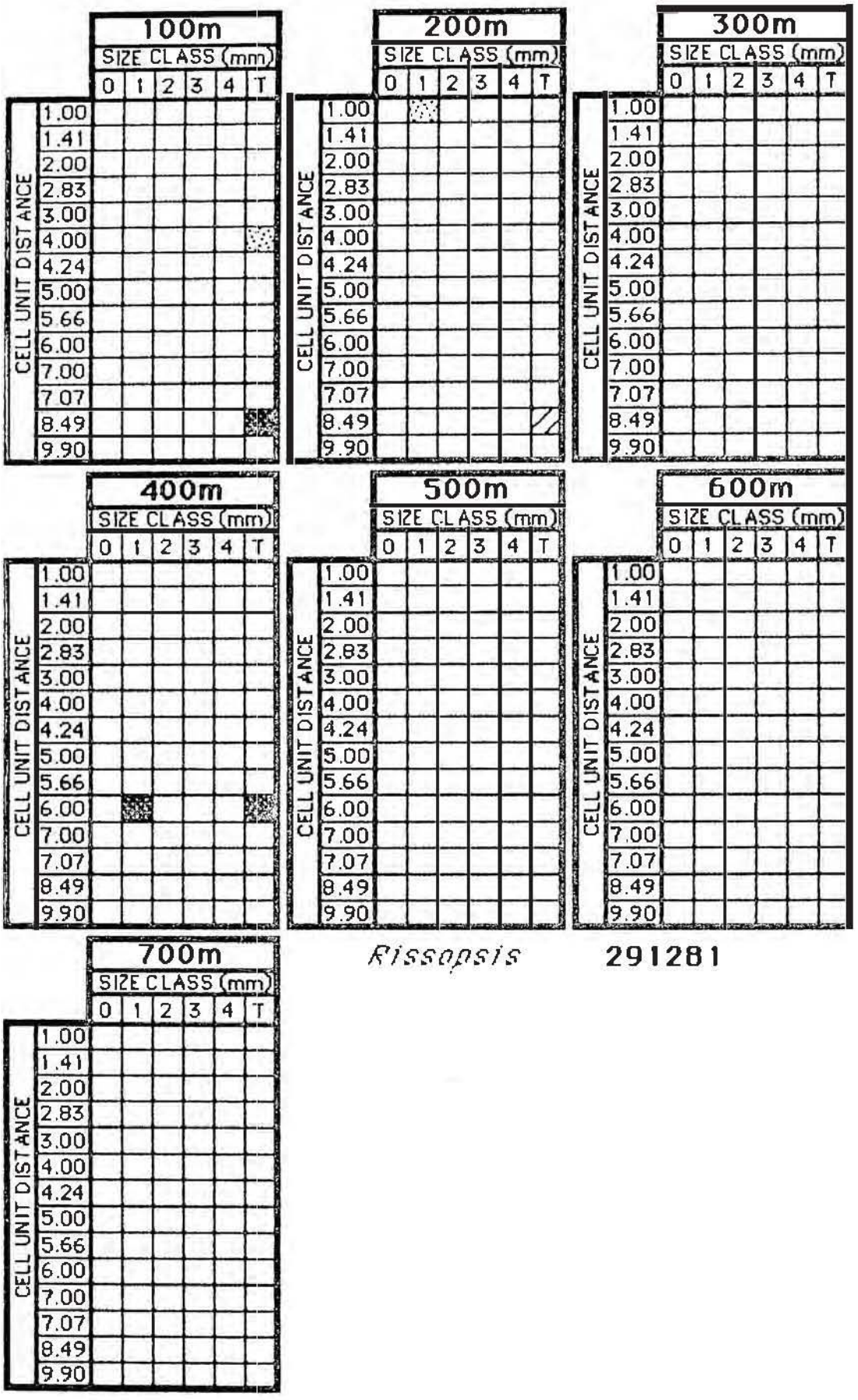

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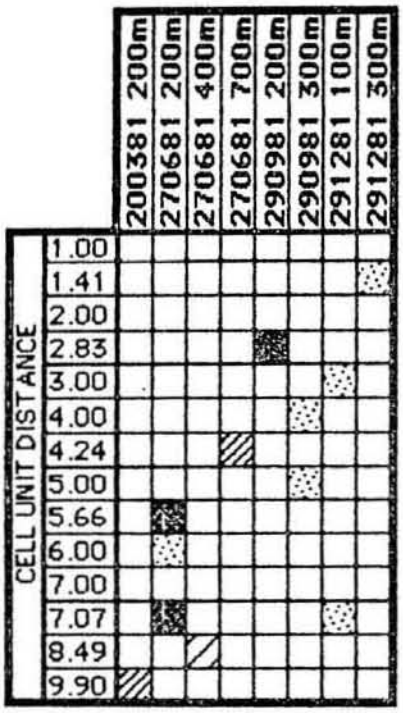

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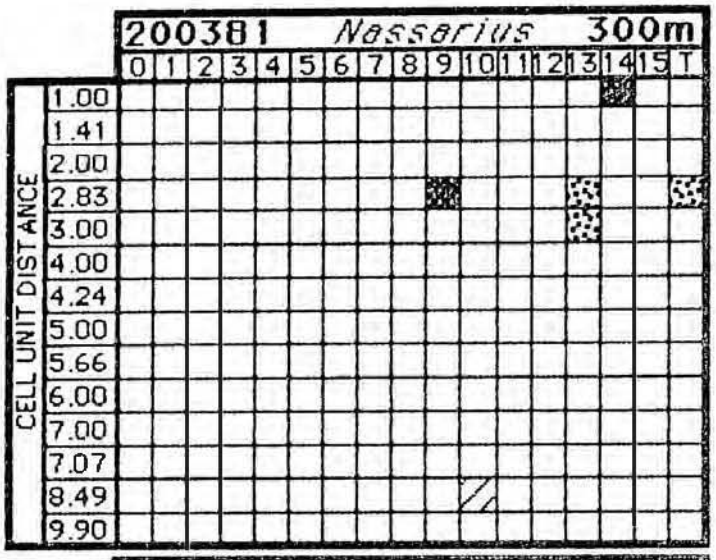
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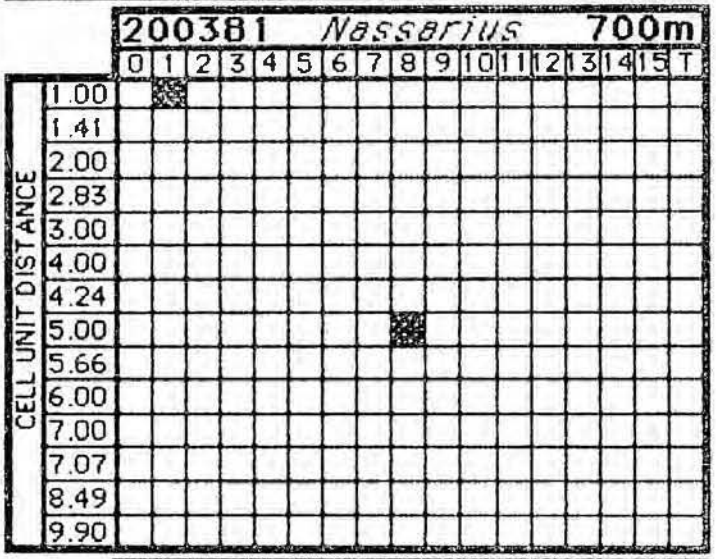
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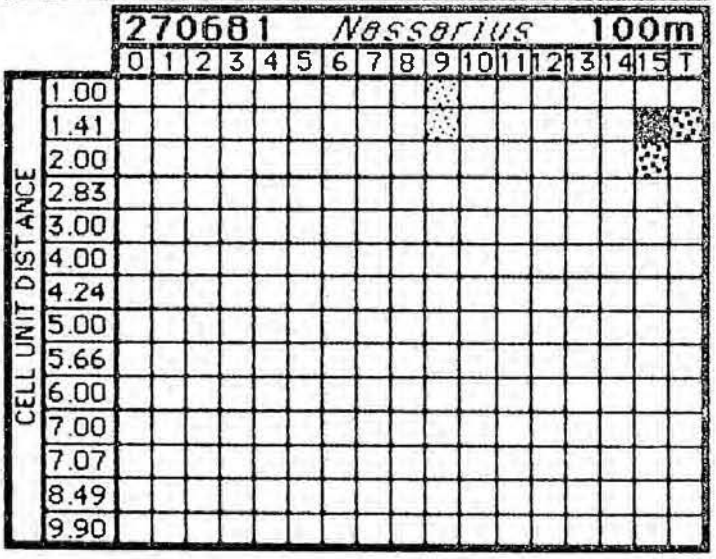
