The Macrobenthos of Selected Habitats From the West Coast of Florida: A Multivariate Analysis[1]

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Trends

"Further, for the mathematics to be manageable, the postulates must be simple; thus a comparative lack of knowledge is almost an asset, since the investigator is not distractkd by a plethora of facts."

- John H. Steele, "The Quantitative ecology of marine phytoplankton", Biol.Rev., 34:129-158 (1959).

"He had bought a large map representing the sea,
Without the least vestige of land:
And the crew were much pleased with they found it to be
A map they could all understand."

- Lewis Carroll, in The Hunting of the Snark.

"When, in mathematics, a trick gains widespread usage, it becomes known as a technique."

- Charles Lyons, over a beer or two.

Preface

This study grew out of a good idea and a lot of data sitting on the shelf. The good idea was to apply a complex statistical technique (principal components analysis) to a largely unfathomable ecological data to yield a simple model of a many sided situation.

This study grew out of a good idea, and grew and grew. Mathematics is not the forte of most descriptive ecologists, nor are most mathematicians interested in things which creep and crawl through the muck. Yet it is a mistake to consider the two sciences miscible in all instances without damage to the principles and assumptions of either. I have accordingly shorn this work of much that is of one side or the other and well presented in countless texts, and concentrated on the construction of a model separate from but true to both. Unfortunately, it is not difficult to forsee that the work will be all but unintelligible to those without (perhaps with) more background in general statistics and ecology than this paper can provide. I can only say I believe the effort is rewarded by the results.

None of the invertebrate data were collected by the author, who prefers to watch quietly living creatures rather than count dead ones. Therefore, I wish to thank John Morrill and his colleagues for the data used in these analyses, and for all his assistance from the inception to completion of this thesis. My thanks also to Donald Tipton for use of the subroutine INFREE, a remarkably useful and time saving program. Special thanks to Charlie the Goldfish for much companionship, and, of course, the nat sci special.

Bob Foster -- March, 1974

Part 1 - Methods and Madness

1. Introduction to history and concepts.

A good discussion of the many terms and analytical techniques as well as the history of the problem is given by Whittaker (1962). In the scope of this work we can only hope to set the framework for our own studies and defend the inherent properties of our methods by reference to others.

The concept fundamental to all ecology perhaps is the community. About even this we find much controversy. Many of our terms, if not our basic thinking about animal communities, are borrowed from the plant ecologist, often with little consideration for real equivalence. As is recounted by Whittaker and others, the beginning of current models lies in two divergent European schools of thought: the Zurich-Montpellier school (influenced by Braun-Blanquet), and the Uppsala school of northern Europe. Briefly, the Zurich-Montpellier school considered vegetation composed of more or less abstract units, usually relying on "characteristic" species as the delimiting factor. These are rare species but found with some "fidelity" within the unit. A "dominant" species is widespread and common. The Uppsala school regarded vegetation as the sum of real units, which were derived by means of simple mathematical tools such as the trellis diagram. The nature of this analysis leads to a dependence on the dominant species. The Zurich school used species lists alone, the Upsalla school species counts. Both schools used as the general ecological group the community, though definitions may have differed. We, like Mills (1969),

tend to prefer a general definition of community as "a group of organisms occurring in a particular environment, presumably interacting with each other and the environment, and separable by means of ecological survey from other groups." We refer to the units of which a community is composed as associations. Note that although the first and third parts of the definition seem to be included in the thinking of the two European schools, the notion of interaction is lacking.

A trend which originally led away from the classification of communities into strict associations is found in gradient analysis. There are many techniques (see Whittaker, 1967 for a review); principal components is one, the more familiar Bray and Curtis measurement another. The methods involve the "ordination" of communities along gradients defined by environmental and other factors. There is a tendency to regard species as more or less independently distributed, with stations compared with one another on the basis of ecological distance. Although the model emphasizes the independence of species and the absence of discrete spatial units, it can, as we shall see, be used to discover these if they exist. Thus we make few assumptions about the nature of the community, considering it a pattern of intergrading units (as small as a single species or site) forming a complex continuum.

Marine zoologists have adapted many of these concepts, usually to fit a particular situation and often with a confusion of terms. Two people stand out. Petersen (1918) characterized benthic communities by reference to a few common species which occurred over a widespread area. Reference is made to the role of sediments and some other environmental factors, but

not to biological interaction. Thus the dominant species were used to separate communities, but any associations which may make up these communities were ignored. Except for the use of dominants, Mills (1969) states there is little evidence for the influence of the northern plant ecologies on Petersen's work.

Next to Petersen, the work of Thorson (i.e. 1957, 1958) has had the most profound influence on marine ecology. It was Thorson who introduced the concept of "parallel communities," i.e. similar groups of species in similar environments regardless of geographic distance. It is unfortunate that this community structure was held to exist only if there were a few clearly dominant species. We shall have more to say on this later. Nevertheless, Thorson introduced, or at least emphasized the role of biological and environmental interaction in the efficient exploitation of the habitat. For example, the production of larvae by a prey species might be coordinated with a passive period in the predator's life cycle. With the discovery of communities in which there are no species distinctly dominant, the situation becomes too complex for simple observational analysis.

2. An aside on diversity.

We have mentioned the occurrence of communities with a few dominant species and those in which no species stand forth. In the recent past much discussion of the meaning of the different states has occupied ecologists. Conceptually, diversity simply refers to a state in which there are a small number of species or the total population is dominated by a few species (low diversity) on through a state of many species with no numerical dominants (high diversity). Howard Sanders and Ramon Margalef are perhaps the major proponents of the diversity index (of which there are many forms) as an ecological tool.

Sanders' (1968) paper is a good review of the subject, although not as definitive as it first seems. Evidently his own index has not turned out to be the answer to what he felt were statistical difficulties. Sanders does point out several significant obstacles in the application of any diversity measurement. Among the problems: a comparison of diversity values must be between the same organisms, habitats must be similar, sampling procedures must be approximately alike, and even then the index does not specify which species will be present. The first three of these considerations can be overcome, but a careful reading of many papers employing diversity indices will show these considerations are often ignored. Statistically, as O'Connor (1972) has pointed out, the significant use of the measurement (in this case the Shannon-Weaver index) is almost precluded by the amount of work necessary to acquire the needed number of observations.

On the theoretical level, discussions of diversity have, at least to us, produced conflicting results. Hutchinson (1958) formalized the theory of the fundamental niche and stated that the number of species that could exist at equilibrium was limited by the number of variable environmental factors. Yet Hutchinson (1961) also points out the existence of a remarkably diverse plankton community in what would seem to be a stable habitat. Patten (1962), by derivation from Hutchinson's set theoretic presentation, demonstrates that it is not possible on this basis to assign high or low diversity to a climax community. Volterra (1926), using simple analytical methods, suggested the principle of competitive exclusion. Based on the Volterra equations, Leigh (1965) concludes that an increase in diversity will lead to an increase in stability, i.e. toward a climax community.

Empirical evidence has a way of changing the minds of even ecologists. For instance, the abyssal zone of the oceans was considered to be populated by few species (see Vinogradova, 1962, for review), and to possess an extremely constant environment, probably the most unvariable habitat on earth. Recently, however, new sampling techniques have uncovered a quite diverse fauna (Sanders, Hessler, and Hampson, 1965; Hessler and Sanders, 1967). The explanation they proposed is based on the interaction of groups of species. We note the possibility that though the rules do not seem to apply to single species, they might apply to groups of species acting in concert.

Margalef (1961) points out what we feel is the only significance to the whole diversity question, i.e. that in a climax community the various species should react to environmental factors in a unified way as opposed to the state in which individual species react independently. His contention that a diverse community can store more information is true in itself, but does not imply alone a high level of organization.

In summary, the concept of organization seems more important than diversity, the two not necessarily correlated. Statistically, the diversity index is of limited value in application beset with sampling restrictions. Theoretically there is little agreement. We conclude that there must be a better way to attack the problem.

3. Numbers

At the present time there are a variety of descriptive techniques and numerical models to use. The rest of this section and thesis is concerned with quantitative and supposedly objective methods. However, we feel traditional ecological survey, in which species lists are compiled and habitat noted, is probably at least as important. Certainly for purposes of primary survey over a wide range of habitats this may be the most efficient.

Numerical techniques are many and varied. It is no small problem to sort the methods, let alone the critters. The matter is complicated further by a tendency of many researchers to apply numerical models blythely unconcerned with statistical reliability or a theoretical basis. We will indulge ourselves and voice the author's personal dislike for researchers in love with numbers reveling at the chance to generate more.

There are several fundamental distinctions to make among the analyses, for example "clustering" vs. "synoptic," and "classificatory" vs. "gradient." A clustering technique will try to reproduce the interrelationships among the variables as accurately as possible. If no groups exist none will be found. Synoptic strategies impose clustering, artificially strengthening boundaries between groups. These are all hierarchial. That is, they proceed by either fusing individuals or successively dividing the population. At least one other distinction exists, namely whether to group stations or group species, known as "Q" and "R" analyses respectively (or "normal" and "inverse") (Stephenson, Williams, and Lance, 1970).

Interesting geographic differences exist among researchers. With some exceptions, of course, most Americans have tended to use classificatory schemes based on clustering models. British and Australian authors often use the more synoptic methods, although it is among these scientists that we find the use of multivariate analysis, the position of which will be discussed later. Americans as a rule use any of the multitude of "indices of similarity," among others those of Jaccard (1912), Sorensen (1948), Webb (1950), Sanders (1960), or Fager and McGowan (1963). A good general reference is Grieg-Smith's Quantitative Plant Ecology (1964).

The method of Fager and McGowan (1963) is based on recurrent groups. Species which show an arbitrary degree of co-occurrence are grouped together. This is an "R"-type analysis. Most of the other similarity measures are founded on the idea that related sites should possess the same species, the degree of similarity determined by the number of individuals of matching species present. They are used in trellis diagrams in which similarity values between each pair of sites is arrayed in a square matrix, which is rearranged so that sites with high values are placed together. This, therefore, is a "Q"-type analysis.

While it is impossible to give a critical review of all methods or even the few mentioned in this paper, some thought must be given to applicability and biological significance. With regard to the above methods statistical properties are often unknown. Perhaps more importantly, several assumptions are imposed on the population. First, all are rank models, numerically dominant species contributing most to the indices.

Second, even after stations are grouped, species associations may be delimited only by reference to the most numerous species at each site group. Finally, no mention can be made of species which have negative effects on each other.

In summary, these methods, described as classificatory and clustering, are usually applied in a Q-type analysis, and make some assumptions which will bear more discussion in a later section.

The use of classificatory and synoptic techniques is confined for the most part to the Australian and British. See for example Lance and Williams (1967) for theory, or Stephenson, Williams, and Lance (1970) for application. Stephenson and his colleagues in the above and many other papers have generated much information about many computer based numerical techniques. We suggest a casual acquaintance with any of the references to Williams, Lance, or Lambert's work that will be found in the 1970 paper, or Stephenson and Williams, (1971), or Stephenson, Williams, and Cook (1972). Applications of analytical methods by Stephenson and his colleagues are characterized perhaps most of all by complexity, and unfortunately receive more attention because of this than for their real merits. Yet, we feel somehow that it would be presumptuous of the author, and Stephenson perhaps, to say just what these merits or faults are. However, there are two comments we consider valid. One is that Stephenson et al study large areas containing a very large number of habitats and species. It is this which necessitates the complexities of analysis. If a small area of relatively few species and uniform habitat were studied, the form

and purpose of the analysis would be different. Another comment concerns the implications of hierarchial strategies. Lambert and Williams, who helped develop these methods, are plant ecologists. To them the idea of mapping large areas by assigning each site or species to a discrete group is quite feasible. Hierarchial strategies are synoptic; they will strengthen boundaries between groups. To this animal ecologist, in any case, it seems necessary to include in the model the possibility of species or sites transitional between one group and another, and to allow for possible negative as well as positive relationships among species. Hierarchial methods place an individual in a single group and no other, all of whose members are positively related. We regard hierarchial techniques most useful for extracting communities from large areas: specifically for use in a Q-type analysis in which similar sites are grouped on the basis of their fauna. This is in fact how the human mind would function on being presented with a large number of facts--sort them out into smaller packages. The fine structure of such packages, namely discovery of associations among communities, is better carried on by other methods. Gradient analysis, perhaps, which is discussed next.

Gradient analysis simply refers to the concept that species are distributed in space along environmental gradients, instead of distinct groups. It may be direct, that is, sampling may take place along deliberately selected gradients, or indirect, where gradients and distributions are reconstructed after sampling. It is this kind of analysis

that we have performed, also known as ordination. Ordination of itself is the opposite of a classificatory scheme, although it can, as will be seen, be used in some cases for the same purpose.

Ordination is often visualized in the following way. Each type of ordination is based on some kind of measure of ecological distance, the object being reproduction of true ecological distance as accurately as possible. For our purposes, ecological distance may be defined in two related ways. Suppose we have N species and M samples. These can be plotted in scatter diagrams as M points in N-space or N points in M-space, R- and Q-type analysis respectively. Distances within these plots are defined as ecological distances. One of the aims of ordination is the reduction of the dimension of the scatter diagrams in hyperspace with as little loss of information (distortion of distances) as possible.

The Bray and Curtis (1957) measurement of the Wisconsin school is the most commonly used, consisting of a simple formula applied in a wide variety of situations. However, Orloci and Austin (1966) demonstrated that it has a rather low retention of distances. Orloci (1966) offers a more reliable method of "position vectors," stating that it has nearly the reliability of principal components while requiring approximately one-fourth the computer time. Principal components analysis will reproduce the multivariate scatter diagram exactly if necessary and include the greatest proportion of information in the smallest number of dimensions. Calculations are, however, complex and time-consuming, relative to other methods. The analysis may be either R- or Q-type, and should

yield equivalent results if the appropriate coefficients are used (Orloci, 1966; Gower, 1966). Since computation time and cost are not a factor at New College, we felt that the theoretical and ecological implications of a principal components analysis made it well worth the effort. It has a certain elegance and beauty not found in most statistics.

4. Principal Components Analysis

Unlike the other techniques in the previous sections, the form of multivariate analysis known as principal component analysis was not developed by biologists. Its first formal presentation was by Hotelling (1933) and has since been used and expanded by psychologists and taxonomists. Interpretations and derivations of the procedures are given by Seal (1964) in a book especially devoted to biologists, by Anderson (1958), and Lawley and Maxwell (1963) inter alia. We will avoid a presentation of mathematical derivation of the method and instead concentrate on the statistical properties in this section, and biological implications in the next.

If two correlated variables are plotted against one another in a two-dimensional scatter diagram, the confidence regions around the mean will be in the form of an ellipse (see Fig. 1,) if the two are normally distributed. If three variables are plotted an ellipsoid is generated, and if N variables are plotted a hyper-ellipsoid in N-space results. The major and minor axes of the ellipse are shown in Fig. 1 as well as the regression lines. Geometrically, the major axis is the longest possible in the ellipse, and the minor axis is at right angles to it, passing through the center.

In principal components analysis the principal axes of the hyper-ellipsoid formed by the scatter diagram are found by calculating the eigenvectors of the matrix representing the product-moment correlation between each of the variables. Statistically, the principal axis defined

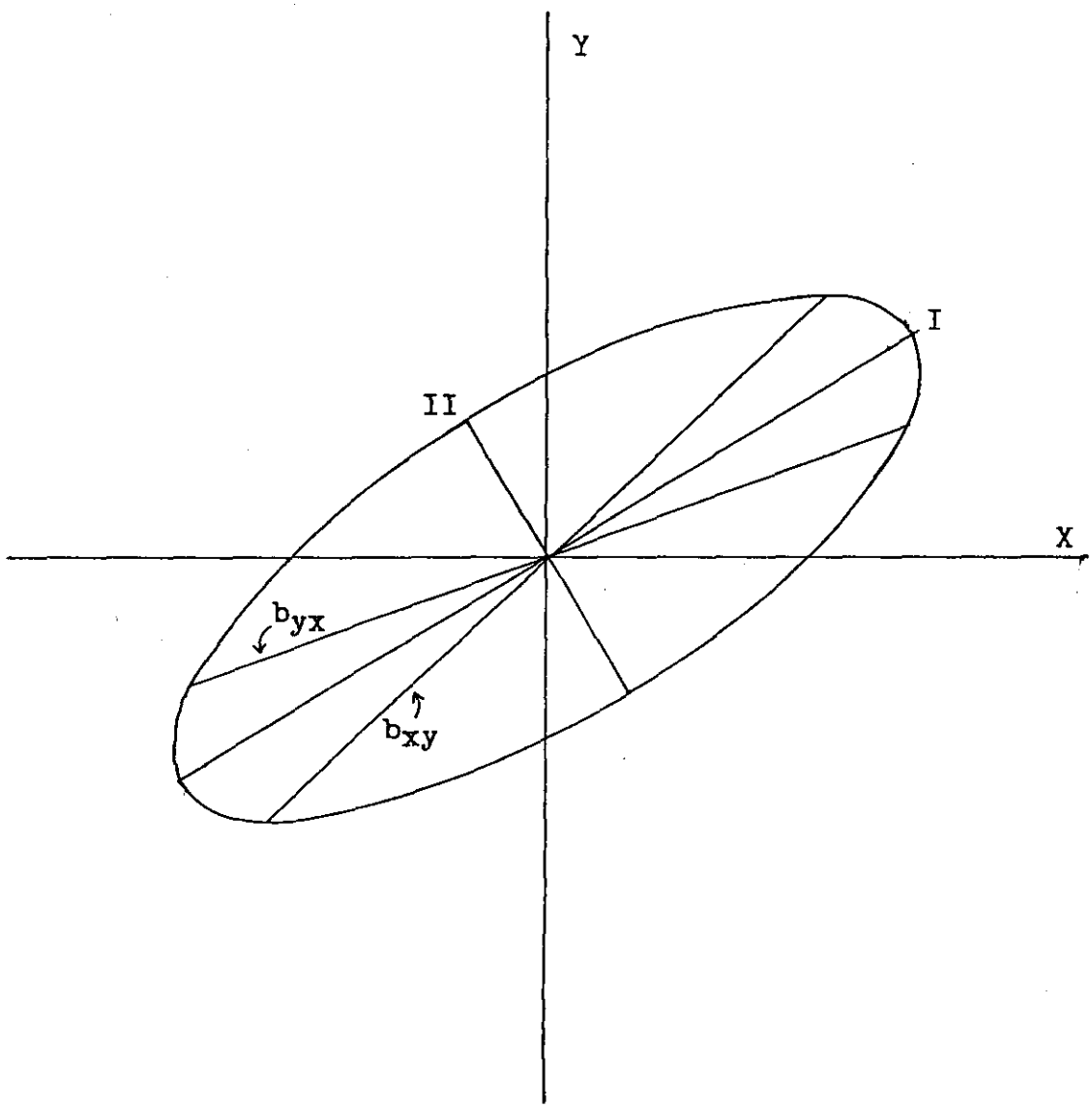


Figure 1. The confidence regions of the bivariate normal distribution of two variables X and Y may be represented by concentric ellipses. Note the difference between the the major and minor axes of the ellipse (I and II) and the regression coefficients b_{xy} and b_{yx}.

by the first eigenvector corresponds to the direction of maximal variation; each subsequent vector conforms to this rule for residual variation. Vectors are ordered by means of their associated eigenvalue, which is the variance of each axis, i.e. its length. Thus each eigenvector may be regarded as a principal component rotating the scatter diagram axis in the direction of maximal variation.