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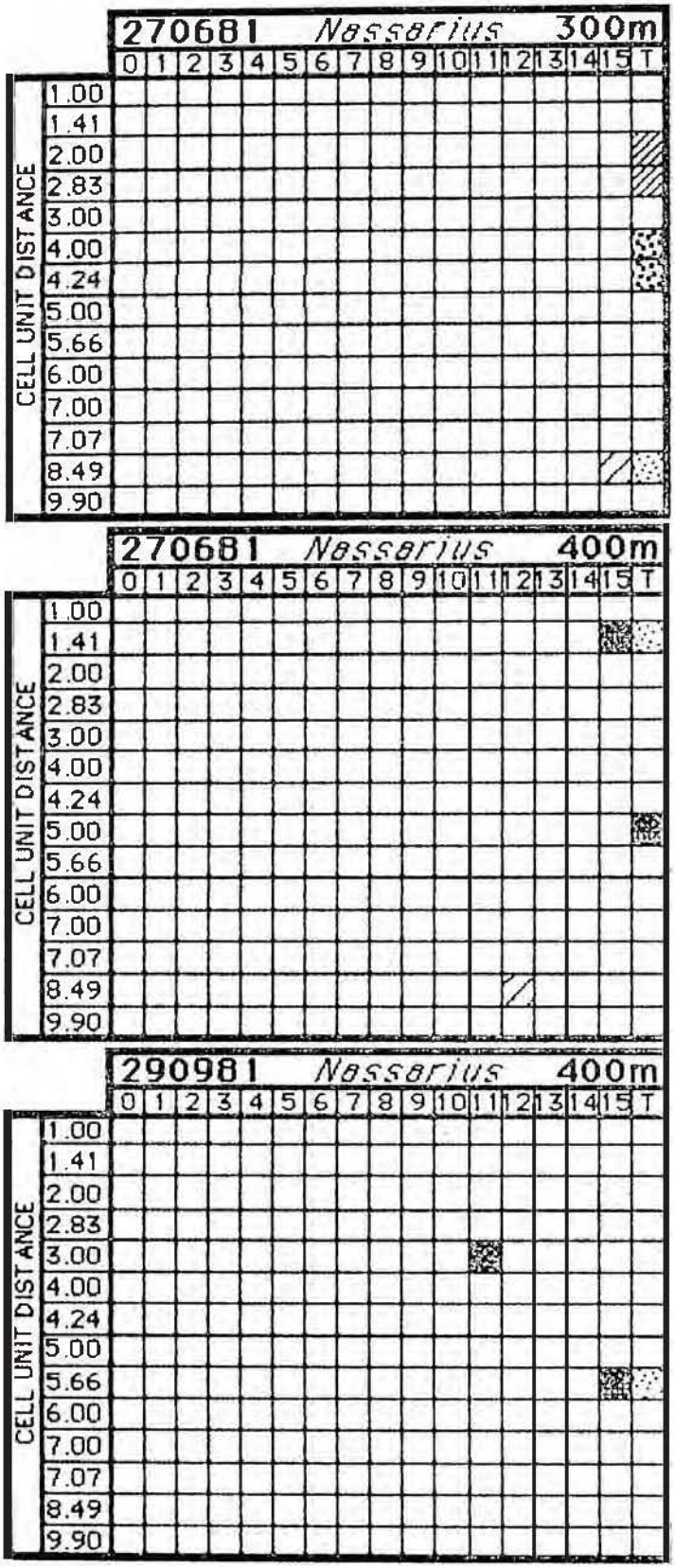
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270681 Nassarius 400m
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290981 Nassarius 400m
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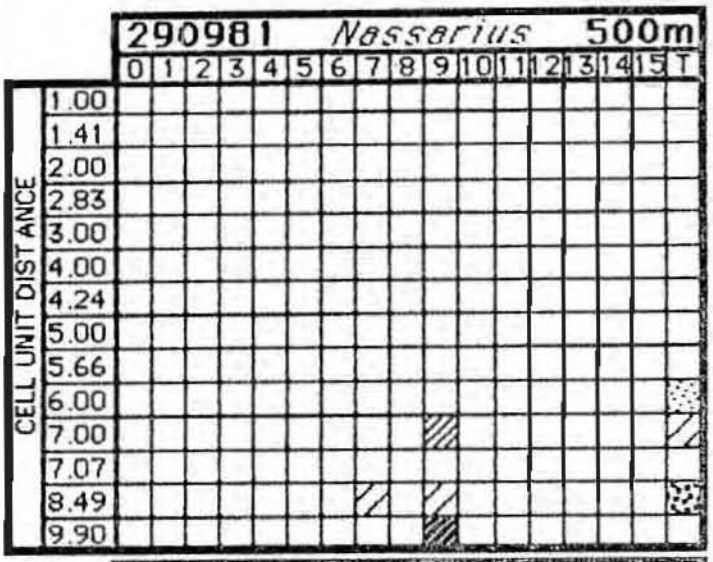
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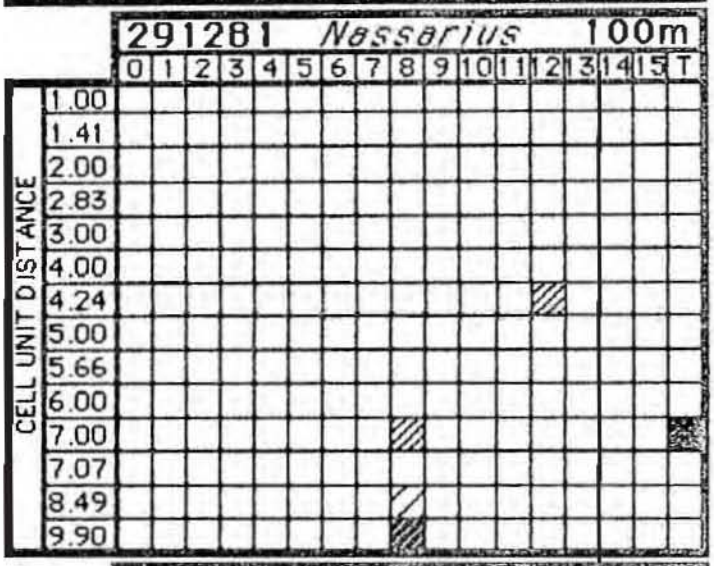