In a correlation matrix each variable is scaled to unit variance. Therefore, the total variance to be explained is equal to the number of variables or the order of the matrix. Since eigenvectors generate only rigid rotation, and each eigenvalue gives the variance of its component, the sum of the values is equal to the order of the matrix. The ratio of an eigenvalue to the order of the matrix then gives the proportion of the total variance explained by that component, an extremely accessible measure of the importance of the component. If all the variables were totally uncorrelated, i.e. the correlation matrix has ones on the diagonal and zeros elsewhere, each eigenvalue would equal one and the scatter diagram would be a sphere. This is the basis of the "sphericity" test for significant departure from total uncorrelation (see Bartlett, 1951; Bartlett, 1954; Lawley, 1956). These and a few other significance tests for principal components have been proposed but their use is questionable. Ordinarily the question of biological significance and interpretation is more important that statistical significance. It must be remembered that one of the foremost goals of principal components analysis is the reduction of the rank

of the model. As a rule we are interested only in the first few components. The statistical significance of the rest may be valid, but of little use.

An important aspect of principal components is that they are orthogonal, at right angles, and uncorrelated. The major problem of all multivariate problems is intercorrelation among the variables. The statistical significance of a single product-moment correlation coefficient in a matrix, or the contribution relative to others of a coefficient in a regression equation, cannot be accurately determined due to the interference of correlated variables. Partial correlation, which calculates the correlation of two variables independent of all other variables in the analysis is one solution. The visualization of this method, incidentally, is found by imagining the shadow of the total multivariate scatter projected on the plane formed by the two variables in which we are interested. The correlation of the points projected on this plane is then calculated. However pretty its visualization, partial correlation is at best a partial solution, chiefly because of the influence of the variables not included in the analysis. It is certainly more rewarding to construct the uncorrelated variables defined by principal components.

The form of these new variables is quite simple. The elements of the eigenvectors are used as coefficients, as in a regression equation; elements of the observation vector are used as data. In practice we often use the deviation from the mean of each observation vector as data.

In symbols:

$$y_{ik} = \sum_{j=1}^{N} (v_{ij} * x_{jk}) \qquad (1),$$

where y is the new variable defined by v_{ij} the jth element of the ith eigenvector, and x_{jk} the jth element of the kth observation. Thus there will be a score for each observation and each component.

In order to compare different scores for the same component and between components easier, we scale each new variable y to the new variable f, such that

$$f_{ik} = y_{ik} \; / \; \text{SQRT}\lambda i \qquad (2),$$

where λ is the eigenvalue of the ith component. The variable f has unit variance and zero mean; y has zero mean but variance equal to λ. It is not necessary to compute both y and f, since equivalent results are given when the eigenvector matrix V is transformed to the new factor score coefficient matrix B such that

$$B = VL^{-1/2} \qquad (3),$$

where L is the vector of eigenvalues. The elements of B may be sugstituted for v in equation (1) to give the variable f.

Perhaps the most useful transformation of the original components, the eigen vectors, is the matrix S defined by

$$S = VL^{1/2} \qquad (4).$$

S is known as the factor structure of factor pattern, and is the primary tool for discerning the composition of the factors and the relationships of the variables to the factors. If in the eigenvector matrix V the vectors are arrayed in columns, with rows related to the original

variables, then the matrix S is similarly arrayed; rows are related to variables and columns to factors. The elements of S represent the correlation of each variable with each factor. Thus an examination of rows will suggest the nature of the variable, and an examination of the columns will give the nature of the factor. Since, as we have said, only the first few factors are of interest, only a very few numbers give a remarkable amount of information about the variables.

It is also possible to correlate the components with variables not included in the eigenvector matrix by a simple equation taken from Cassie (1963):

$$r_{hi} = \lambda_h^{-1/2} * \sum_k (l_k * r_{ki}) \qquad (5)$$

where r_{hi} is the correlation of the hth principal component with the ith external variable, λ_h is the hth eigenvalue, l_k is the kth element of the hth component, and r_{ki} is the correlation of the ith external variable with the kth internal one. This ability to correlate components with outside variables is useful in discovering the nature of the component.

In addition to principal components analysis there are two related forms of multivariate analysis: discriminant and factor analysis. Discriminant analysis was originally developed by Fisher (1936) for use in taxonomic research. It seeks to generate a single function which will discriminate between two populations, based on a number of variables measured for each opoulation. It is extremely useful if there is some a priori reason for separating the population into two groups. This

was not the case in our studies, but might be of use if the situation were to arise in studying the mixing of, for example, fresh and marine oriented organisms in an estuary. Factor analysis is the name for a number of different methods which generate a specified number of factors, like the components of the previous discussion, which are orthogonal but satisfying other criteria than principal components. Perhaps the most significant difference of these two methods, at least from the viewpoint of application, is their relative robustness. As Lawley and Maxwell (1963) state, in principal components analysis no assumption need be made of the variables for the criteria of the model to be satisfied (some assumptions are made on practical grounds), if significance tests are not to be used. Factor analysis, on the other hand, makes a variety of assumptions about the variables, and depending on which method is used to calculate the factors has rather strict requirements for multivariate normality and linearity. Another problem is that different methods often give different results. These difficulties make it unsuitable for the present analysis.

5. Principal Components and the Ecologist

Apparently there have been only a handful of instances in which component analysis has been applied to ecological problems. Goodall (1954) used this method in the study of percentage cover data in plant communities of Australia. Cassie (1963) used both principal components and a discriminant function in the study of plankton communities from Wellington Harbor in New Zealand, and Reyment (1963) gives us "An example from paleoecology." Colebrook (1964), together with Colebrook and Robinson (1964), based their work on long term changes in plankton populations in the North Sea and northeastern Atlantic on correlational and component analysis. Orloci (1966) and Austin and Orloci (1966) used principal components analysis as a reference technique for comparison with other methods of ordination in plant communities. Cassie and Michael (1968) make, as far as we can determine, the only application of principal components to benthic invertebrates. Howarth and Murray (1969) employed a variety of methods, including components, in their study of foraminifera from Christchurch Harbour, England. An interesting note on the above references is that none are American researchers.

All analyses in this work are of the R-type; species are variables, stations are individuals. Justification for this choice is found on two levels. First, for a variety of statistical reasons, product-moment correlation is not appropriate in a Q-type analysis. Although Gower (1966) inter alia has suggested that the correct coefficient (the similarity coefficients in common use are not sufficient for multivariate

statistical work) can be derived, and that R- and Q-type analysis of principal components should lead to equivalent conclusions. However, the properties of these coefficients, or indeed their form, have not been well investigated. Second, we think it unlikely that either species or stations can be definitely assigned to discrete groups in all cases, but in the case of small relatively uniform and interconnected habitats (such as the ones in this work), species are more likely to show such units than stations. Since in R-type analysis it is in fact species that are most readily grouped, and since product-moment correlation is a simple and well-known statistic, it has been employed exclusively in this study.

There are a number of practical and theoretical considerations which make traditional forms of multivariate analysis, especially component analysis, more useful than the primitive methods developed strictly for ecological problems. For instance, two variables have more discriminating power than one. Horton, Russell, and Moore (1968) for example, demonstrate effective use of multivariate analysis of covariance in obtaining a number of tests of many possible ones which are capable of distinguishing changes in the micro-topography of soil where a single test will not. This technique, incidentally, would certainly be of use in ecological problems where simple discrimination of sites is required and labor must be conserved.

As Cassie (1963) suggests, any mathematical model of communities based on survey should group species without assuming an undirectional effect, i.e. species may have both positive and negative effects on

one another; it should distinguish between negative effects and lack of effect. Surely a negative effect such as competition for resources is as valid an ecological reality as positive effects based perhaps on the richness of the habitat. The model should also allow species groups to be correlated with outside influences, rather than force each species to be treated individually. In addition, although a species should be assigned to a definite group, it should also be possible to view species which may belong in some degree to more than one group.

Most, perhaps all, of the similarity coefficients do in fact assume only positive effects, and fail to discriminate between non-association and negative association. None (a multiple correlation is always possible) allow immediate correlation of species groups with environmental factors. Many, especially the hierarchial strategies, do not permit a single species to exist in more than one group. Principal components analysis conforms to all of the model requirements.

There is the question of the units of the observation vector, and the manner in which the technique weights the importance of the various species. In most similarity coefficients the most numerous species or the ones with the greatest biomass contribute most to the measurements. In our opinion there is no justification for equating numerical abundance with ecological significance, the latter of which should be the criteria for the grouping of species and mapping of habitat. In the principal components-correlation model all species are given unit variance and zero mean, thereby drastically eliminating the effects of relative

abundance and limiting grouping tendencies to the ability of a species to explain changes in other species. The significance of these relationships is best left to observation of the critters themselves. Although we can still put species on equal footing, there remains some question of the best manner in which to quantitate species data. An interesting study is that of Erman (1973), who used respiration rate as the measure of importance, and the Orloci (1966) method of position vectors to analyze the data. In an earlier paper, Erman and Helm (1971) noted that ranking of species based on respiration and numerical abundance or biomass differed significantly. It would therefore seem important to de-emphasize the unit of measurement. With regard to Erman's study there seems to be a number of practical difficulties in applying respiration measurements to the Florida environments. Erman dealt with relatively few species and calculated respiration from previously determined relationships between body length and respiration rate. At the very least, the rate equation should include a term for temperature variations, since different species do not respond to temperature changes in the same way. There would also have to be some attempt to relate laboratory activity levels of the animals with their average activity in a natural setting.

Compared with analysis based on diversity indices, principal components permit some useful statements to be made. Although from our biased human viewpoint, a diverse community should be more stable and capable of complex interation, there is little empirical evidence to support the

claims. Principal components provide an explicit measurement of organization in the sum of the variance of the vectors representing all or most of the species, compared as a percentage to the total variance. Since principal components are not plagued by most of the problems of diversity measurements, notably the effect of different sampling methods, comparison of different communities is readily feasible. In addition, diversity allows only extrapolation; no mention can be made of which species will be found at any given site. Principal components, on the other hand, do permit such interpolation, and can be used to predict the distribution of species.

6. Principal Components and the Niche

The last section compared principal components with other methods, with favorable conclusions; their versatility may be more apparent in the applications of sections after this. But first we would like to explore some relationships between the inherent properties of component analysis and traditional niche theory.

Even a brief review of niche theory and its literature is beyond the scope of this paper, and perhaps the knowledge of the author. Still, let us present a possible model for practical if not theoretical application.

As a beginning, we will consider Hutchinson's (1958) formalization of niche theory. Begin by examining a single environmental factor, such as temperature, and designate on a single axis the ranges of temperature in which the species under consideration can survive and reproduce. Now examine another environmental factor and plot as orthogonal axes the points which satisfy the two conditions, survival and reproduction. When all factors have been plotted, a hypervolume results which is known as the niche space or N-space. Hutchinson's original presentation was in the language of set theory, an extremely useful formalization in terms of succinct statements, but unnecessary for this discussion. Moreover, although set theory permits very pretty manipulation of the theory, it has not produced many tangible results.

Consider the principal of competitive exclusion, proposed by Gausse many years ago and embodied in the classical niche theory. The conclusion

of the principal is that if two species in physical contact have niche spaces which overlap, one or the other would be eliminated at equilibrium. Now the condition of equilibrium in an ecological situation is at best mystical, and at worst clerical. If it does exist anywhere, it is probably in the abyssal zone of the ocean. Yet as Dayton and Hessler (1972) have pointed out, the bottom of the sea supports quite a number of different species, all of which seem to get their daily bread in similar ways. The two supposedly antithecal ideas of extreme niche overlap and species diversity at apparent equilibrium seem to coexist. Interestingly, Dayton and Hessler explain the phenomena in terms of the interaction of groups of species, the basis of our contention for the usefulness of association analysis.

Another problem with the simple form of the niche space is the widely divergent modes of life in the juvenile and adult forms. McConnaughey (personal communication) has pointed out the interaction of coral and sea star in the southern Pacific. Here the coral feeds on the larval sea star, while the adult sea star feeds on the coral. Perhaps the most significant difficulty is that niche space, even if it takes into account the vagaries of the infant, does not imply distribution in the habitat. Unfortunately, spatial distribution is the only thing we normally have to go by.

Obviously, within the bounds of survival and reproduction, an environmental factor may have positive, negative, or no effect. These distinctions are not represented in the model niche. Indeed they would present a formidable problem were each species of a typical marine community, for example,

to be considered individually. Yet in principal components we have at our means a method for making these distinctions if we substitute for the classical niche of a single species the niche space of all species combined. As said before, the axes of species distribution scatter diagram may be correlated with environmental factors, giving us the positive, negative, and no effect distinction. Further, since principal components are uncorrelated, they are statistically, at least, independent, a property of non-overlapping niches. Thus we could shade the original N-space with the factor scores of each of the associations which, if we could see in N dimensions, would give us a succinct and vastly more informative picture of ecological realities in a complex system than a combination of individual classical niche spaces. For practical purposes a correlation is sufficiently difficult to explain.

One possibility which is not explored in this paper but which could be of use when the species of the communities are to be examined individually is the use of components to determine niche breadth. Previously proposed measures of niche breadth (see Levins, 1968, for example) are usually based on the relative proportions of a species over a range of differing environments. Disregarding the general problem of selecting "differing" environments which would permit equitable comparison of a number of species, on the small scale of our investigations valid reasons might be found for considering all or none of the stations different. Species are affected in varying degrees by environmental factors. What might appear to us as a significant change in the habitat might have no

effect, or worse and more likely, have different effects on different species. However, both theoretically and in practice, principal components do represent independent partitioning of the habitat. A species receiving high weighting in more than one component is obviously affected by more than one environmental factor and in a sense exists in a wider niche. Note this is a real departure from previous concepts of niche breadth. If a species exists over a wide range of habitats but is affected only by changes of a few factors, it would possess a traditionally wide niche but a narrow component niche. The difficulty is significant and perhaps beneficial. On the small scale we would tend to think limiting our investigation to only those factors which have some effect on the species to be more enlightening, while large scale environmental investigations require less detailed information useful in preliminary study.

7. "For the Snark was a Boojum, you see."

In summary, an analysis of benthic invertebrate populations by means of principal components will have the following features:

1.) As a form of ordination it is the standard of efficiency (in the sense it causes no distortion of scatter diagram), approximately four times as efficient as the Bray and Curtis measure, somewhat more than Orloci's position vectors.

2.) It tends to de-emphasize the unit of measure of species abundance, and eliminates the ranking problem.

3.) Unlike diversity indices, it allows interpolation with regard to species distribution, it is not affected by sampling procedures as such, and appears to be a useful tool in comparing species of different communities.

4.) The model permits both positive and negative relationships between species, and distinguishes between negative effects and no association.

5.) An examination of the factor structure matrix will suggest community fine structure:

    a.) species associations

    b.) positive, negative, and non-interactions

    c.) niche breadth

    d.) degree of organization

6.) Associations defined by the principal components can be correlated to environmental factors, identifying possible causes for the distribution of the organisms.

7.) Factor scores can be plotted for each sample on orthogonal coordinates or on location maps to help distinguish site groups and species distribution.

Plate 1. View of Bayside development, with the Grand Canal in the background and Coconut Bayou at the extreme right, looking toward the West.

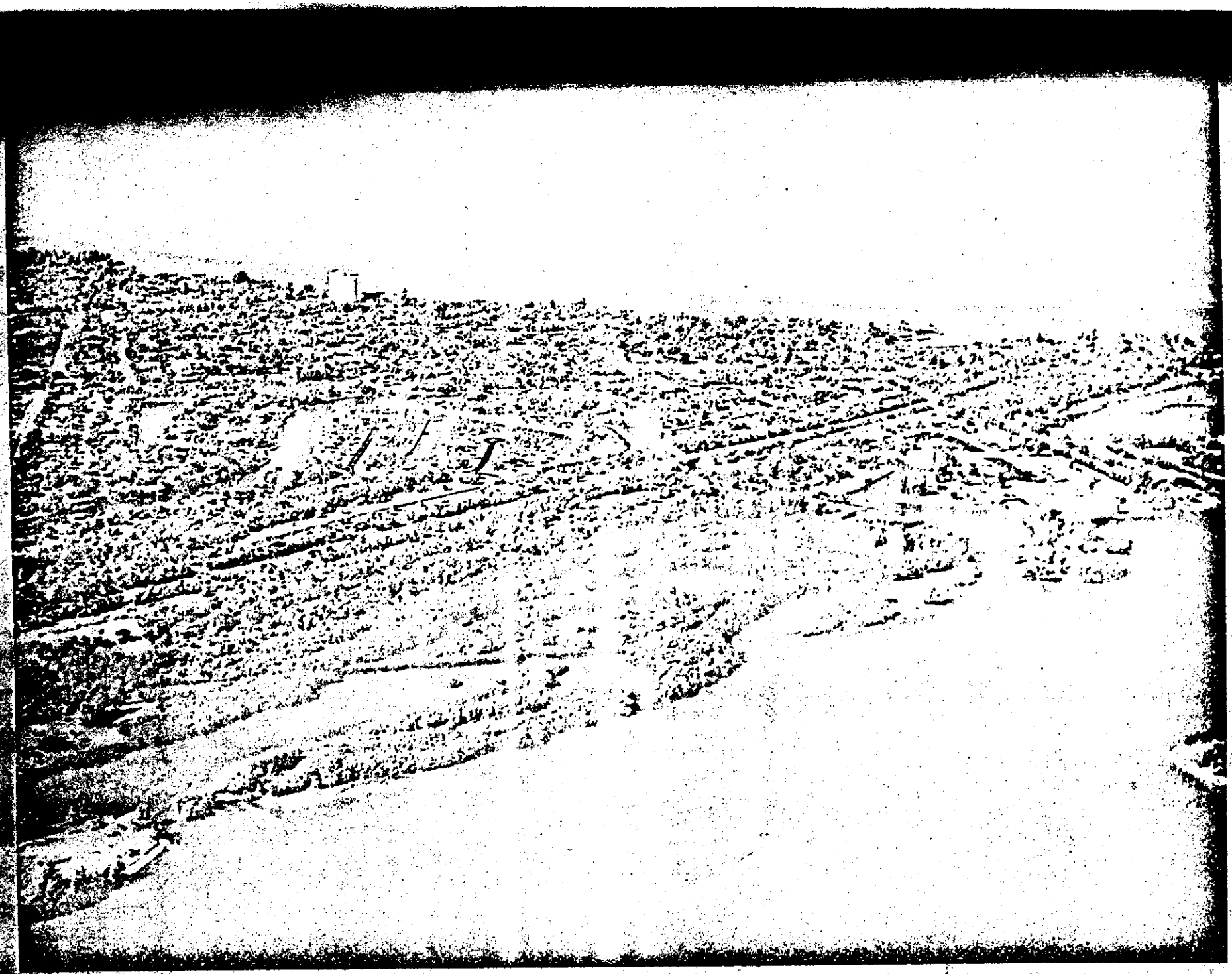


Plate 2. The Grand Canal, with Coconut Bayou in the background, looking North.

Part 2 - Matter

1. Introduction

Data on the macrobenthos of four separate areas were collected. An observation consisted of the pooled species counts from four core samples each of 1/64 m^2, screened by a 1/8 inch wire mesh. Although it is not known precisely if this procedure completely accounts for all organisms at a station, it does tend to reduce the problems of micro-distribution. Further, since rarely occurring species contribute little to a community analysis (though their ecological contribution is undetermined), the principal components analysis is limited to those species which occurred in at least four samples in any one area. All study areas are considered separately.

We note that difficulties with mesh size, sampling area, and other sampling procedures are not as significant to the component model as to, for example, diversity models. Although new species may be included in any given analysis by decreasing mesh size, for example, groupings of previously included species should not be altered, since the model is based on intercorrelations among species and not some accumulated function of all species.

We have adopted in all analyses a transformation of species counts whereby a new variable is defined by

$$x = \log (\text{count} + 1).$$

It is for this new variable "x" that correlations and principal components are calculated. There is a good deal of justification for this

transformation. One, although it is true that the principal components model is not dependent on the distribution of the variables, the manner in which they are grouped sometimes is. In any case, the transformation by logarithms can be observed to give more variables their highest factor structure weightings in the first few components, i.e. will place more species into distinct associations. Two, the log transformation itself can be regarded as a conservative application on two levels. It is a common method of removing the dependence of mean and variance, an obvious problem in species data (see Sokal and Rohlf, 1969, for instance). Also, it has been known for some time that species counts are approximately log normal (Preston, 1948; Cassie, 1962; inter alia). This transformation has been applied in principal components analysis by Colebrook, 1964, and Cassie, 1963, 1968. While data reduction and transformation do tend to eliminate adverse effects of species occurring infrequently or in small numbers, associations of these species should be considered carefully before acceptance.

Complete lists of data used in these analyses are to be found in the appendix. There also will be found lists of most of the programs used by the author, in Fortran IV for the PDP-11.

Before looking at the studies themselves, we caution the reader not to place too much faith in them. Although we believe the methods employed here to be the most acceptable of all the numerical techniques, none should be accepted blindly. In the words of Mr. Spock, "The computer is a useful tool, but I have no wish to serve under one." At

best it can point the way to an intelligent and effective natural historic approach, that is, if the ecological situation is of interest at all. If all that is required is an objective and technical description of the distribution of those little things at the bottom of the bay, perhaps with the idea of looking at the changes incurred when someond digs a big hole through one's study area, then we heartily recommend blindness.

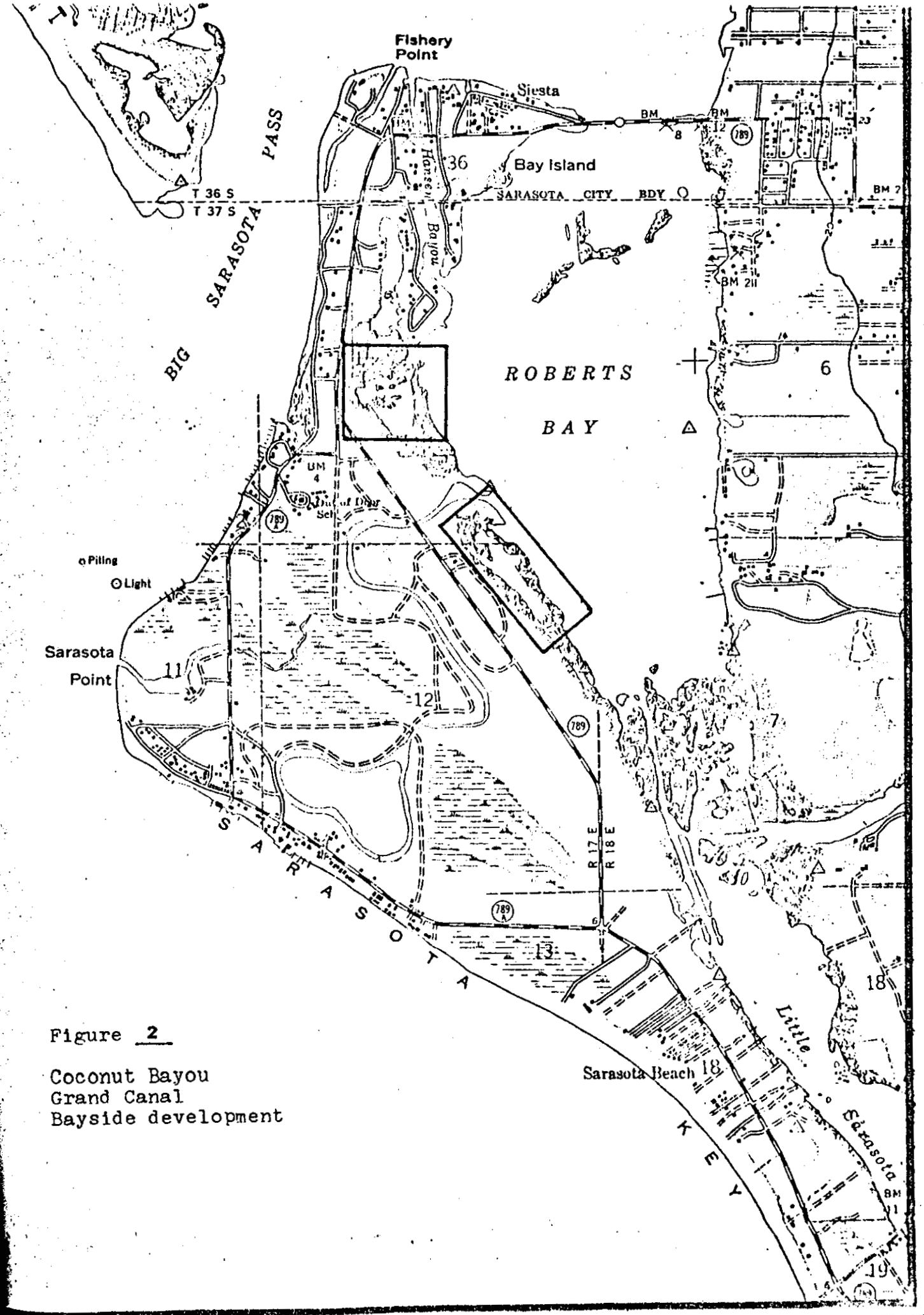


Figure 2

Coconut Bayou
Grand Canal
Bayside development

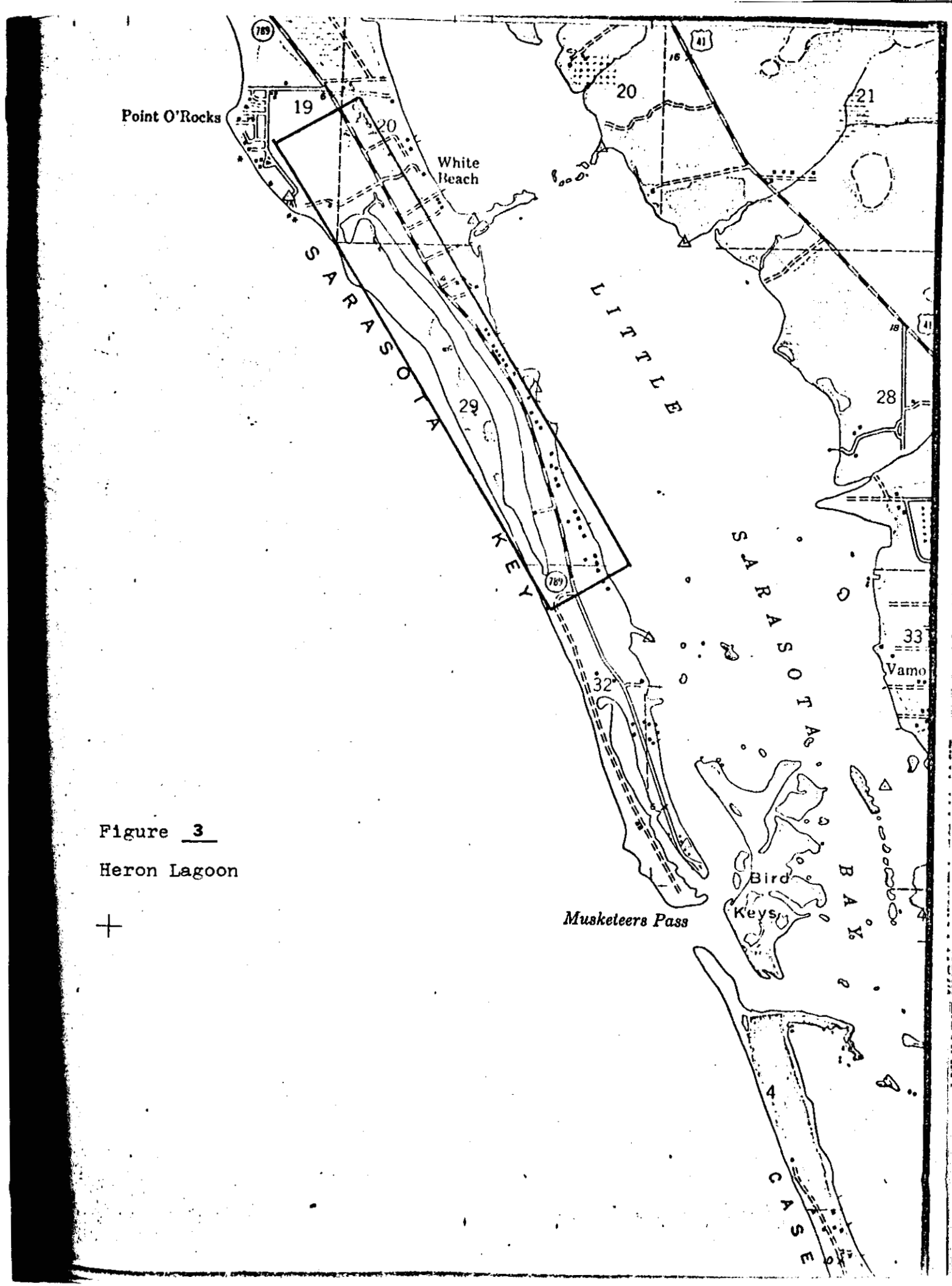
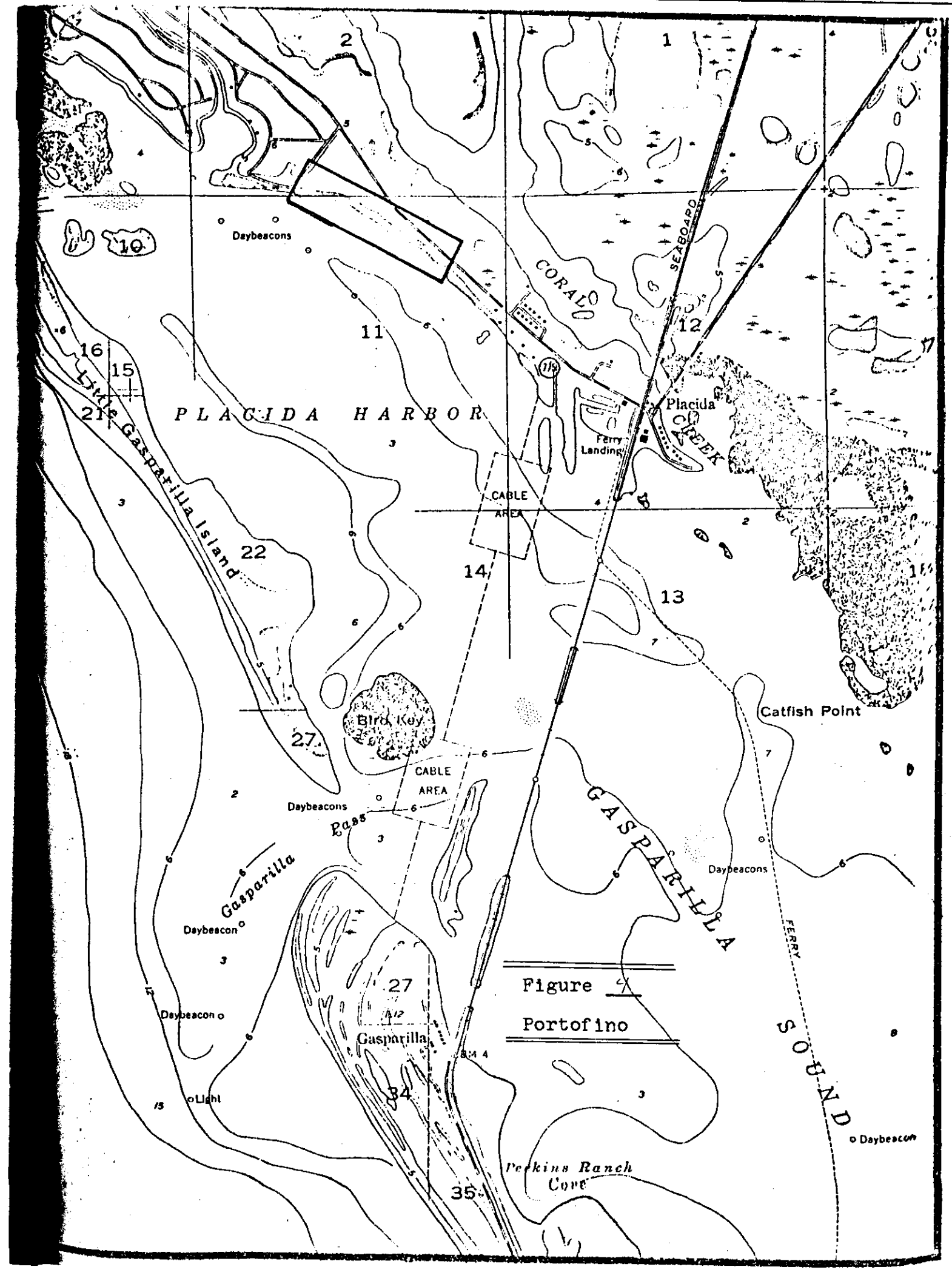


Figure 3

Heron Lagoon


Daybeacons
CORALO
SEABOARD
Placida
CREEK
Ferry Landing
PLACIDA HARBOR
CABLE AREA
Little Gasparilla Island
Bird Key
CABLE AREA
Daybeacons
Pass
Gasparilla
Daybeacon
Daybeacon
Light
Gasparilla
Catfish Point
GASPARILLA
Daybeacons
FERRY
SOUND
Daybeacon
Figure 4
Portofino
Perkins Ranch
Core

2. Coconut Bayou

Coconut Bayou (Fig. 2 and Plate 2) is a relatively simple, shallow canal system of moderate age, bordered by natural banks and mangroves, and possessing mangrove islands in its center. All three of the common marine grasses are present: Thallasia testudium (turtle grass), Diplanthera wrightii (Cuban shoal weed), and Ruppia maritma (Widgeon grass). A listing of dry weight biomass of these grasses for the 24 stations of this study (see Fig. 5) will be found in the appendix.

Although some dredge bucket samples were taken in the channel and some samples were taken along the shore, this study includes only the plug samples in and around the central mangrove islands. Approximately 90 live species were found over the entire area, of which 26 occurred in at least four of the 24 stations. These species provide the substance of our analysis, and include 14 polychaetes, four gastropods, four bivalves, two ophiuroids, and the grouped classifications of nemertines and sipunculids.