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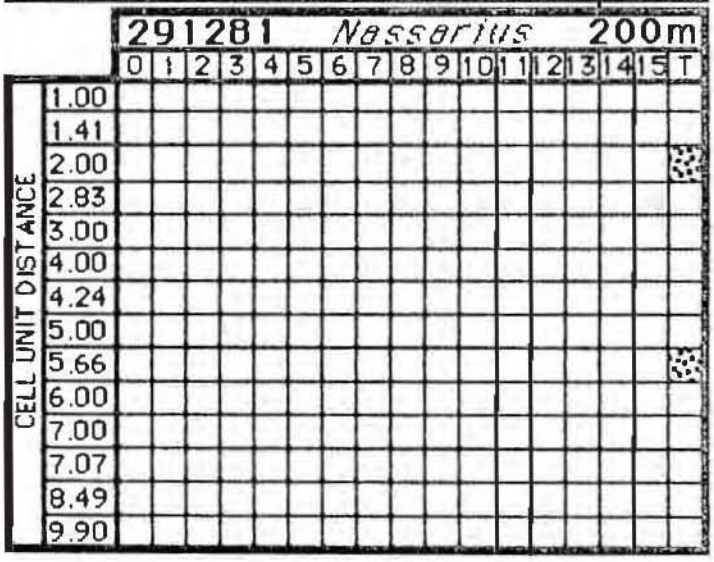
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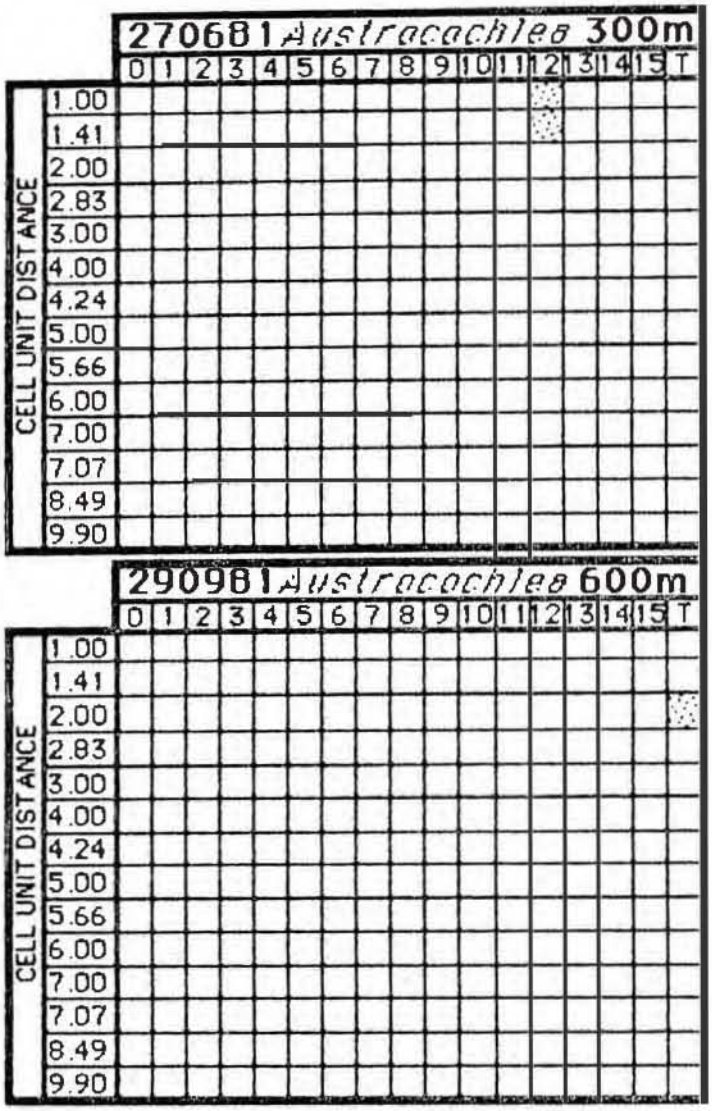
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290981 Austrocochlea 600m
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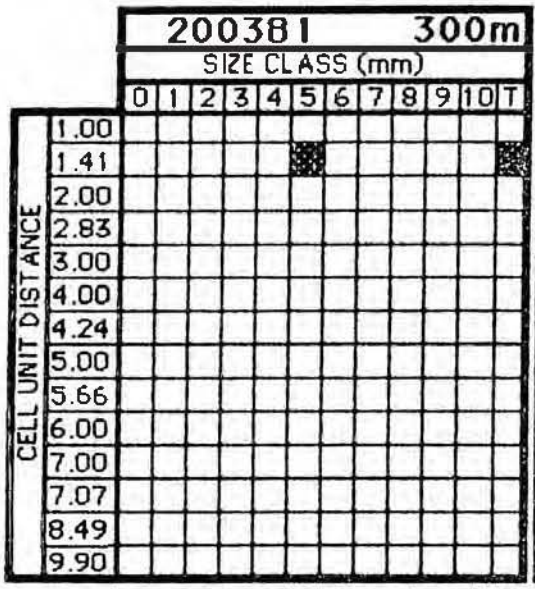
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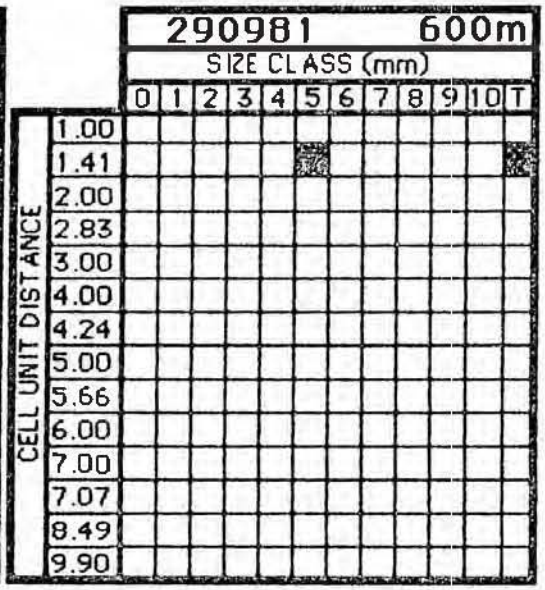