Coconut Bayou appears to represent a relatively complex invertebrate community. An examination of the factor structure matrix reveals at least five components to the community; the first five vectors of this matrix are shown in Table 1. Remember that these figures give the correlation of each of the species with the independent components. Maximum correlations for each species are underlined, but a single species may be highly correlated with more than one component. Such species may be thought of as bridging the statistically independent associations,

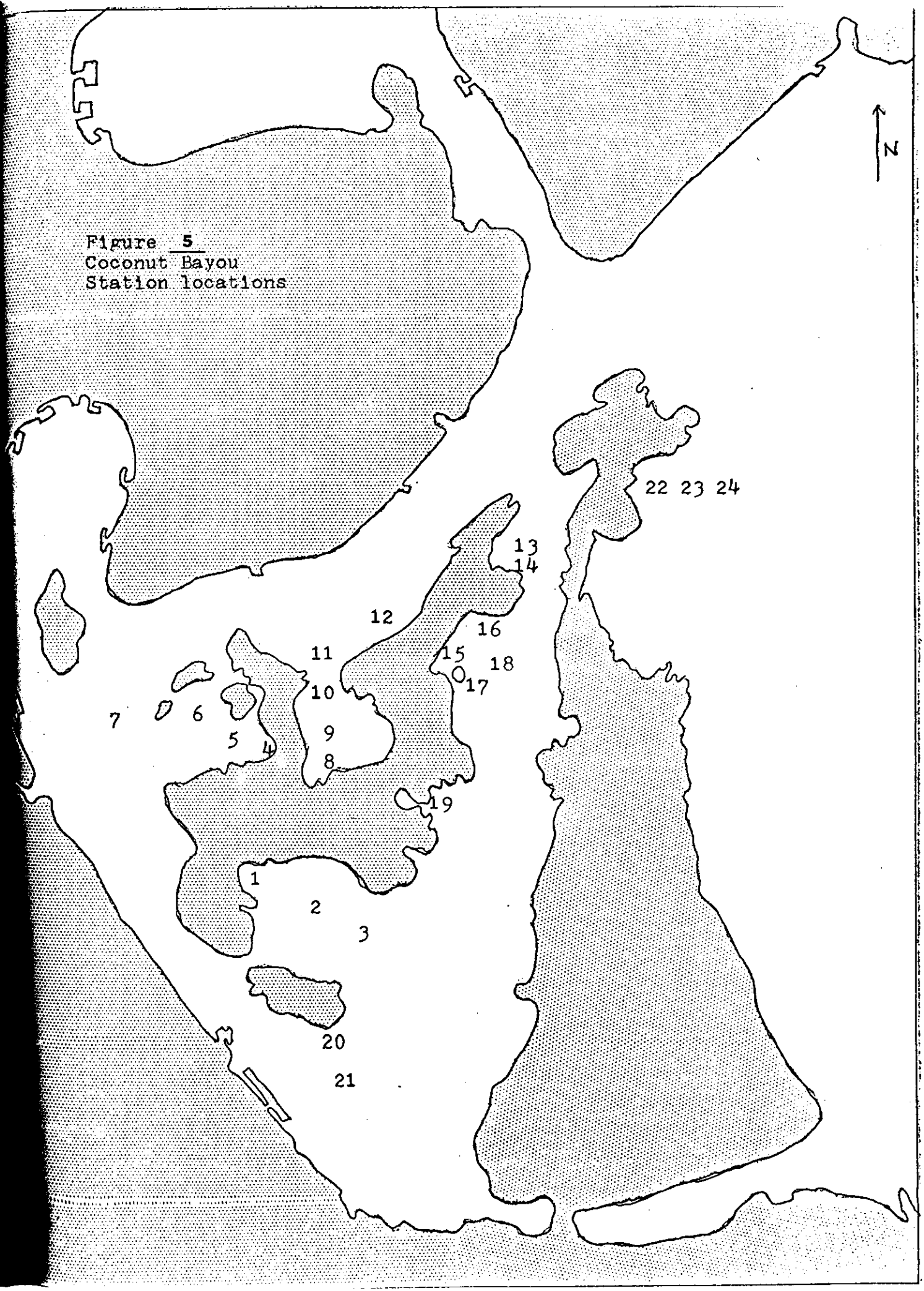


Figure 5
Coconut Bayou
Station locations

TABLE 1 - Associations: Coconut Bayou

Species	Feeding type	Factor Structure Vectors				
Capitella capitata	NSDF	.42	-.18	-.46	-.10	.07
Diopatra cuprea	C,S	-.09	.74	-.25	-.14	.13
Ehlersia sp.	C	-.38	.61	-.37	-.04	-.09
Eunice rubra	C,S	-.03	.32	.05	-.60	-.07
Haploscoloplos foliosus	NSDF	.14	.25	-.46	.06	.41
Onuphis eremita	NSDF	.09	.67	-.30	.10	-.06
Branchiomma nigromaculata	SF	-.27	-.02	-.29	.19	.47
Cirriforma filigera	SDF	-.77	-.02	.21	-.20	.13
Loimia medusa	SDF	-.00	.28	-.09	.61	-.20
Loimia viridis	SDF	-.17	-.33	-.66	-.11	.12
Maldane sarsi	SDF	.07	.39	.62	.16	.07
Melinna maculata	SDF	-.34	.48	-.25	.02	.46
Pista cristata	SDF	-.81	-.24	.01	-.34	-.08
Cerithium muscarum	S	-.77	-.34	.01	-.02	-.16
Crepidula fornicata	S,SF	-.72	-.40	.21	.21	-.10
Pleuroploca gigantea	C	-.02	-.01	.18	-.35	.19
Prunum apicum	S,C	-.47	-.04	.03	.60	.44
Anomalocardia cuneimeris	SF	-.73	-.13	.20	.10	.05
Chione cancellata	SF	-.29	.42	-.53	.23	-.18
Modiolus papyria	SF	-.04	.58	.18	-.53	.21
Nuculana acuta	SDF	-.64	.33	-.29	-.28	-.11
Amphioplus abditus	NSDF	.16	-.01	.01	.24	.57
Ophiophragmus filograneus	NSDF	.20	.29	.05	.19	-.66
Spiochaetopterus sp.	SF	-.53	.34	-.15	.29	-.16
Nemertines	C	-.08	.34	.18	.38	-.15
Sipunculids	NSDF	-.72	-.00	.40	-.13	-.15
Variance of component =		5.05	3.42	2.48	2.28	1.90

Sum of variance = 58% total

Key to feeding types: C - carnvore; S - scavenger; SF - suspension feeder;

SDF - selective deposit feeder; NSDF - non-selective deposit feeder.

Table 2 - Correlations of environmental variables with components: Coconut Bayou.

	Components				
Grass species	1	2	3	4	5
Thallasia testudium	-.11	-.50	.01	.09	-.10
Diplanthera wrightii	.09	.35	.07	-.43	-.03
Ruppia maritima	.00	.05	.41	-.17	.04
Detritus	-.05	.10	-.29	-.08	.08
Total grass biomass	-.08	-.34	.19	-.13	-.09

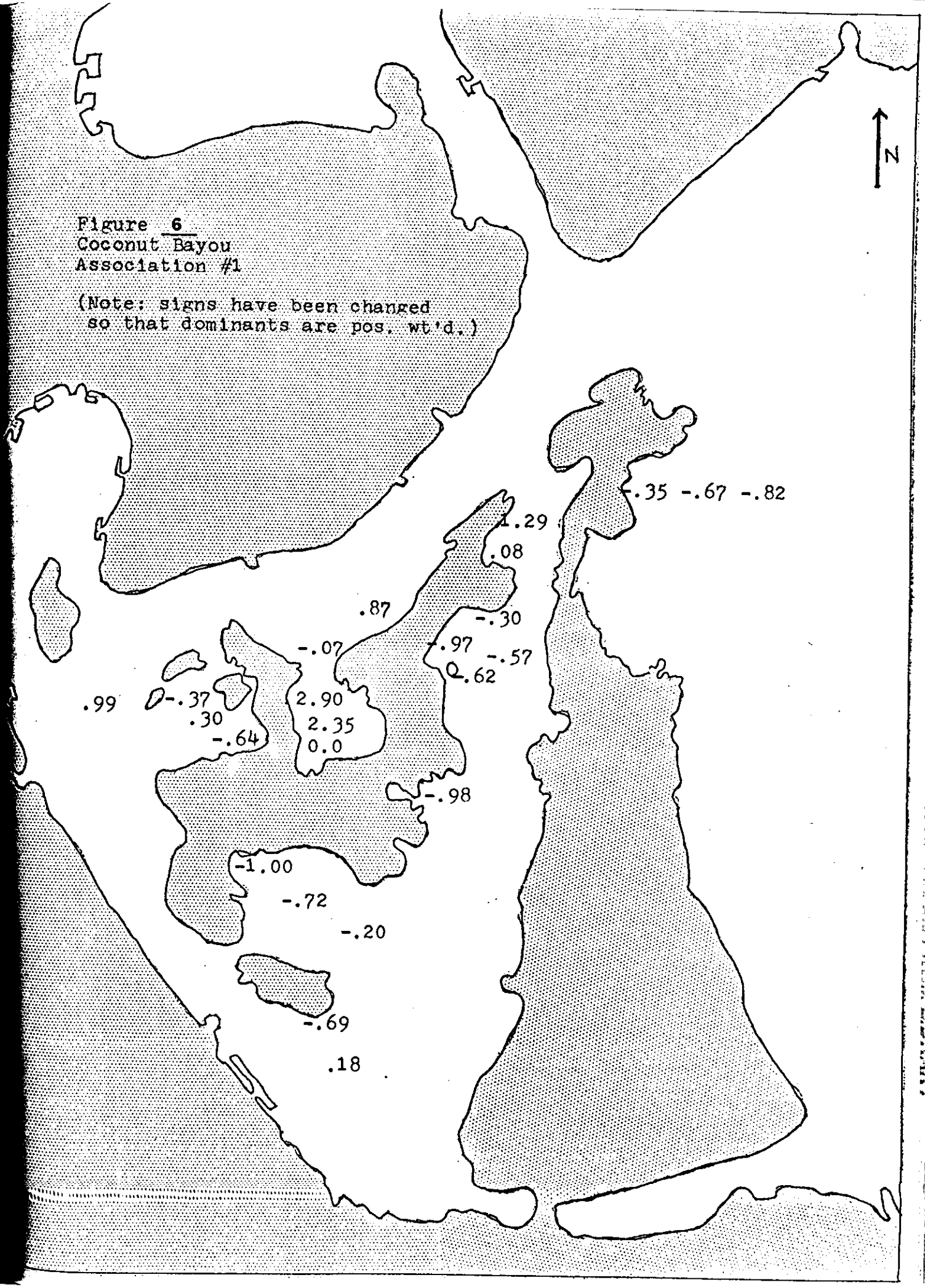


Figure 6
Coconut Bayou
Association #1

(Note: signs have been changed so that dominants are pos. wt'd.)

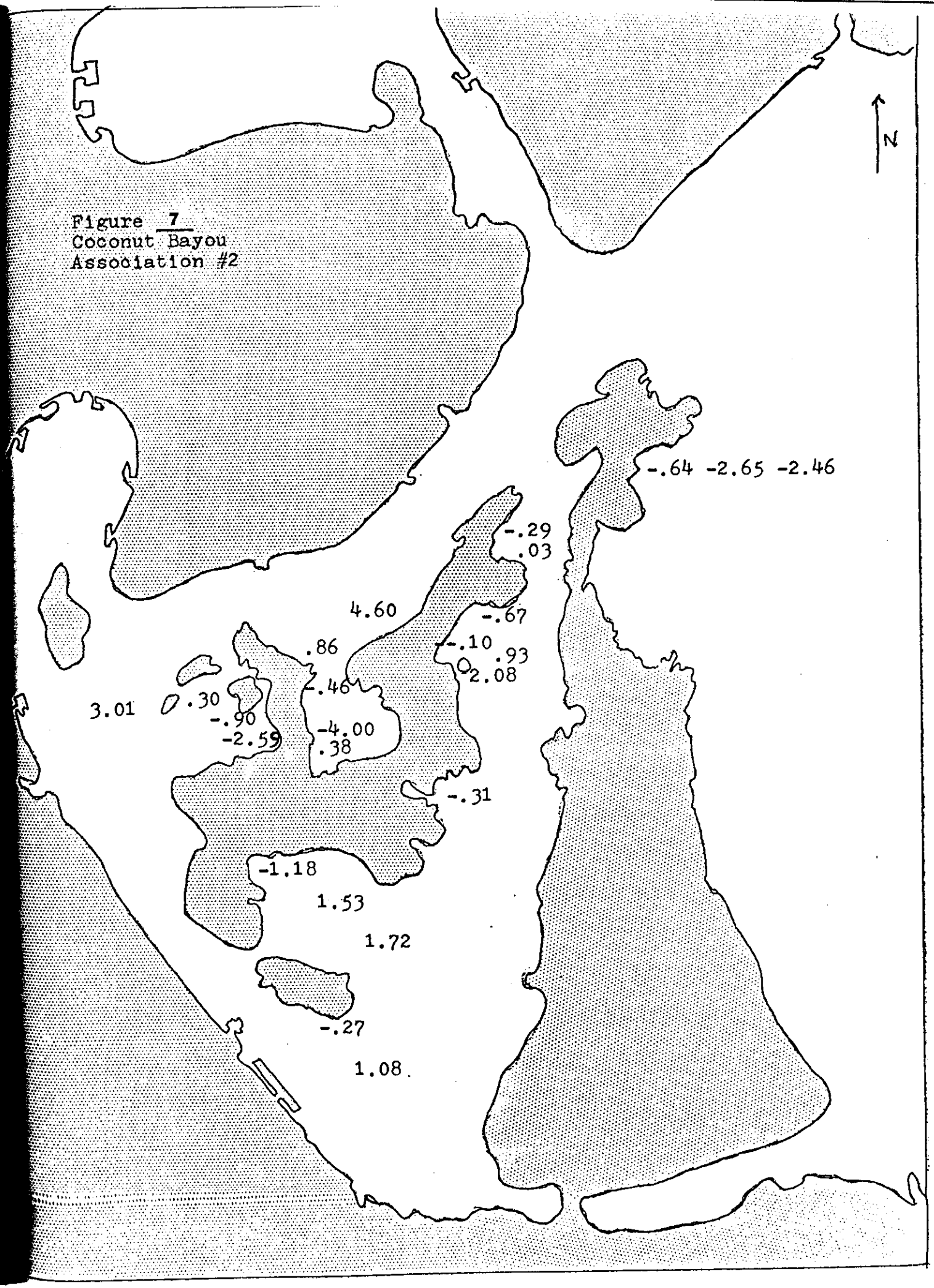


Figure 7
Coconut Bayou
Association #2

permitting one helluva Finagles constant to be employed. Table 2 shows the correlation of each of the five associations with the grasses. The summed variance of the five factors is 58% of the total; 23 of 26 species may be reasonably accounted for.

The first association is uniform, i.e. only species of one sign are included in the association. Eight species are most highly correlated with this component. None of these seem particularly correlated with any other factor, indicating the independence of the association. It does not have any significant correlations with the marine grasses, nor with detrital content. (Note: none of the associations seem correlated with detritus.) Feeding types, according to the classifications proposed by Sanders (1960), indicate a predominance of suspension and deposit feeders. It may be that the distribution of this association, shown in Fig. 6, is related to sediment type or current conditions. Of the two, we feel currents the more significant.

The second association is also uniform, consisting of four polychaetes and a single bivalve. Among the five species all feeding types are represented. These species form a Cuban shoal weed oriented association, or at least one which avoids turtle grass, judging from correlations in Table 2. Still, in certain instances Cerithium and Crepidula occur in relatively large numbers in turtle grass. This association is linked to the fourth association via the bivalve Amygdalum, and with the fifth association via the polychaete Mellina. A map of the distribution of the second association is found in Fig. 7.

Association #3 would seem to be a Widgeon grass oriented group (Fig. 8). It is not uniform, being divided into groups of two and three species. Again, four are polychaetes and one is a bivalve. Of the polychaetes, all are deposit feeders, both selective and non-selective. Interestingly, the two selective feeders have opposite sign, as do the two non-selective deposit feeders. This may indicate some competition for resources.

Association #4 (Fig. 9) is negatively correlated with Cuban shoal weed. It is clearly weighted for three species, two of like sign; also at least one species, Amygdalum, has a bridging capacity. Negatively weighted species are found in Cuban shoal weed, positively weighted species occur in areas with no shoal weed. All species in this association are relatively rare in occurrence.

The fifth association (Fig. 10) includes the two brittle stars, which are oppositely weighted and uncorrelated with any of the grasses. Amphioplus is fairly common, Ophiophragmus much less so, but the competitive or at least exclusive nature of their relationships seems to be valid on the basis of present data. The polychaete Mellina, a fellow deposit feeder, occurs with Amphioplus sufficiently to bridge associations 2 and 5.

Three species cannot be grouped with any of the associations nor with each other. They are: Branchiostoma nigromaculata--the only sabellid in the analysis; Plueroploca gigantea--a large gastropod carnivore whose range probably extends over the whole area and whose size is not suited to the sampling technique; and the nemertines, also carnivores.

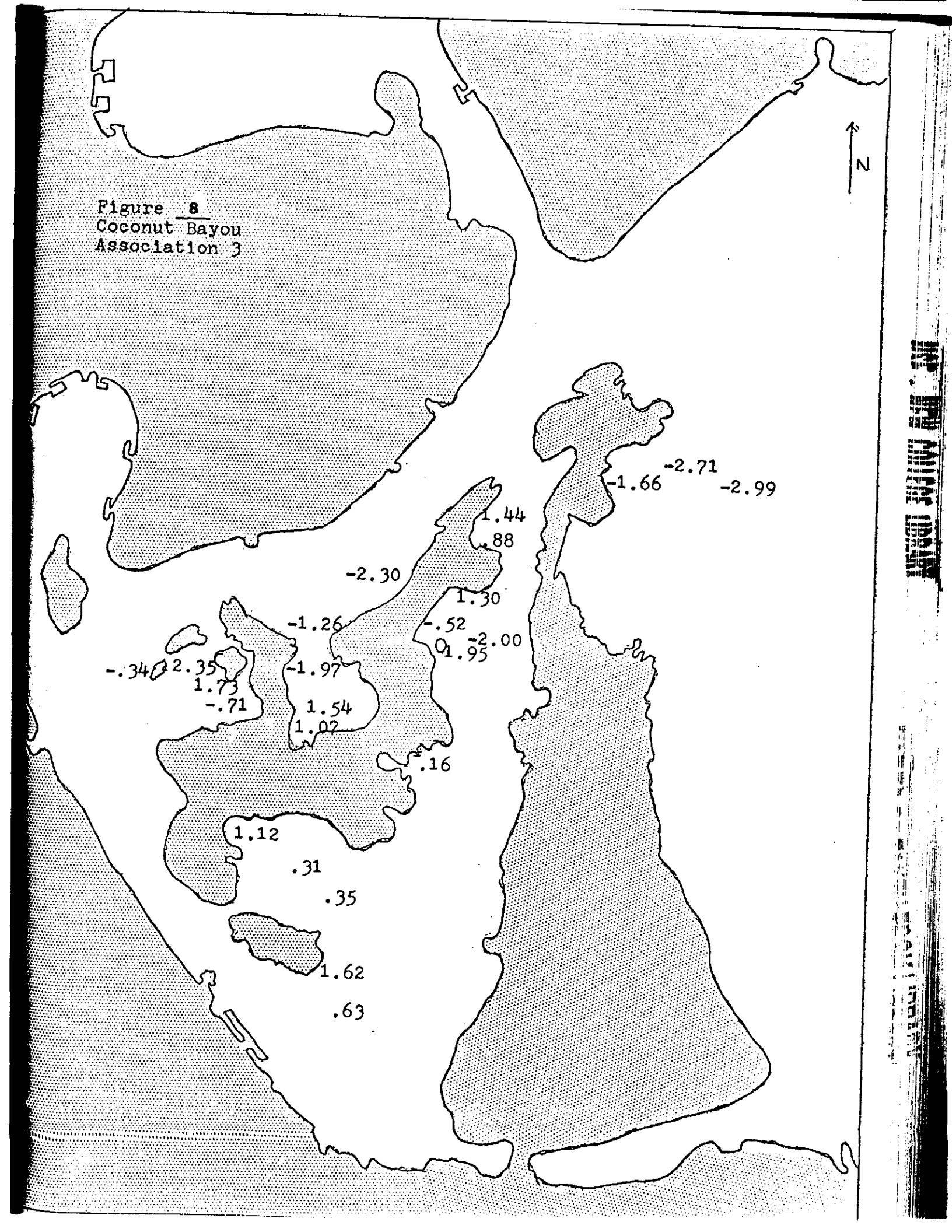


Figure 8
Coconut Bayou
Association 3

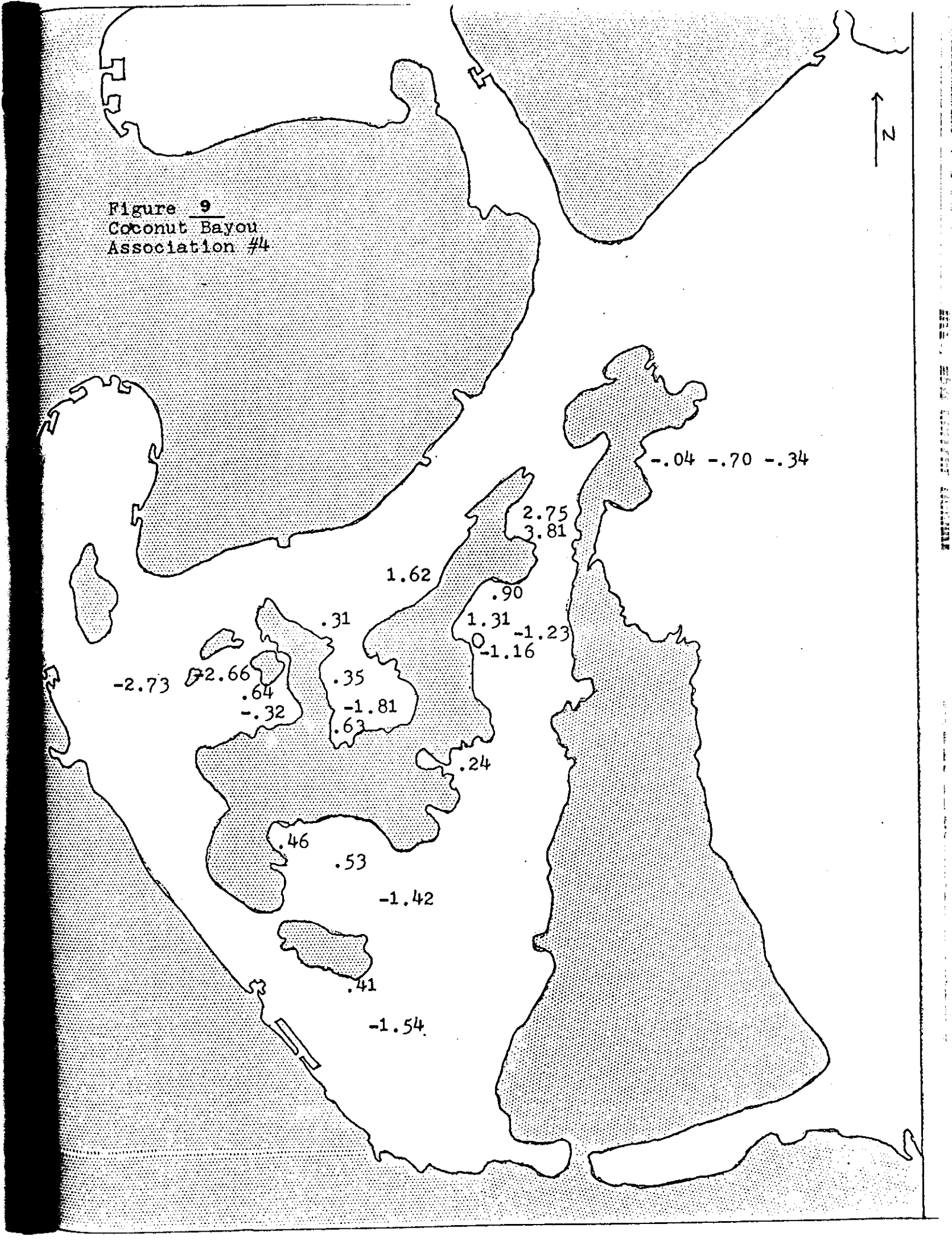


Figure 9
Coconut Bayou
Association #4

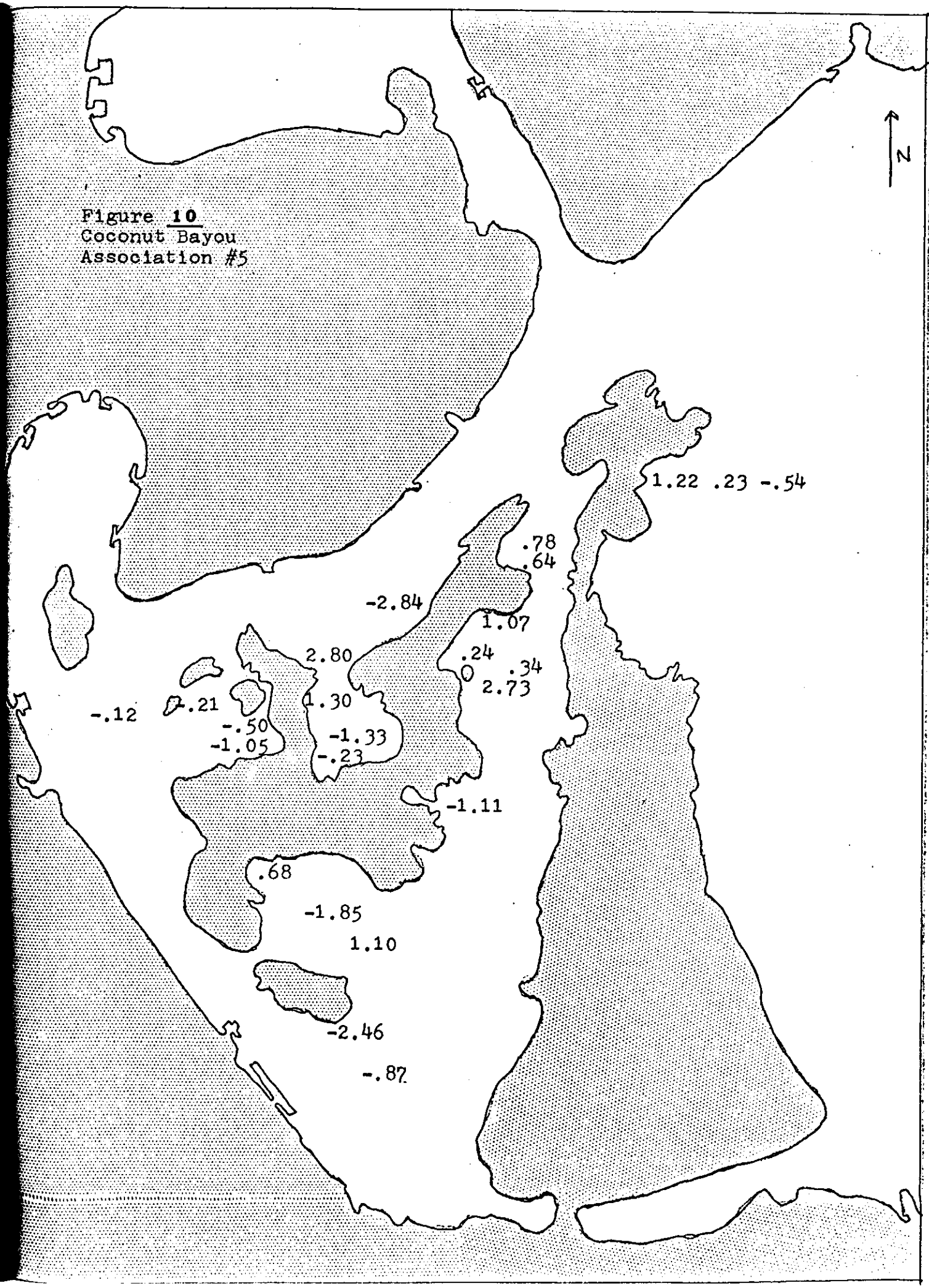


Figure 10
Coconut Bayou
Association #5

In summary, Coconut Bayou possesses a complex community, at least around the central islands. Twenty-six of the 90 or so species present occur frequently enough to be included in the analysis. Of these, 23 may be grouped into five associations. Cuban shoal weed and Widgeon grass each possess distinct associations; turtle grass would not seem to affect distributions except in a negative fashion with association #2. The first association is general both in feeding and distribution. Associations 2 and 4 are affected by grass biomass, and tend to place similarly feeding species into competitive positions in the component. The fifth association consists of the echinoderms, is unaffected by the grasses, and also indicates some form of competition between the two species. Associations 1 and 3 appear the most independent, while 2, 4, and 5 possess bridging species.

3. Heron Lagoon

Heron Lagoon consists of the natural lagoon (Fig. 3) and the man-made canal system to the north of the original lagoon (Fig. 11). The canals have, for the most part, natural banks or sea walled lawns. The only connection with open water at the present time is through a single culvert leading to a boat basin on Little Sarasota Bay. Circulation does take place, but in a limited and complex manner. Locations of the eight sampling stations of the study are seen in Fig. 11. At each station three separate samples were taken: one at MLW (approximately one foot), one at LLW (approximately two feet), and one at maximum channel depth at that station (four - five feet); these are labelled A, B, and C respectively in all tables. Marine grasses are infrequent, and the measurement of detrital content seems to parallel water depth--higher content in the upper zones, lower content in the lower zones. Twenty-one samples are included in the analysis; a total of about 50 species were found, of which 13 occurred in at least four samples. Eight are polychaetes, five molluscs. Table 3 presents the factor structure for Heron Lagoon; immediately the striking division of the organisms is visible. Well, maybe not immediately... hell.

In the first association all but one of the polychaetes may reasonably be included. The second association consists of all the suspension feeding molluscs plus Tellina (with the bridging species Lysarete), the third of the deposit feeding molluscs. The fourth is weighted for the ramaining polychaete Brachiosyhchus americana. It would seem that differing modes of life in this enclosed system define remarkably strict division of the niche space.

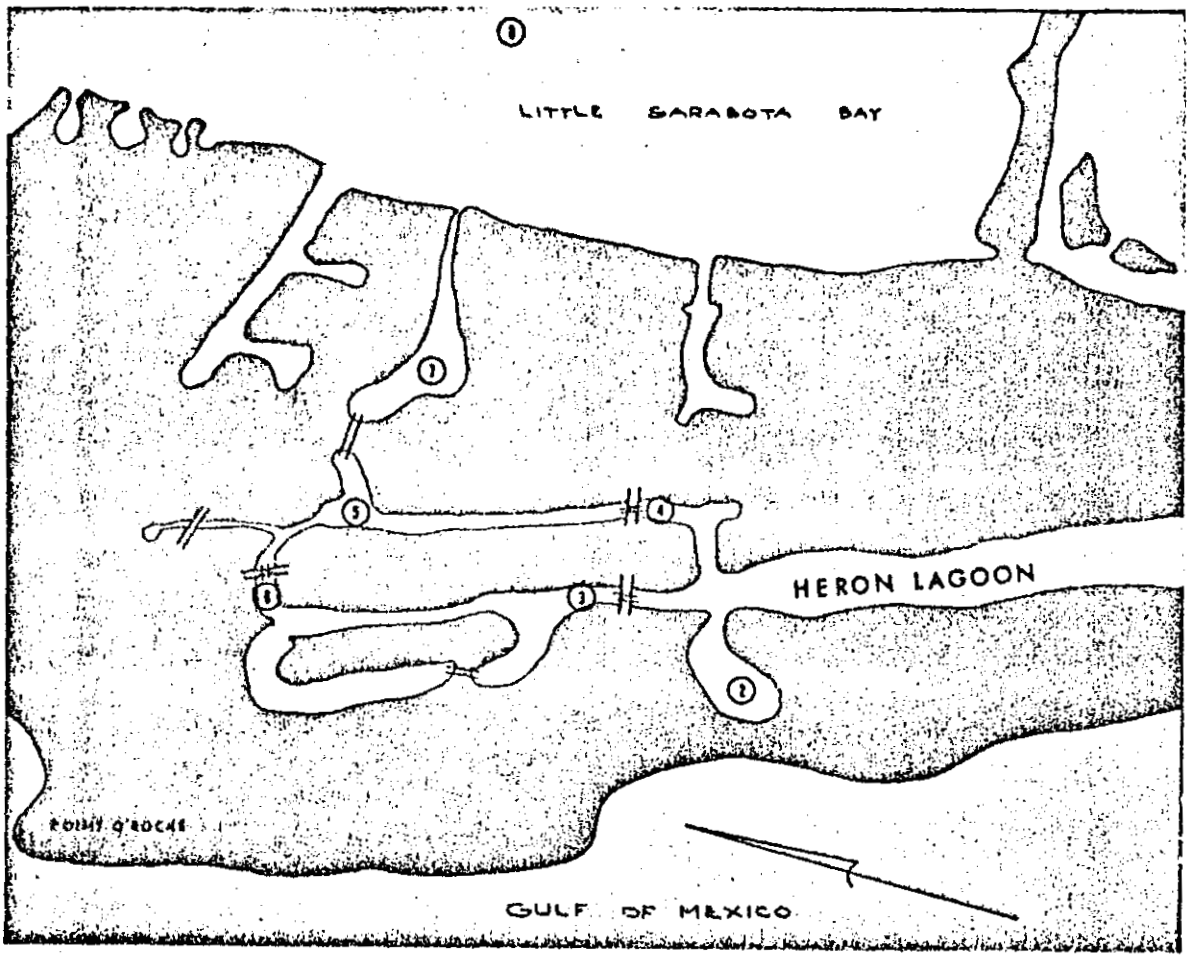


Figure 11. Invertebrate sampling stations.
(Station 1 at southern end of lagoon)

TABLE 3 - Associations: Heron Lagoon

Species	Feeding type	Factor Structure Vectors			
Brachiosyhchus americana	NSDF	.34	-.12	.38	.73
Cirratulus sp.	SDF	.77	-.30	-.10	-.11
Cirriformia filigera	SDF	.87	.28	-.22	-.10
Diopatra cuprea	C,S	.61	-.02	-.19	.51
Lysarete sp.	C	.62	-.64	-.10	-.18
Mellina maculata	SDF	.84	-.18	-.04	.16
Onuphis eremita	NSDF	.82	.13	.16	-.33
Spiochaetopterus sp.	NSDF	.68	-.47	.22	.10
Anomalocardia cuneimeris	SF	-.01	.55	.36	.51
Modiolus tulipus	SF	.49	.61	.41	-.35
Semele proficua	SDF	-.13	-.44	.64	-.31
Tagelus gibbus	SDF	-.19	-.33	.71	-.00
Tellina lineata	~~SF~~ SDF	.49	.78	.19	-.13
Variance of the components =		4.61	2.44	1.57	1.48

Sum of variance = 78% total

TABLE 4 - Factor scores: Heron Lagoon

Factor	1			2			3			4		
Location	A	B	C	A	B	C	A	B	C	A	B	C
Stations 1	-.73	-.67	-.66	.14	.08	.47	-1.39	-1.16	-1.24	-.67	-.22	-.39
2	-.73	-.60	-.39	.14	.22	.19	-1.39	0.00	-.35	-.67	.49	2.37
3	-.55	-.69	-.45	-1.26	.25	.35	2.61	.79	2.44	-.75	1.56	2.20
4	2.24	-.91	-.85	-2.76	-.60	.03	-1.29	-.14	-1.27	-.51	-1.18	-.62
5	-.62	-.81		-2.08	-.52		1.86	-.11		-1.34	-.30	
6	.97	.51	-.26	3.79	2.75	1.02	1.53	-.32	-1.29	-1.93	-.83	1.01
7	1.50	1.50		-1.60	-2.25		.67	-.91		-1.65	1.42	
8	.15	2.04		-.10	2.45		.61	.32		.65	1.37	

Table 5 - Correlations of environmental variables with components: Heron Lagoon.

	Components			
Variable	1	2	3	4
Detritus	.40	-.55	.34	-.47

Correlations with detritus are shown on Table 5. As we have pointed out, this measurement is related to tidal zonation. From the lack of correlation with detritus in the Coconut Bayou study and our own feeling of the inadequacy of the measure, we infer these correlations are probably more indicative of a partitioning of the environment and not an effect of the detritus itself.

It is difficult to show distribution of the associations in a spatial map, therefore they are shown on Table 4. Examination of these and the correlations of Table 5 leads to the following conclusions. The first and third associations, polychaetes and deposit feeding molluscs, show a preference for the upper tidal zones, while the second and fourth associations are likely to be found in the lower zone. This would seem to be the reason for the division of Brachiosyhchus from the rest of the polychaetes.

The division of species according to feeding type, according to tidal zonation; the enclosed nature of the system; the fact that only 13 species can be included in the analysis; the apparently high level of organization among these species (78% of the total variation accounted for by the four associations); what would seem to be a large number of associations, well linked by bridging species, for so few species--we can reach the following conclusions:

1) Heron Lagoon possesses relatively poor faunal diversity compared to other nearby systems.
2) The system has reached a high level of diversification for that system, i.e. interrelated organization combined with maximal partitioning of the niche space

Our samples were taken one month after a hurricane had subjected the area to severe stress. Although we have no data on the previous condition of the lagoon, the attributes described above suggest themselves as part of a colonizing community. The work of Simon and colleagues at Tampa Bay supports the facts of polychaete predominance and the independent behavior of molluscs in the colonizing period.

4. Bayside Development

The Bayside development is an area of mangrove swamp and grass flat destined to provide waterfront property just as the two previously considered areas currently do. The development is seen in Fig. 2 and Plate 1; the sampling stations for this study are shown in Fig. 12. Data on the invertebrates were collected in 1969 by John Morrill and Claudia Blair. Since then much work has been done, with limited results. Bayside is a perplexing yet continually enticing system.

This study consists of analysis of observations from 49 stations (two empty stations were eliminated). A total of approximately 50 species were found; 24 were included in the analysis. Of these, 19 of the 24 may be accounted for by the first four components, representing a combined variance 49% of the total. However, examination of the raw data shows that the four species of factors 3 and 4 are rather rare, thus casting doubt on the validity of the associations. The first two components account for 23% and 12% of the total variance, respectively.