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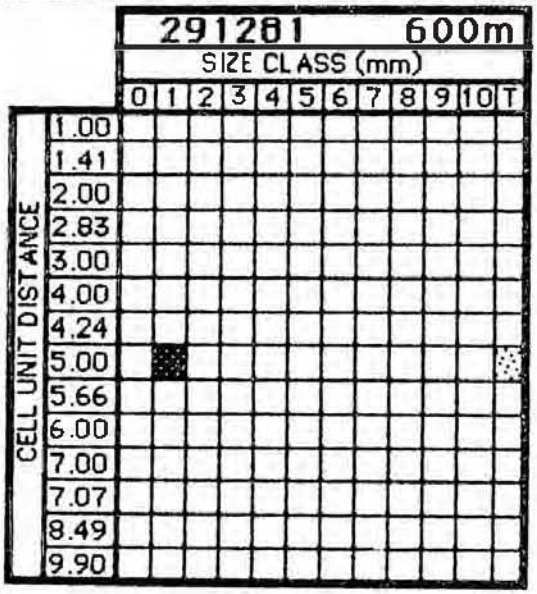
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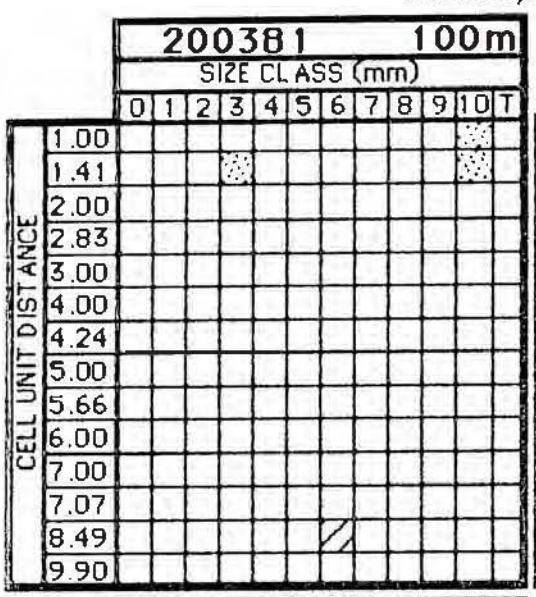
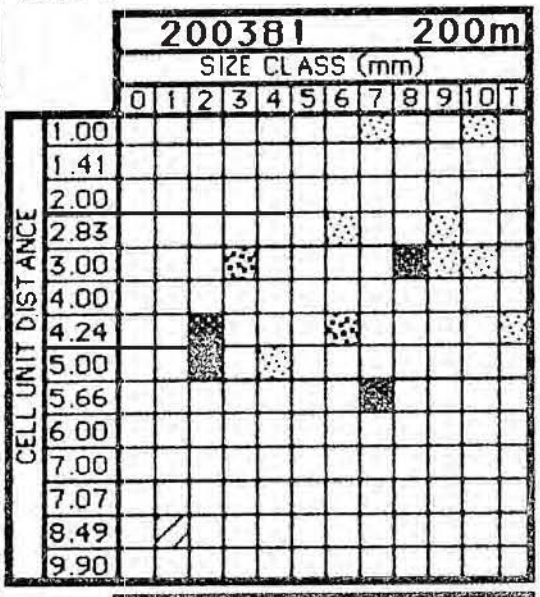
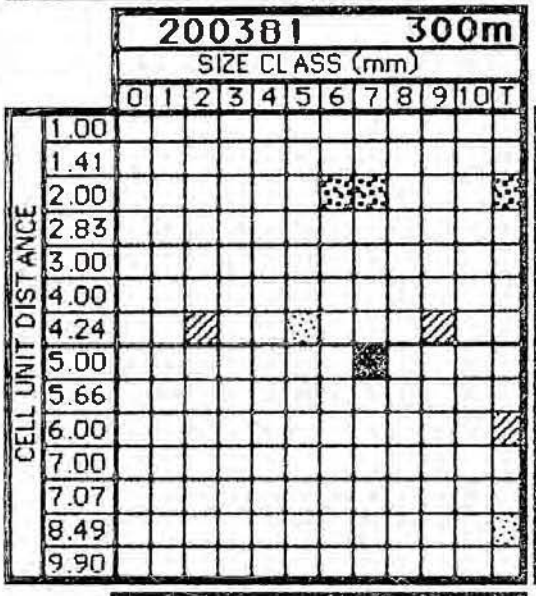
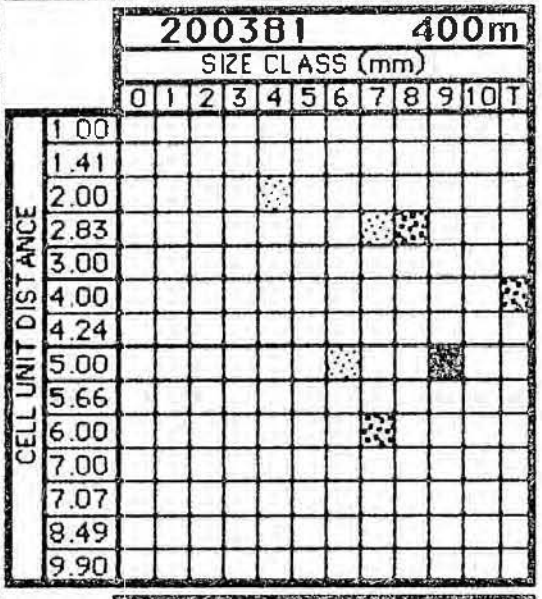
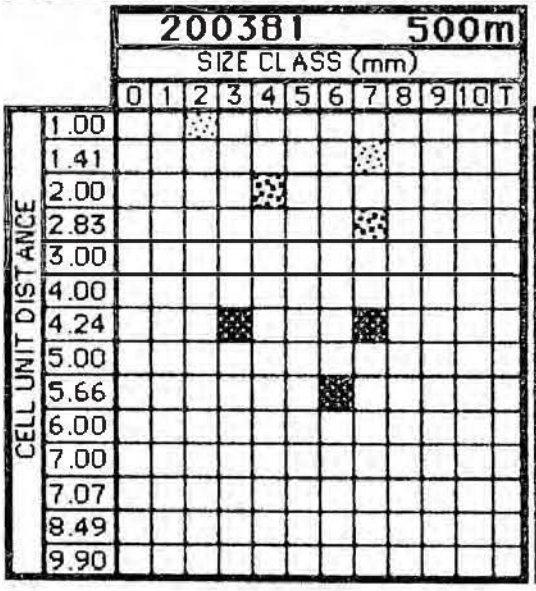
Anthopleura

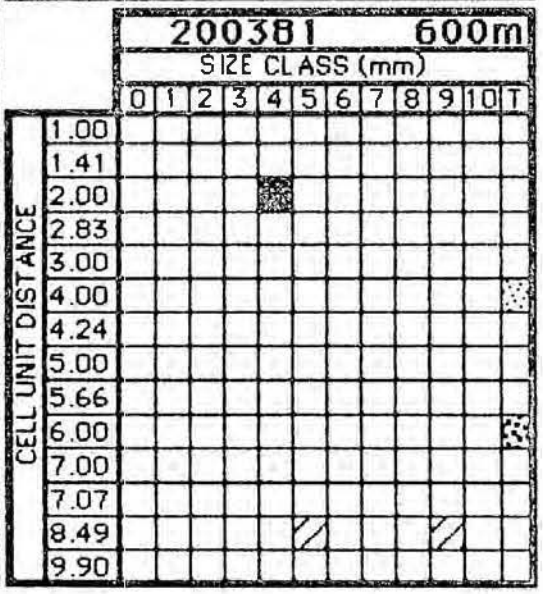


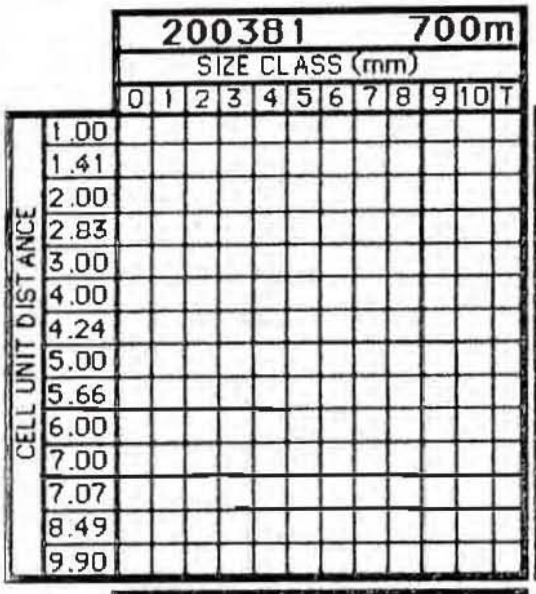








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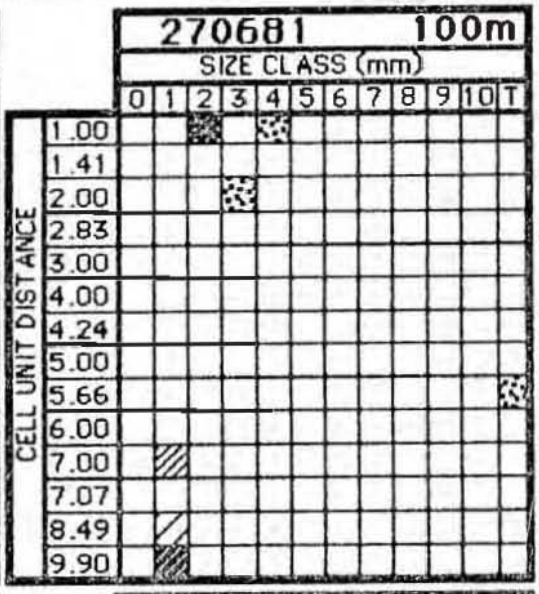
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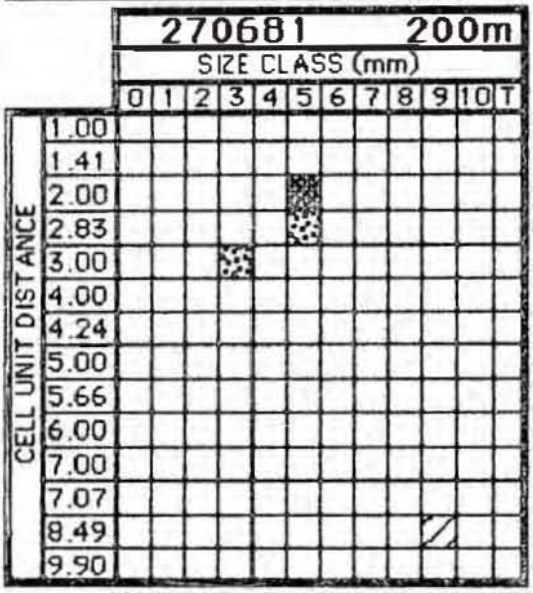
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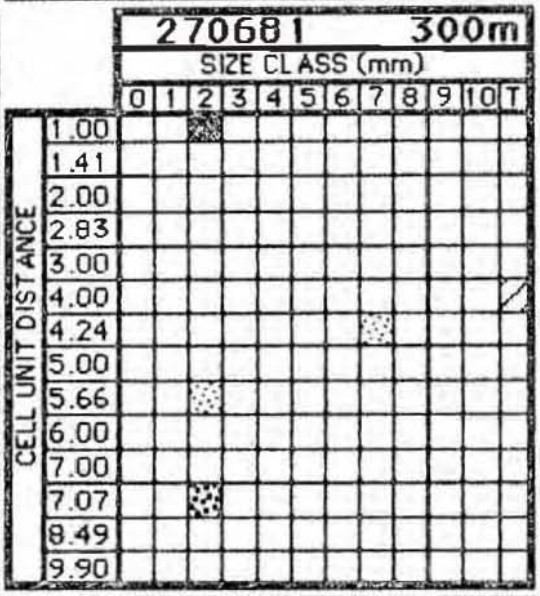
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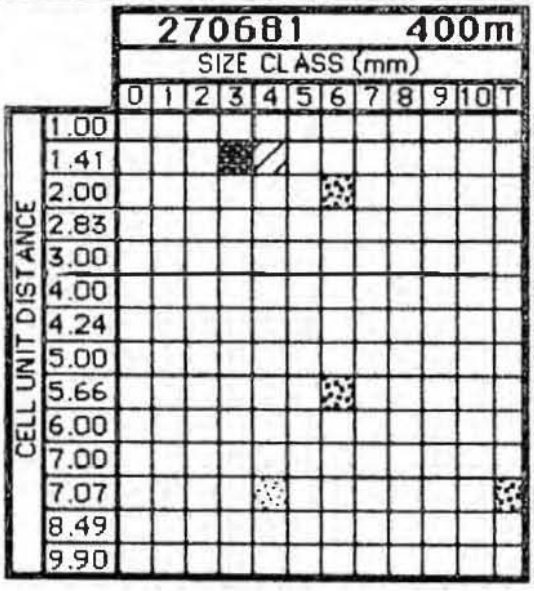