The first association is uniform, possessing a variety of feeding types and phyla, and correlated most strongly with Cuban shoal weed (see Tables 6 and 7). Eleven species are included. An examination of the distribution of this association (Fig. 13) clearly shows the tendency of the organisms if this association to exist in the grass flat bordering the mangroves.

The second association (Fig. 14) includes four, possibly five, species. All are deposit feeders except the carnivore Nasarius vibex.

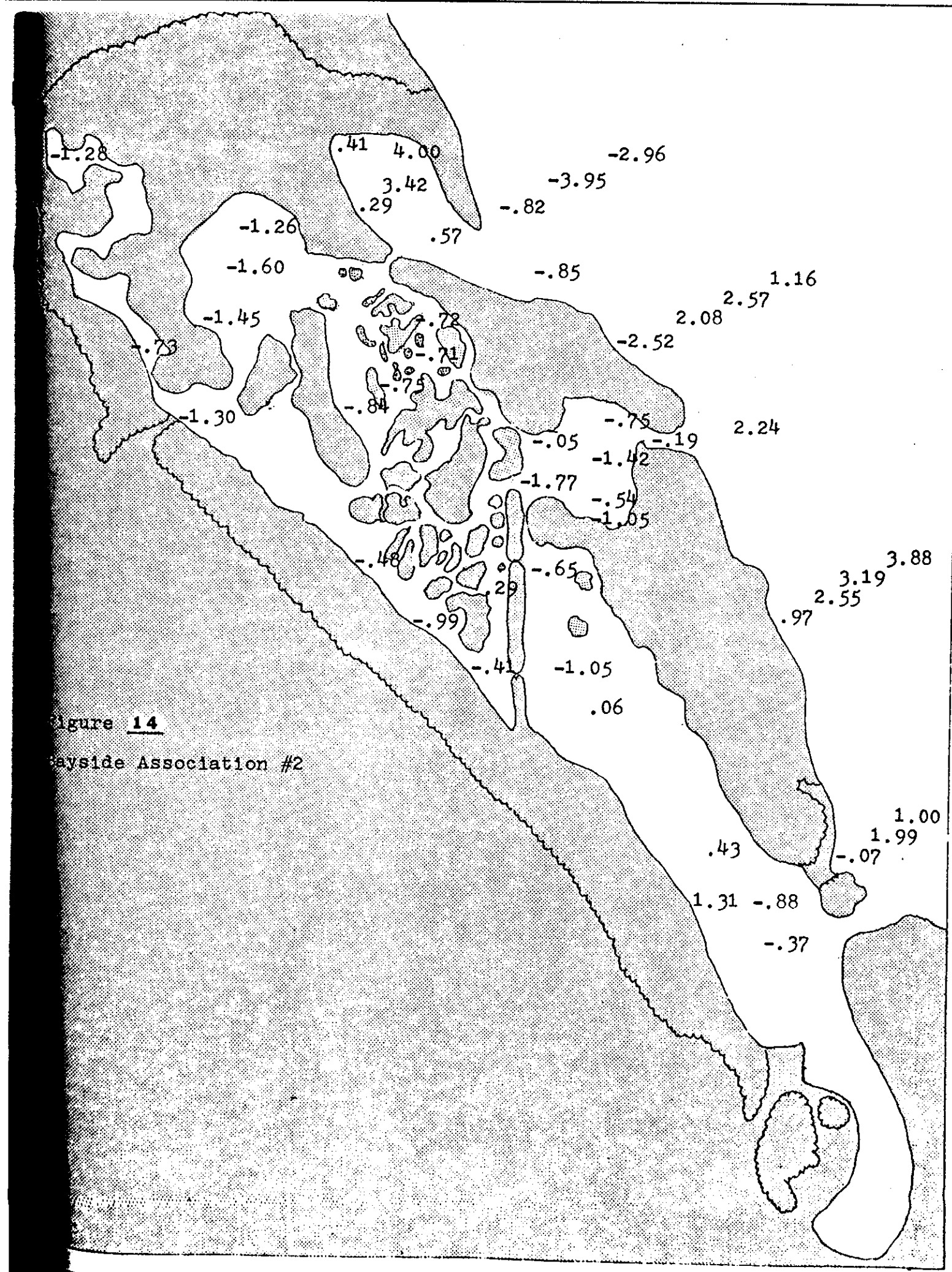


Figure 14

Bayside Association #2

Table 7 - Correlations of environmental variables with components. Bayside Development.

	Components			
Grass species	1	2	3	4
Thallasia testudium	.28	.10	.12	.02
Diplanthera wrightii	.48	-.06	-.01	.13
Ruppia maritima	-.16	-.03	-.15	.09
Total grass biomass	.41	.07	.08	-.18

TABLE 6 - Associations: Bayside Development

Species	Feeding type	Factor Structure Vectors			
Amygdalum papyria	SF	.68	.00	.31	.34
Anachis transliterata	C	.70	-.50	.12	-.10
Mussel	SF	.28	.07	-.68	-.17
Nassarius vibex	S,C	.38	.56	-.35	.08
Arenicola cristata	NSDF	-.09	.08	-.49	.01
Cistenides gouldii	SDF	.47	.27	.02	.38
Diopatra cuprea	C,S	.67	.43	-.12	.02
Glycera americana	C,NSDF	.05	.21	.21	-.73
Laeonereis culveri	C	-.32	-.24	.19	.06
Mellina cristata	SDF	.71	-.10	.12	-.20
Nereid	C,S	-.17	.18	.44	-.48
Onuphis cremata oculata	NSDF	.69	.13	-.14	-.11
Onuphis magna	NSDF	.14	.57	.27	.36
Pista sp.	NSDF	.83	-.10	.03	.01
Sabella melanostigma	SDF	.75	-.18	.12	-.10
Spiochaetopterous sp.	NSDF	.10	.61	.32	-.21
Maldane sarsi	SDF	-.25	-.38	.13	.03
Nemertine (white)	C	-.17	.01	-.42	.07
Nemertine (red)	C	.13	.05	.03	.39
Phoscolian sp.	NSDF	.53	-.34	-.13	-.14
Amphioplus sp.	NSDF	.37	-.35	.14	.18
Amphiodia pulchella	NSDF	.28	.75	-.02	-.18
Amphipoda	S	.50	-.39	-.32	-.30
Hermit crab	S	.57	-.17	.24	.13
Variance of the components =		5.42	2.87	1.83	1.43

Sum of variances = 49% total

Although the association shows a general trend toward open waters, it is uncorrelated with marine grasses. Current conditions would not seem to underly distribution since areas with supposedly similar currents sometimes have widely divergent scores. Probable causes entail a combination of current and sediment factors. However our inability to explain the distribution of the association, an interesting fact is the opposite relationship which exists between Maldane sarsi and the other species of the association. It is a fact that this species exists in the shallow lagoons of the swamp proper (check observations for stations 9, 10, 14, 19, and 21-27 for instance). This is by far the most common species in the swamp itself, and perhaps the only one which truly thrives in the variable conditions among the mangroves.

Of the species unaccounted for by the first two components, most are rather infrequent. One notable exception may be the nemertines which are somewhat more common. It will be remembered that nemertines found at Coconut Bayou were also not grouped with any of those associations.

There is a temptation, whether writing grant proposals or petitions, to speak of the "value" of a natural and relatively untouched piece of the Earth. On the basis of our analysis of invertebrate data, we might conclude that the shallow swamp of mangroves which comprises Bayside development is of minor importance. A rather small number of species is found, and these seem poorly organized. Such associations which do not exist are oriented toward open water.

Yet the area supports a wide variety of life other than invertebrates. Fish, especially mullet, are often seen. The author has seen many species

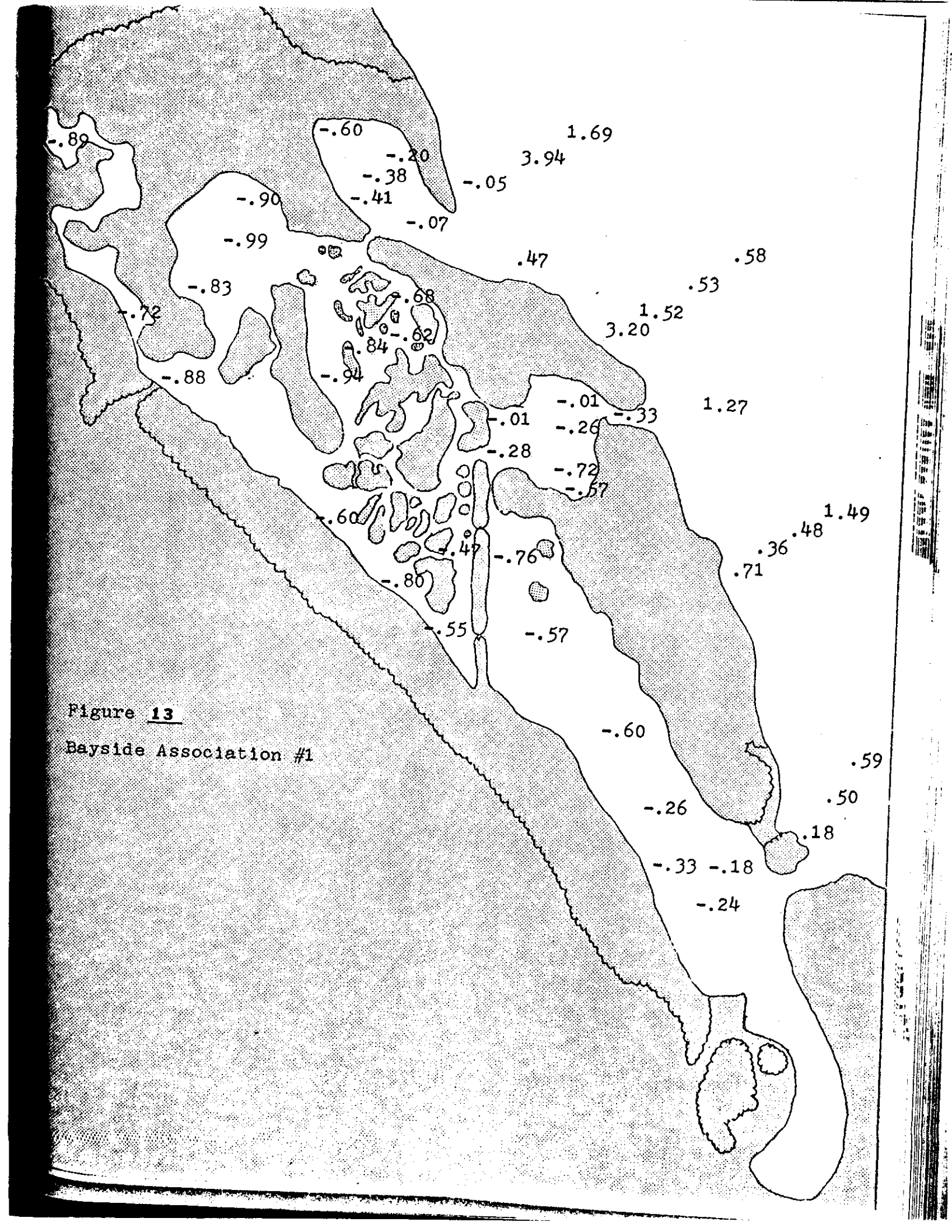


Figure 13

Bayside Association #1

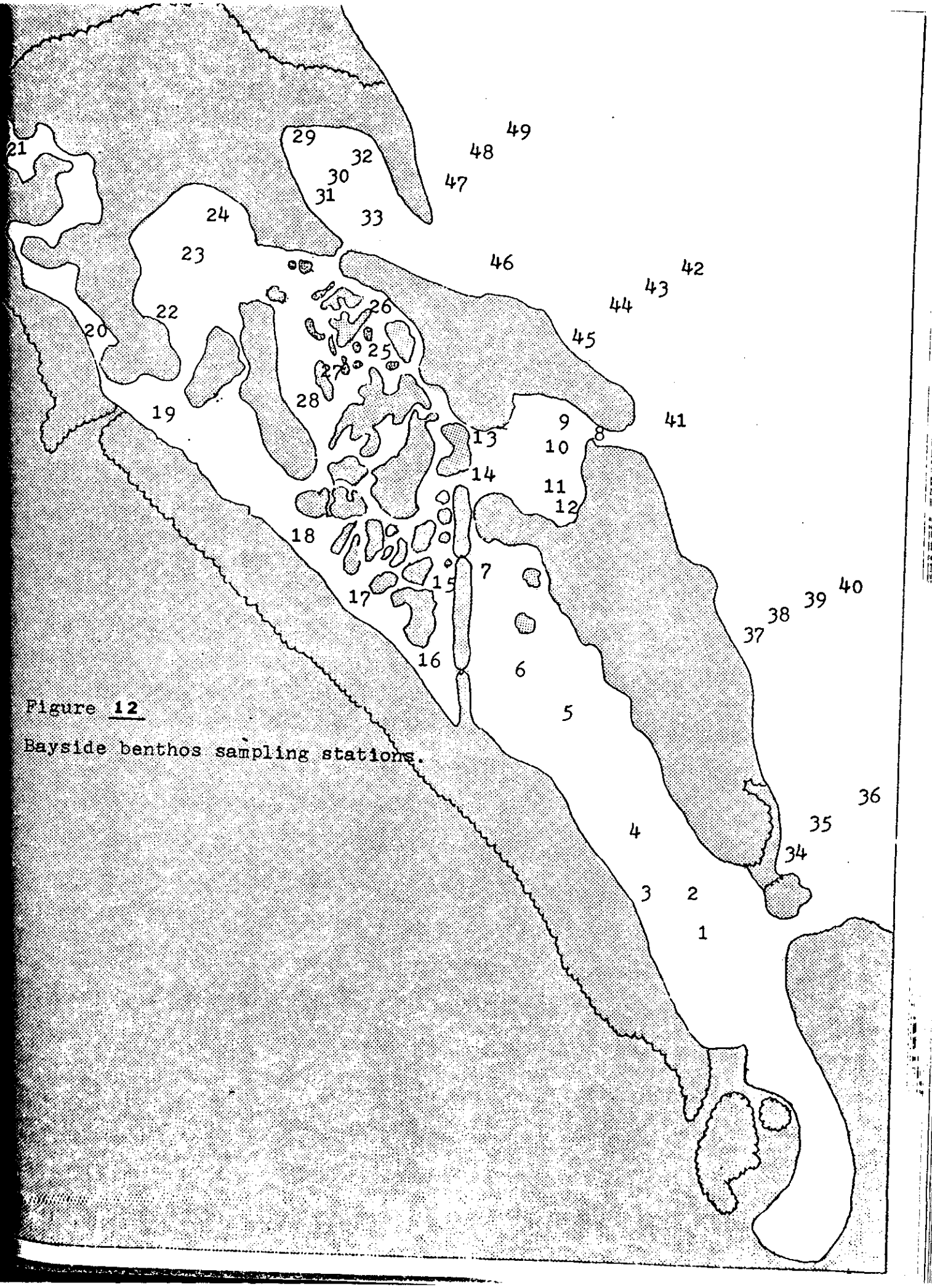


Figure 12

Bayside benthos sampling stations.

of birds at various times, including common and snowy egrets, white and wood ibises, little blue, great blue, green and Louisiana herons, black crowned and yellow crowned night herons, roseate spoonbills, as well as sundry collections of plovers, terns, sandpipers, gulls, pelicans, doves, and Lord knows what else. From time to time through the year blooms of the algae Gracilaria, Acanthophora, and Cladophora cover the bottoms of the interior lagoons.

In view of this and our general impression of the area, we would recommend only minor manipulation, carefully considered. The feeding habits of some birds and the high primary productivity of shallow lagoons would argue against any drastic changes in the water depth or current patterns in the swamp. However, as seen in Coconut Bayou, the increase in currents produced by a dredged channel of moderate depth lends itself to a rather rich, organized, and populous community. Therefore, it may in fact be desirable in this situation to effect an increase in water exchange with the bay by opening channels to open water. This would effect a deepening of the lagoons as fine sediments washed away. We feel that it is the lack of sufficient current conditions which leads to build-up of soft sediments, combined with the extreme ranges of environmental factors such as salinity, temperature, and bacterial populations that prohibits the macroinvertebrates' existence in the swamp. It must not be forgotten, however, that the invertebrates of our study are a single component of a much larger system. Manipulation in a natural system is in our opinion regrettable, but can at least be attempted with as much regard for the flourishment of life as possible.

5. Portofino

The study area which we refer to as Portofino (see Fig. 4 for location) consists of sandy beach and grass flat bordering on mangrove stands (Fig. 15). In 1960 the Board of County Commissioners of Charlotte County approved the establishment of a bulkhead line (Fig. 15) between three and four hundred feet offshore. In 1962 spoil was deposited in the intertidal area, and eight years later in 1970 the benthic invertebrates and marine grasses were sampled by John Morrill and Nancy Needham.

The spoil created an upland of approximately five acres, bordered by 2.7 acres of sandy beach. The spoil itself initially covered an area vegetated by Cuban shoal weed: fine silt runoff has covered former turtle grass beds with soft clay-like silt up to 18 inches in depth. These areas lie just off the spoil and to the south, and have been repopulated mostly by Cuban shoal weed. It would seem that the more slender leaves of the Cuban shoal weed make it a better colonizer of soft sediments than turtle grass. Almost all the turtle grass in the area lies outside of the bulkhead line.

Morrill and Needham suggested the existence of at least four distinct ecological zones at Portofino, namely intertidal sandy beach, a zone of short Cuban shoal weed (and small amounts of Ruppia maritima), a zone of tall Cuban shoal weed in slightly deeper water, and the turtle grass beds. Nineteen stations were selected representing all these zones.

Casual examination of the data shows Portofino to be quite rich in fauna. Each station possesses a relatively large number of species from the 60 or so found in the entire area. Twenty-five of these were included in the analysis.