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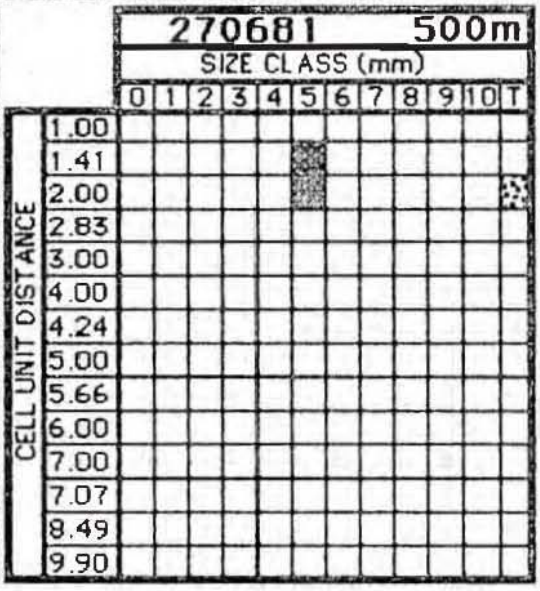
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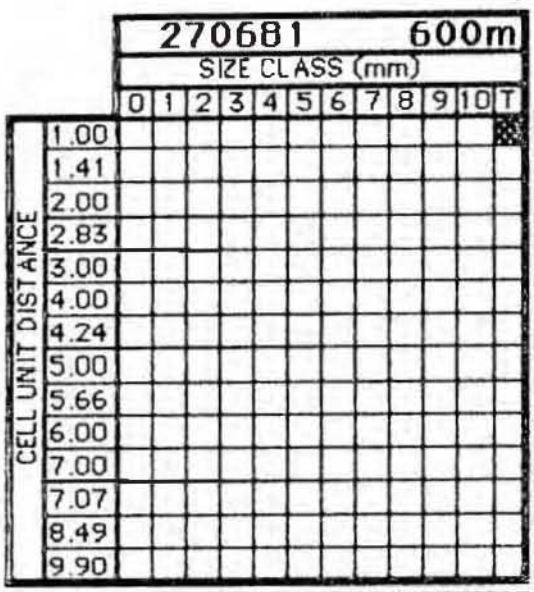
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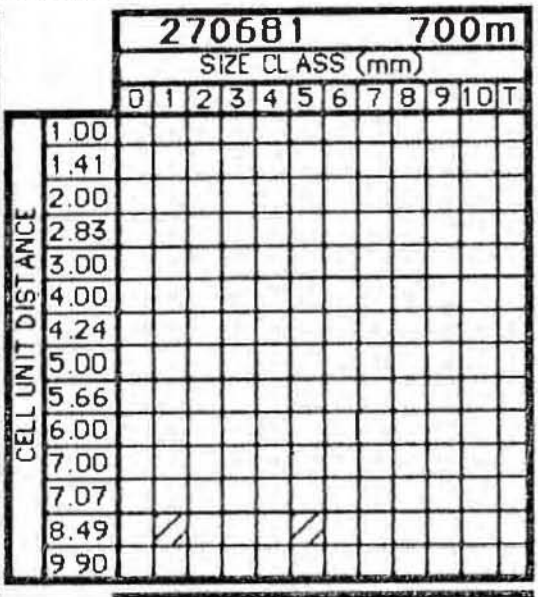
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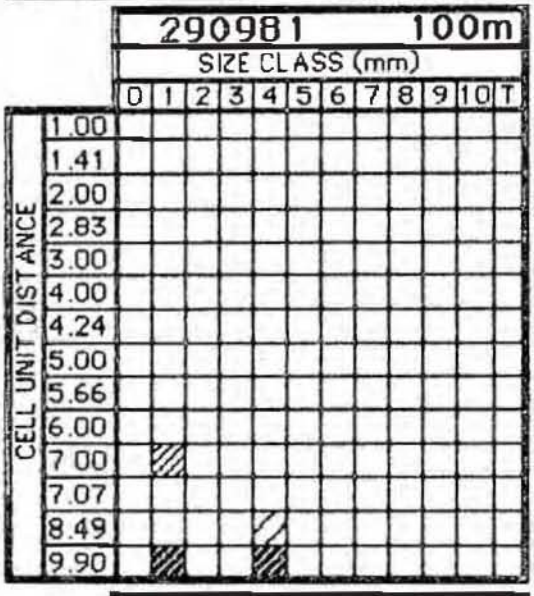