Figure 15

Portofino

(note position of bulkhead with respect to turtle grass)

Table 8 — Associations: Portofino

Species	Feeding type	Factor Structure Vectors		
Anomalocardia cuneimeris	SF	.73	.01	.01
Anachis avara	C,S	-.70	-.04	-.03
Bulla occidentalis	C	-.67	-.24	.44
Battilaria minima	S	.09	.83	-.12
Cardita floridana	SF	-.69	-.32	.10
Cerithium floridana	S	-.42	.70	.08
Crepidula fornicata	S,SF	-.68	.09	-.41
Monilispira leucocyma		-.61	.20	-.55
Modulus modulus	S	-.83	.24	.16
Nassarius vibex	C,S	-.42	.61	.03
Olivella pusilla	C	-.17	-.16	.25
Phacoides nassula	SF	-.65	-.30	-.42
Prunum apicum	S,C	-.69	.27	.45
Tellina mera	SF&OF	.12	.36	-.56
Vermicularia fargoi	S	-.31	.47	.64
Cistenides gouldii	SDF	.09	-.16	-.03
Cirriforma filigera	SDF	-.58	.05	-.25
Diopatra cuprea	C,S	-.57	-.63	.21
Loimia medusa	SDF	-.39	.06	.54
Phascolosoma sp.	NSDF	-.32	.58	-.05
Bugula sp.	SF	-.49	-.24	.10
Ophiostigma isacanthum	NSDF	-.19	.54	-.32
Ophiophragmus sp.	NSDF	-.18	.30	.22
Hermit crabs	S	-.66	-.25	-.32
Crabs	S	-.65	-.43	-.35
Variance of components =		6.96	3.81	2.68
Sum of variance = 54% total				

Table 9 - Correlations of environmental variables with components: Portofino.

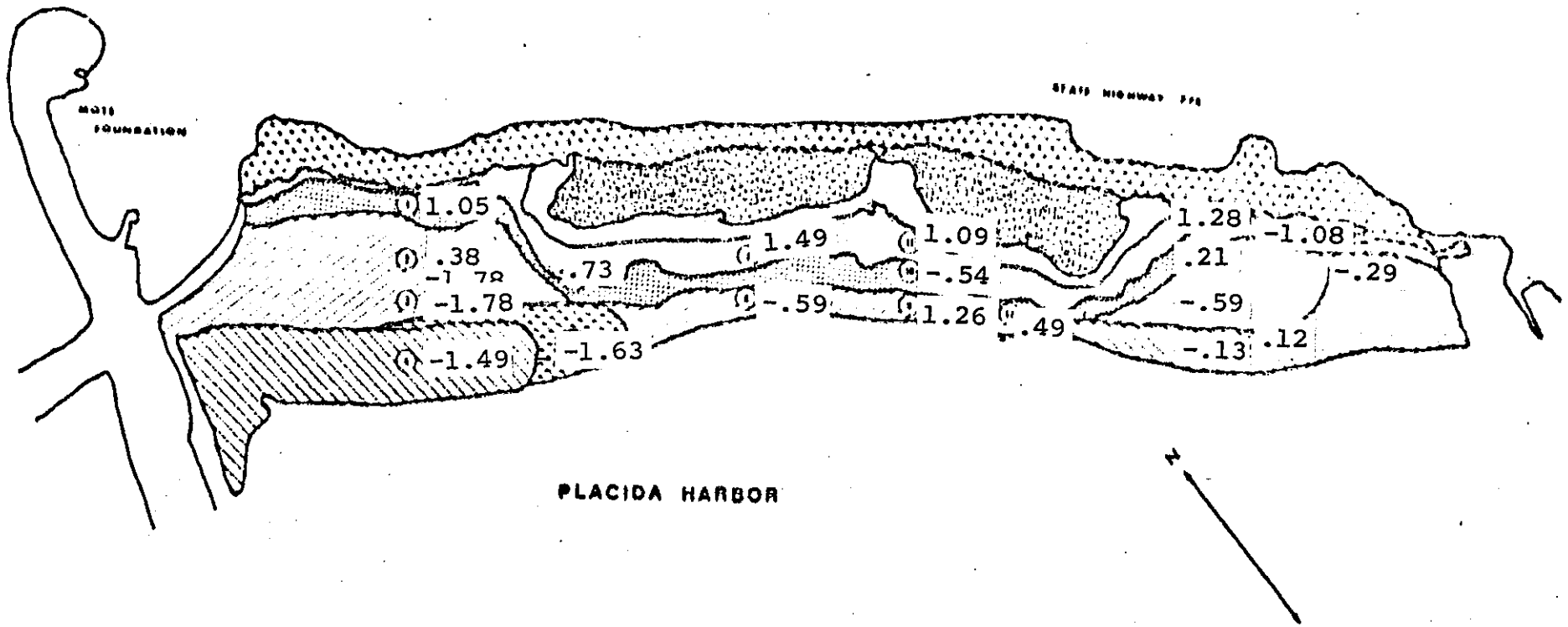
	Components		
Grass species	1	2	3
Thallasia testudium	-.41	-.40	.13
Diplanthera wrightii	.00	.36	-.01
Total grass biomass	-.46	-.25	.06

Examination of the factor structure matrix clearly shows that there are at least three distinct associations accounting for 54% of the total variance and 22 of the 25 species. The first three vectors of the factor structure matrix are shown in Table 8; Table 9 shows correlations of the grasses with these components.

The first association includes 13 species, all similarly weighted except Anomalocardia. All feeding types are represented. This is a turtle grass association, at least in terms of response to changes in biomass, since it shows no correlation with shoal weed even though many of its species occur there. Correlation with total grass biomass is somewhat higher than for turtle grass alone, indicating some orientation to the general grass habitat. Anomalocardia has a preference for upper and intertidal zones. Distribution of the association is shown in Fig. 16.

The second association contains 6 species, again all alike in weighting except one, this time the polychaete Diopatra. Correlations strongly suggest this to be a shoal weed association. Diopatra is a bridging species from association #1 and probably accounts for some of the negative correlation with turtle grass. This association is comprised of rather motile, scavenging organisms. Its distribution is seen in Fig. 17.

Association #3 would appear to be minor, consisting of three fairly infrequent species and showing no correlation with the grasses. However, examination of Fig. 18 shows quite different scores for similar areas north and south of the spoil zone suggesting an effect of the sediment character or distribution. We can detect for the first two associations no such effect that cannot be explained in terms of grass changes. This



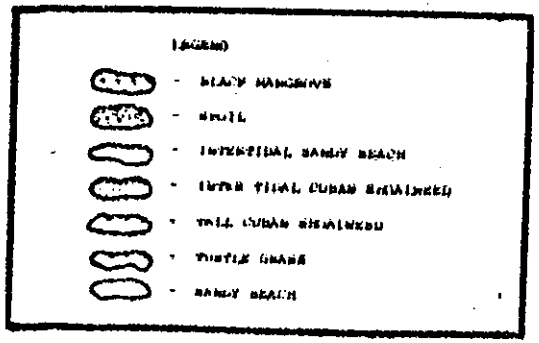
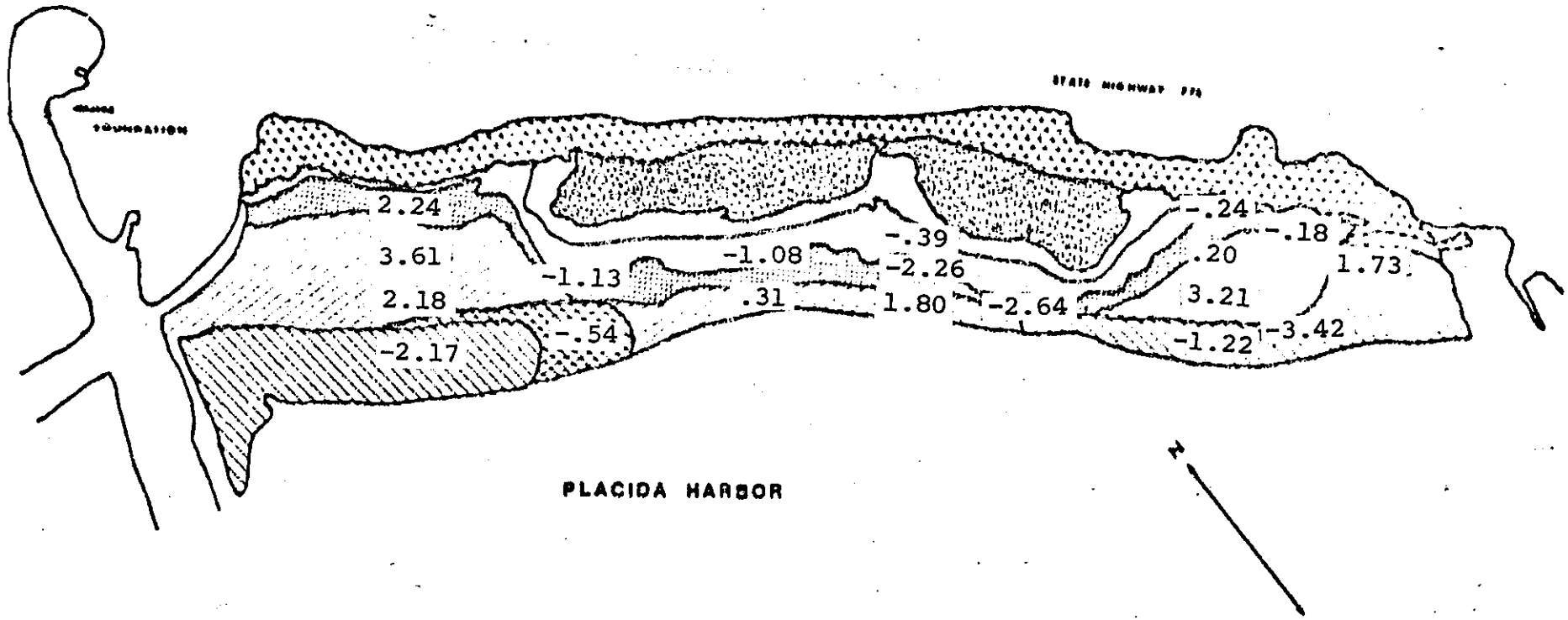


Figure 16

Association #1



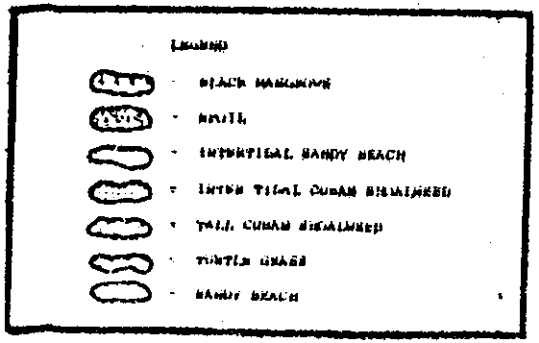
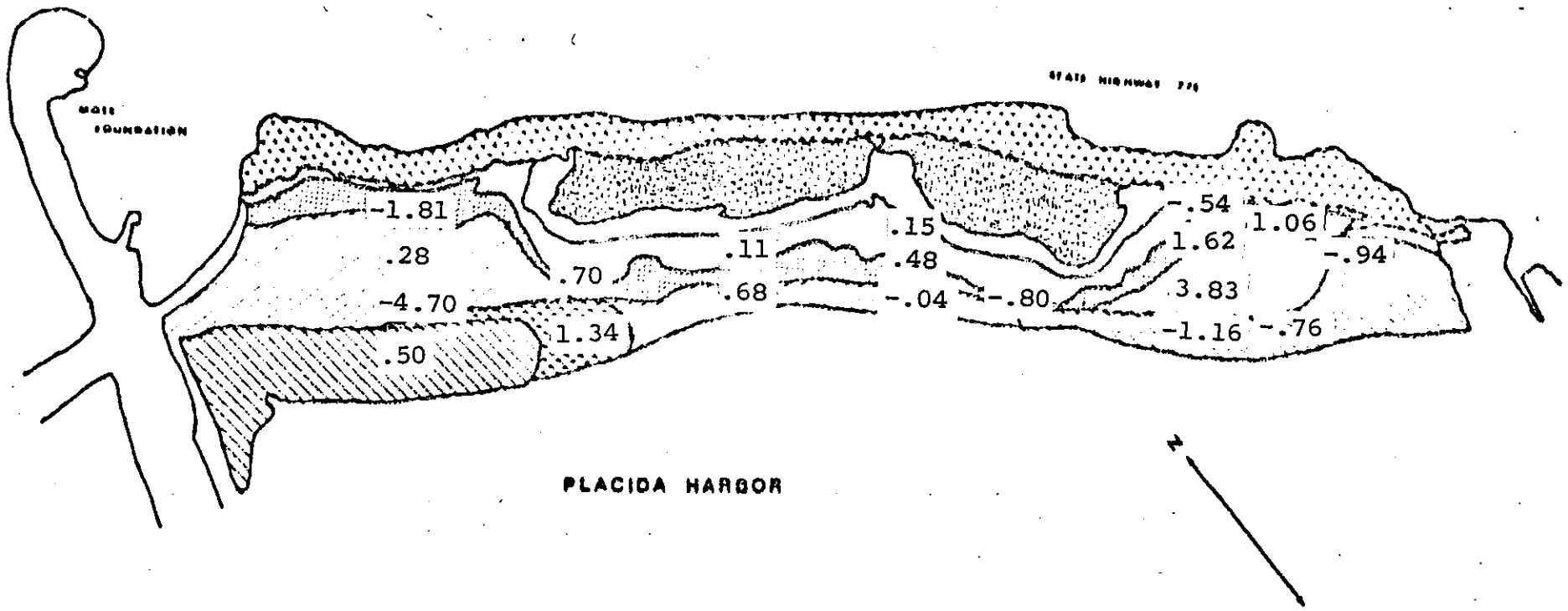


Figure 17

Association #2



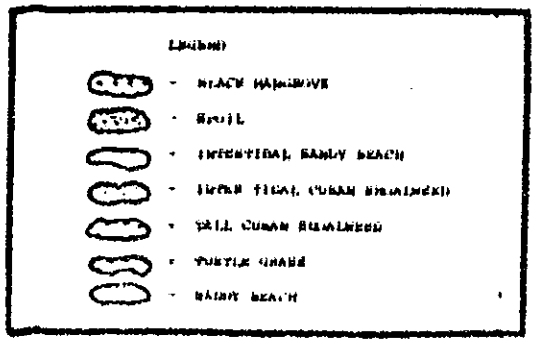


Figure 18

Association #3

association is bridged with the first, at least, by the mollusc Monilispira.

The three species unaccounted for by the first three factors appear in components 5 and 6, statistically significant but of questionable ecological importance.

Portofino, then, is a rich, fairly well organized comminity of grass and sand habitats. Each species of grass has its own association, with the deeper water turtle grass association perhaps dominant. Compared with the grass flats off Bayside, Portofino shows a good deal more organization, in terms of partitioning the habitat and resources, as well as the higher percentage of species existing in associations, and the clear bridges between associations. All in all, an area of reasonable health, probably better off without the spoil but showing the potential for recovery.

6. In addition

We have subjected the data of Bloom, Simon, and Hunter (1970) to the same analysis as our own data, with the following results. Their study area consisted of non-vegetated sediments of various character. Stations were established on three transects at upper, middle, and lower tidal zones, and sampled at times roughly reflecting fall, winter, and spring conditions. Thus there were nine stations with 27 observations. Of almost 60 species found, 22 were included in the analysis.

The animal community appears to consist of four associations, accounting for 21 of 22 species and 58% of the variance. The remaining species, Scoloplos rubra, might reasonably be included with the third association since its correlation with this component is only slightly less that the species' maximum, though low for the association itself. The first four vectors of the factor structure matrix are shown in Table 10. Table 11 presents correlation of the first four components with sediment conditions.

We note here that these correlations are between components and the untransformed variates consisting of the mean particle size in phi units, the sorting coefficient (a measure of distribution of particle sizes), and the percentage weight of each fraction of the sediment. Percentage data is often subjected to an arcsin transformation (see Sokal and Rohlf, 1969; for applied instance, see Cassie and Michael, 1968), which corrects for deviation from normality among the higher and lower percentages. We have calculated correlations both with and without transformation and find the pattern and magnitude of the coefficients to be essentially the same.

TABLE 10 - Associations: Bloom, Simon, and Hunter

Species	Feeding type	Factor Structure Vectors			
Ophiophragmus filograneus	NSDF	.12	.45	.55	.17
Ptchodera sp.	NSDF	.31	.61	-.07	-.07
Rhynchocoel	C	-.51	.42	-.32	.01
Branchiostoma caribaeum	SF	.55	.56	.06	-.25
Arabella iricolor	C	.02	.01	.67	.28
Clymenella muscosa	SDF	-.48	-.07	.46	-.06
Diopatra cuprea	C,S	-.54	.27	.31	-.52
Glycera americana	C,NSDF	-.53	-.06	.70	.09
Onuphis eremita oculata	NSDF	-.84	.07	.40	-.02
Pectinaria gouldii	SDF	-.65	-.21	-.19	-.17
Scoloplos rubra	NSDF	.25	.21	.39	.22
Amphipoda	S	-.11	.70	-.15	.36
Pinnixia sp.	S,C	.03	.78	.01	-.22
Shrimp	S,C	-.13	.04	-.46	.53
Upogebia affinia	SF	-.56	.25	-.23	.05
Bittium varium	S	.05	.36	-.15	.54
Ensis minor	SF	-.62	.23	-.04	-.09
Macoma constricta	SDF	-.55	.05	-.59	.10
Nassarius vibex	S,NSDF	-.25	.45	-.20	.65
Prunum apicum	S,C	-.11	-.30	.46	.65
Tagelus divisus	SDF	-.16	-.66	-.42	.05
Tellina tampaensis	SF	.13	-.50	.12	.39
Variance of the components =		3.81	3.55	3.12	2.31

Sum of variances = 58% total

Table 11 - Correlations of environmental variables with components: Bloom, Simon, and Hunter.

	Components			
Sediment characteristic	1	2	3	4
Mean particle size	.07	-.21	.24	.18
Sorting coefficient	-.16	-.26	-.05	.23
%wt. -2 to -1 phi	.25	-.21	-.07	-.10
" -1 to 0 "	-.31	-.01	-.32	.05
" 0 to 1 "	-.54	.27	-.25	.01
" 1 to 2 "	-.27	.25	-.10	-.03
" 2 to 3 "	.15	.05	-.03	-.12
" 3 to 4 "	.14	-.13	-.02	.00
" 4 to --	-.04	-.26	.38	.47

The first association consists of at least the seven species which receive their highest weighting in the first component, with the possible addition of two bridging species included in other associations. It is correlated with the smaller particle sizes centering around the 0-1 phi fraction. The first association is linked to the second via Branchiostoma and the third by Macoma and possibly by a lesser degree by Glycera. The association contains a variety of feeding types and phyla, indicating a general attack on the habitat.

The second association, which contains six species, seems rather more complex. It is divided into groups of four and two species of interesting feeding type, but rather uncorrelated with the sediments. There is a weak tendency to be negatively correlated with the extremes of particle size and positively correlated with the mid-range. The division into two subassociations is based on two phenomena. In the case of Branchiostoma and Tagelus, the species have partitioned the habitat in some way and do not overlap in space. However, the amphipoda and Tagelus do overlap considerably but have an inverse relationship, due to some form of competition or mutual avoidance. We judge at least that the basis for the distribution of this association is not sediment characteristics.