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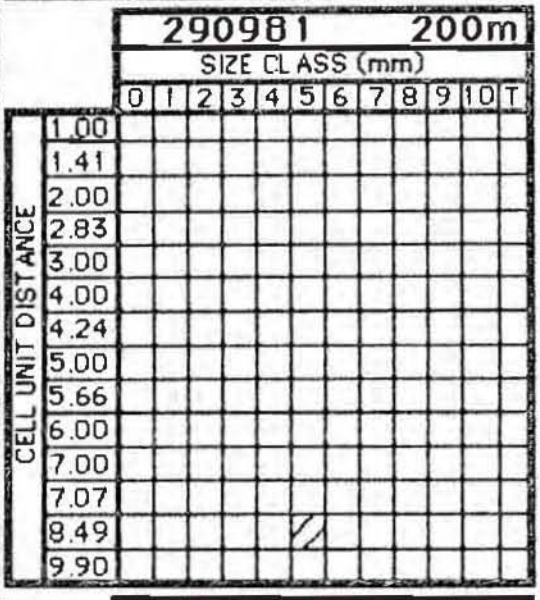
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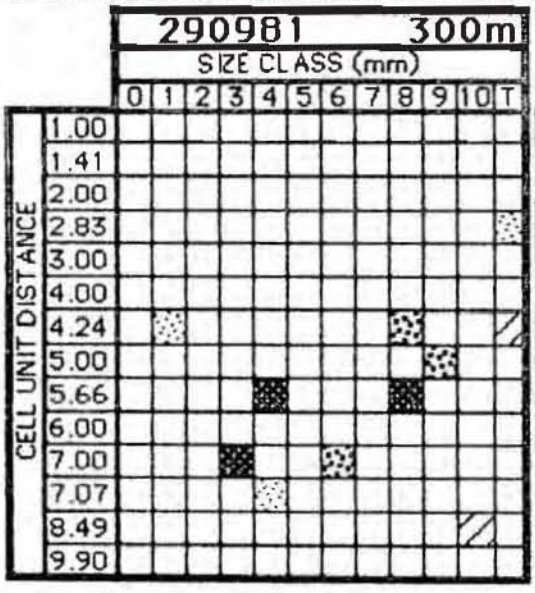
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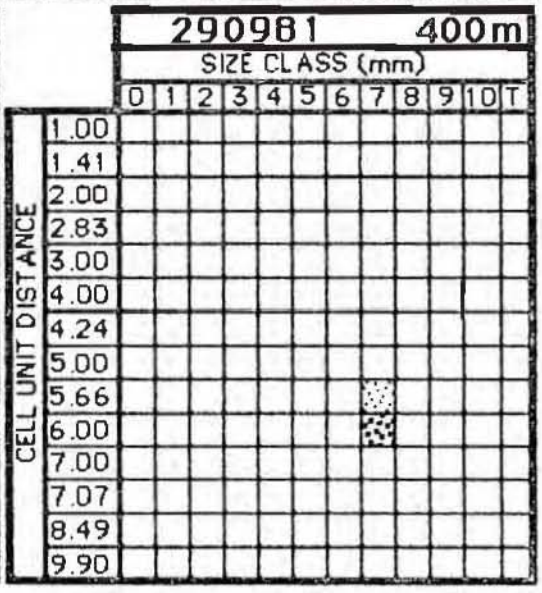
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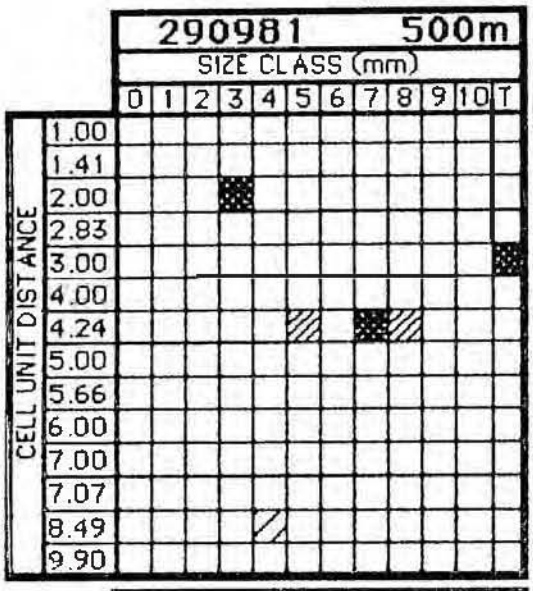
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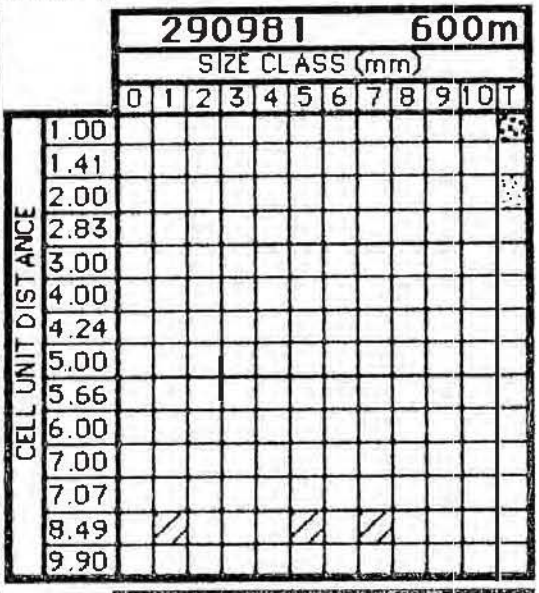
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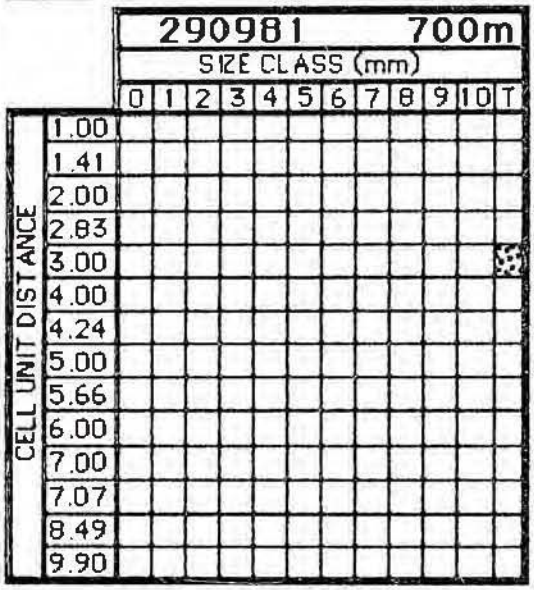
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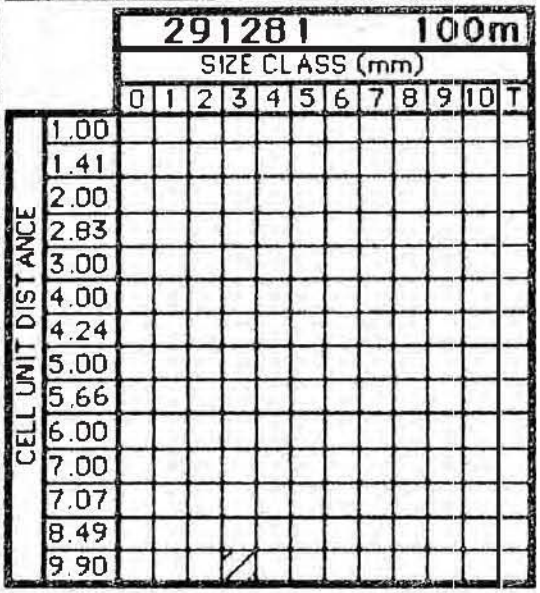
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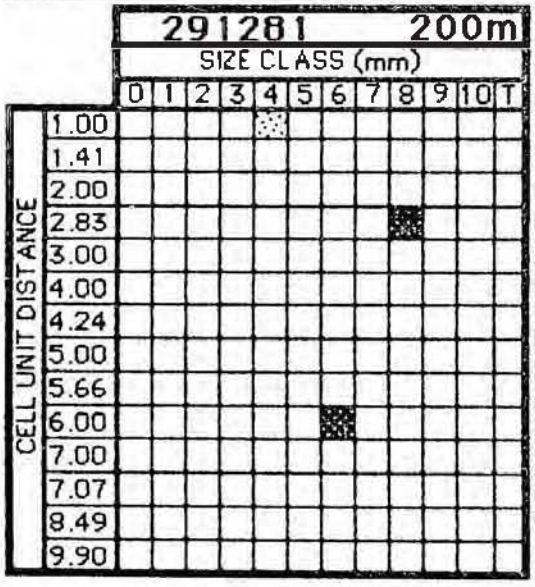
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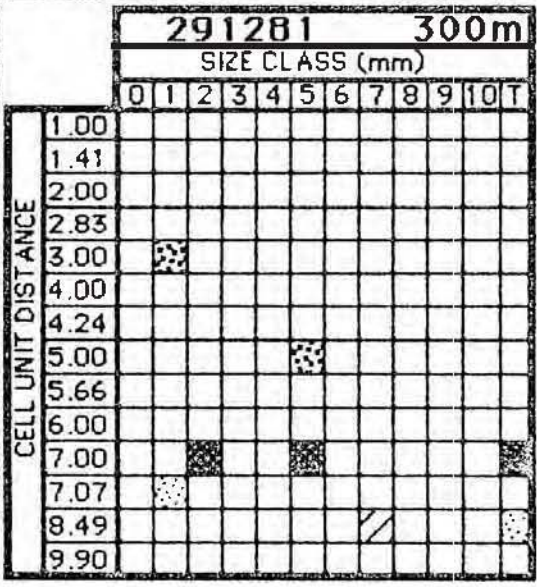
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