Association #3 consists of four species, one (Macoma constricta) of opposite sign and bridging tendencies. Feeding types lean toward carnivorous and deposit feeding. There is quite a definite trend in correlation with sediments; values are positive for the above four phi fraction, increasingly negative as one proceeds to the smaller particle sizes.

The organisms of the last association are all carnivores or scavengers and are strongly correlated only with the largest particle sizes.

Site groups and possible seasonal effects are more difficult to establish than species groups. Since Bloom, Simon, and Hunter do perform a Q-type analysis, we have attempted in Fig. 19 to illustrate ecological distances between stations based on the factor scores for the first two associations.

Stations appear to resemble themselves through the year more than they resemble any other site. The change from winter to spring would seem more drastic than from fall to winter. There are definite trends in the seasonal changes, but they are not constant. For instance, at transect #1 the upper and middle stations tend to become more negative to the first association (indicating an increase in the negatively weighted dominants), while the lower station becomes more positive. We hesitate to speculate on so few observations, but it may be that some sort of complex shifting of species occurs throughout the year that more extensive observations and principal component analysis could distinguish. Certainly there are patterns in the spatial distribution of organisms in the current study, but we leave these to the imagination of the interested reader. We list complete factor scores for all associations in the appendix for your amusement.

One thing we would like to point out is the absence of any inverse relationship between suspension and deposit feeding organisms in our analysis. Frankly, although we do not doubt the validity of the relationship

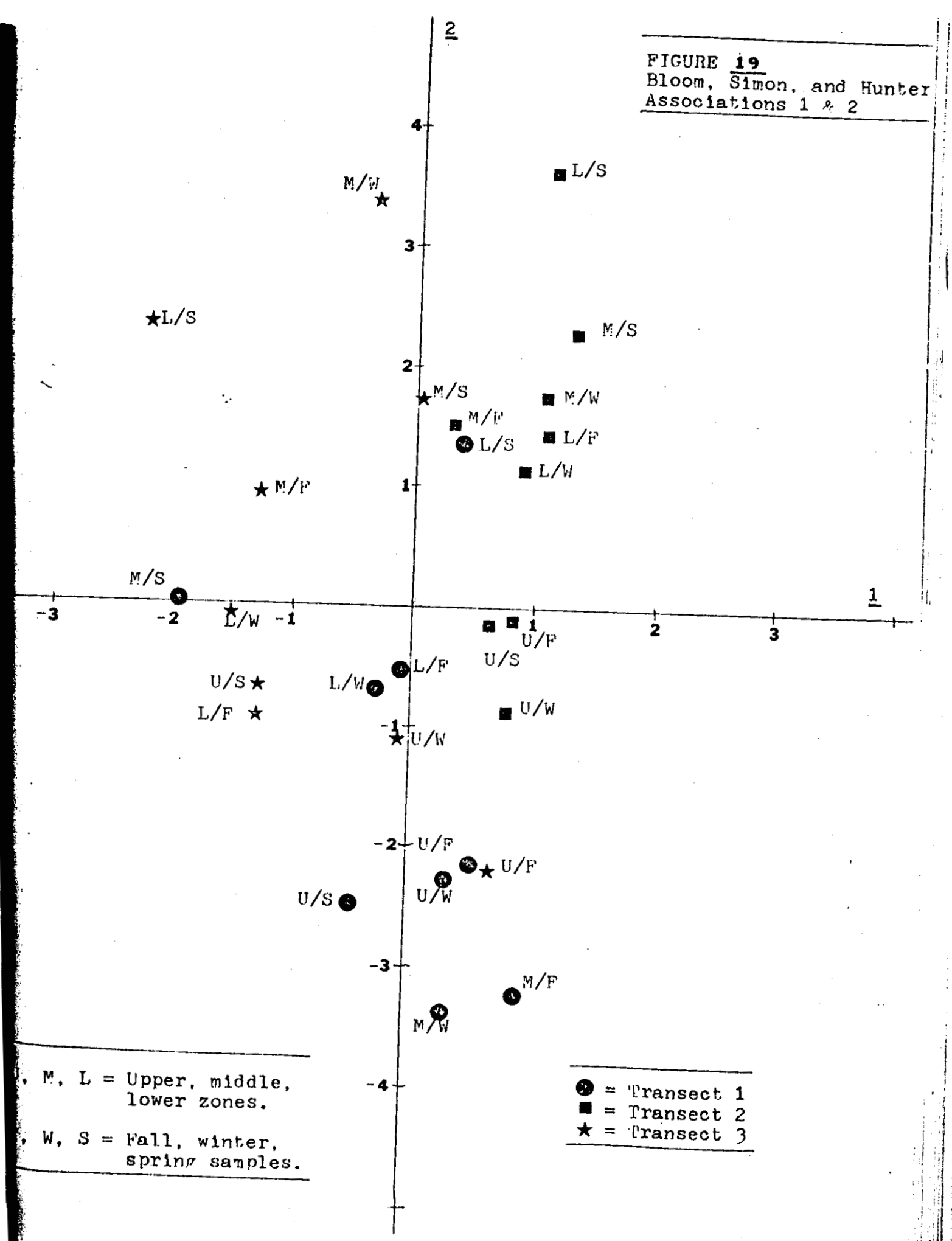


FIGURE 19
Bloom, Simon, and Hunter Associations 1 & 2

, M, L = Upper, middle, lower zones.

, W, S = Fall, winter, spring samples.

● = Transect 1
■ = Transect 2
★ = Transect 3

on the large scale, we do not feel it to be as significant in the partitioning of small scale habitats. Such biological interaction is not the underlying basis for distributions, though they may often occur due to other factors.

Part 3 - Analysis of Chemical Data

In the summer of 1972 the author conducted assays for ten chemical or hydrographic parameters of water samples from the Sarasota area. The samples were taken from three areas already discussed: Coconut Bayou, Heron Lagoon, and Bayside development, as well as the Grand Canal. The Grand Canal is a relatively deep dead end canal system, the mouth of which is located between Coconut Bayou and Bayside. In addition, several reference samples were taken from open bay and gulf waters. The raw data used in the following study will be found in the appendix. In all, 71 observations were considered, after stations with missing data were eliminated.

Salinity was measured with a hydrometer, dissolved oxygen with a standard polarographic cell, pH was measured both in the field with the Hydrolab, and in the lab with a Corning Model 12 Research pH meter. Strickland and Parsons (1968) provided the methods to calculate dissolved CO_2 from alkalinity, and measure concentrations of inorganic phosphate, nitrate, and nitrite in 0.8 micron Millipore filtered samples. Chlorophyll a was measured in an extraction with 90% acetone using the SCOR/UNESCO equations for converstion. Dissolved organic phosphate was determined by difference after all phosphates in the filtered sample had been transformed to the inorganic form by oxidation with persulfate according to the method of Menzel and Corwin (1965). This last technique, by the way, is a great deal more comfortable than the more drastic methods of sulfuric-nitric or perchloric acid digestion, and yields comparable results at least on filtered samples. All optical measurements were made on a Gilford 240 spectrophotometer.

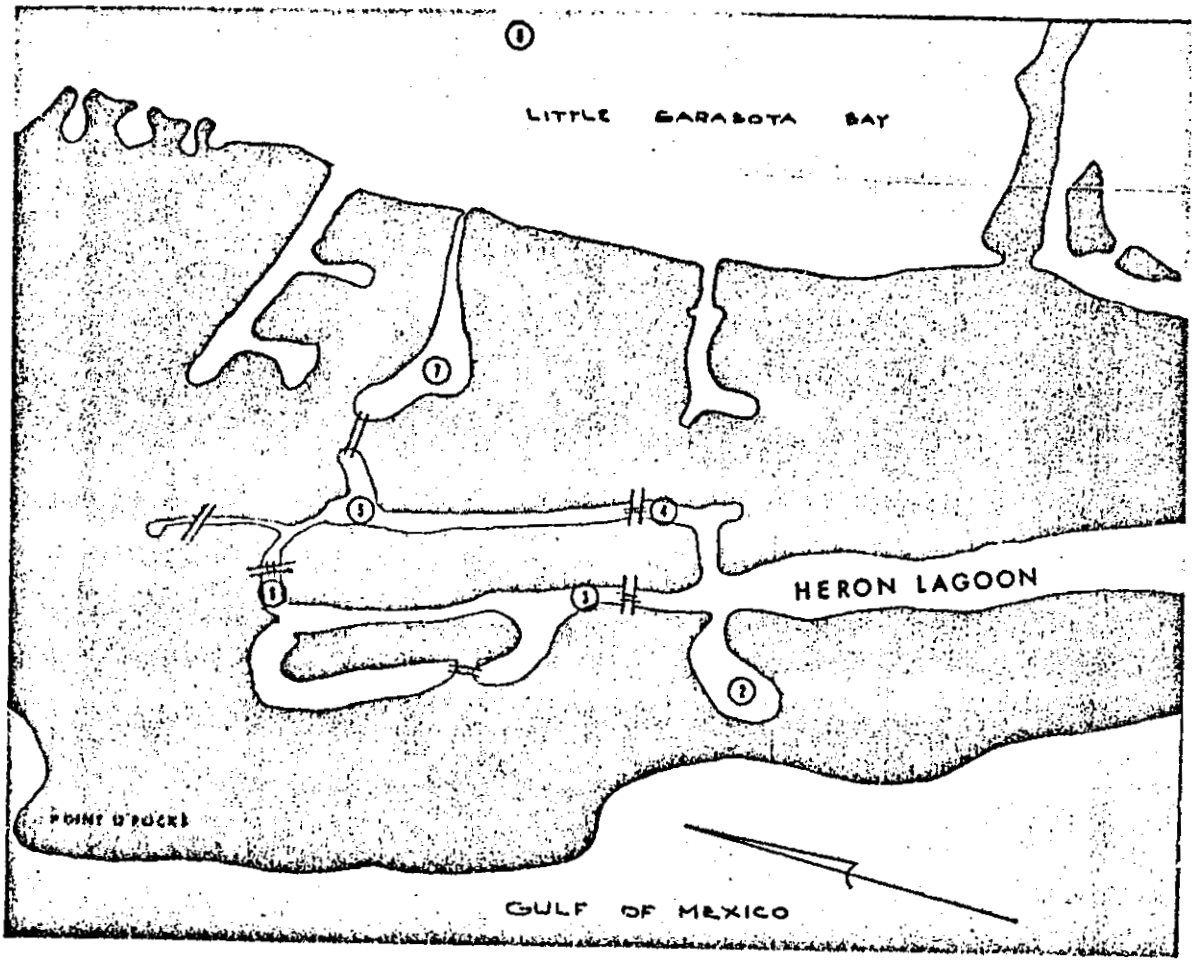


Figure 20. Chemical sampling stations.

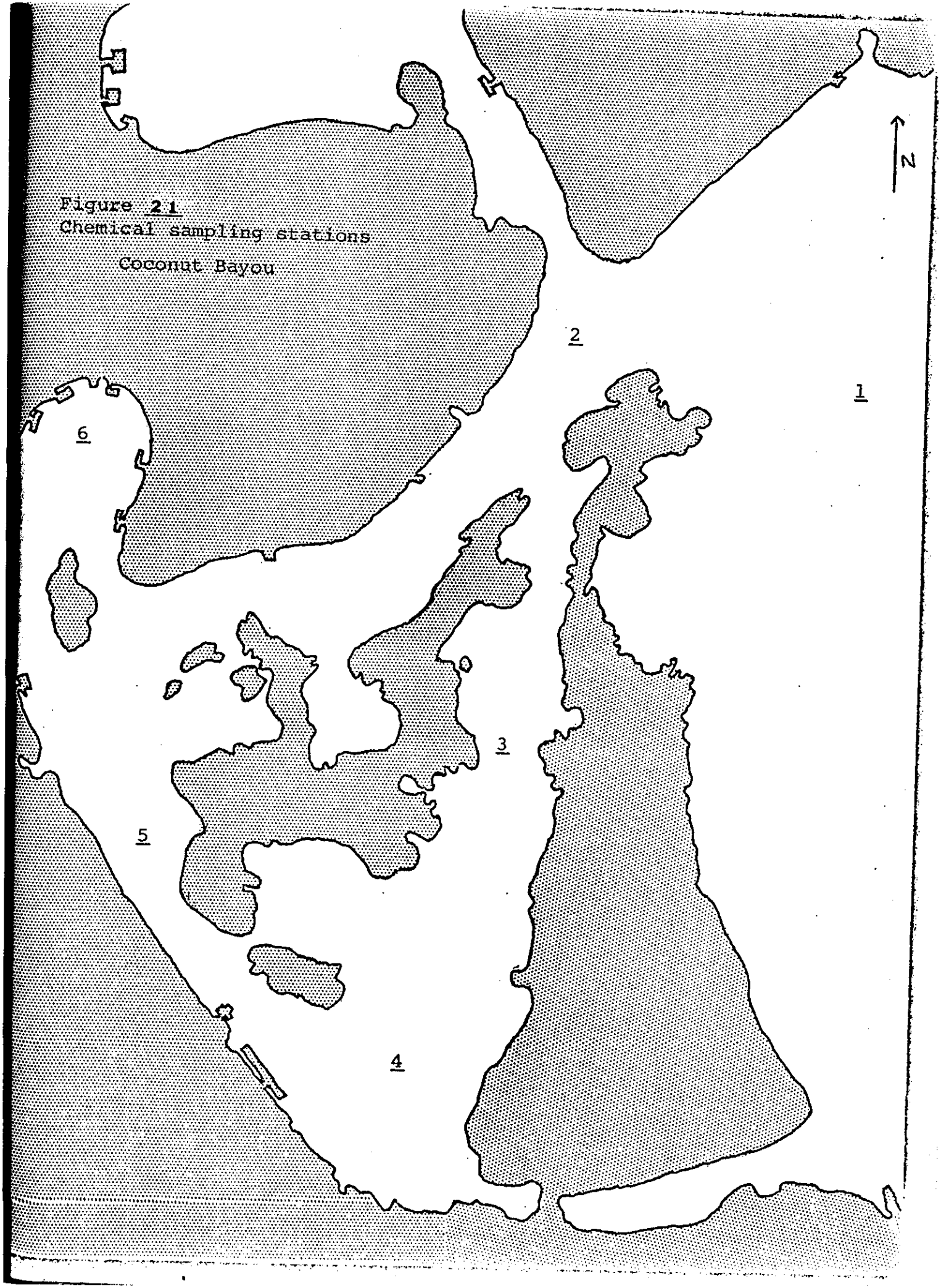
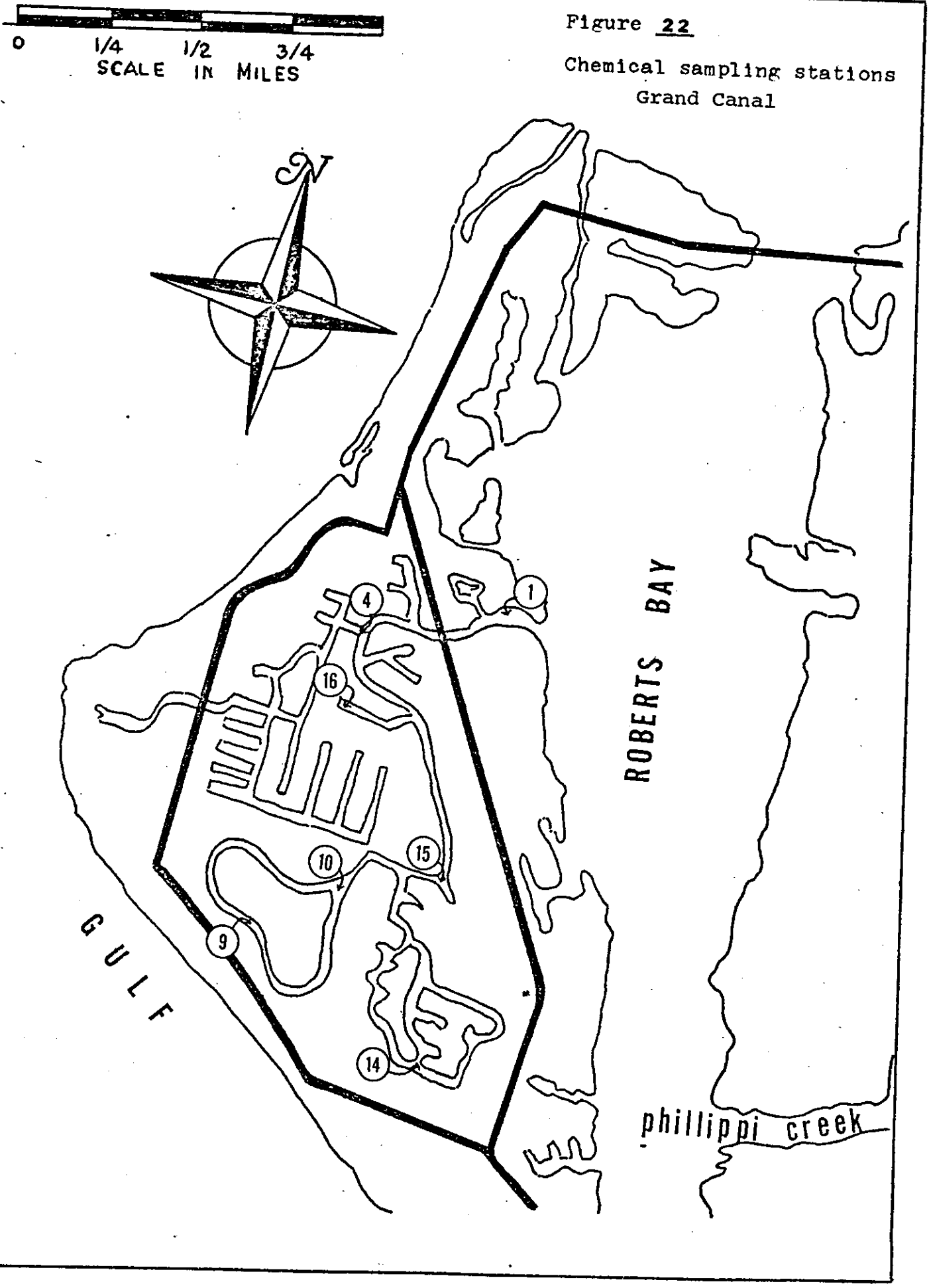


Figure 21
Chemical sampling stations
Coconut Bayou

Figure 22

Chemical sampling stations
Grand Canal



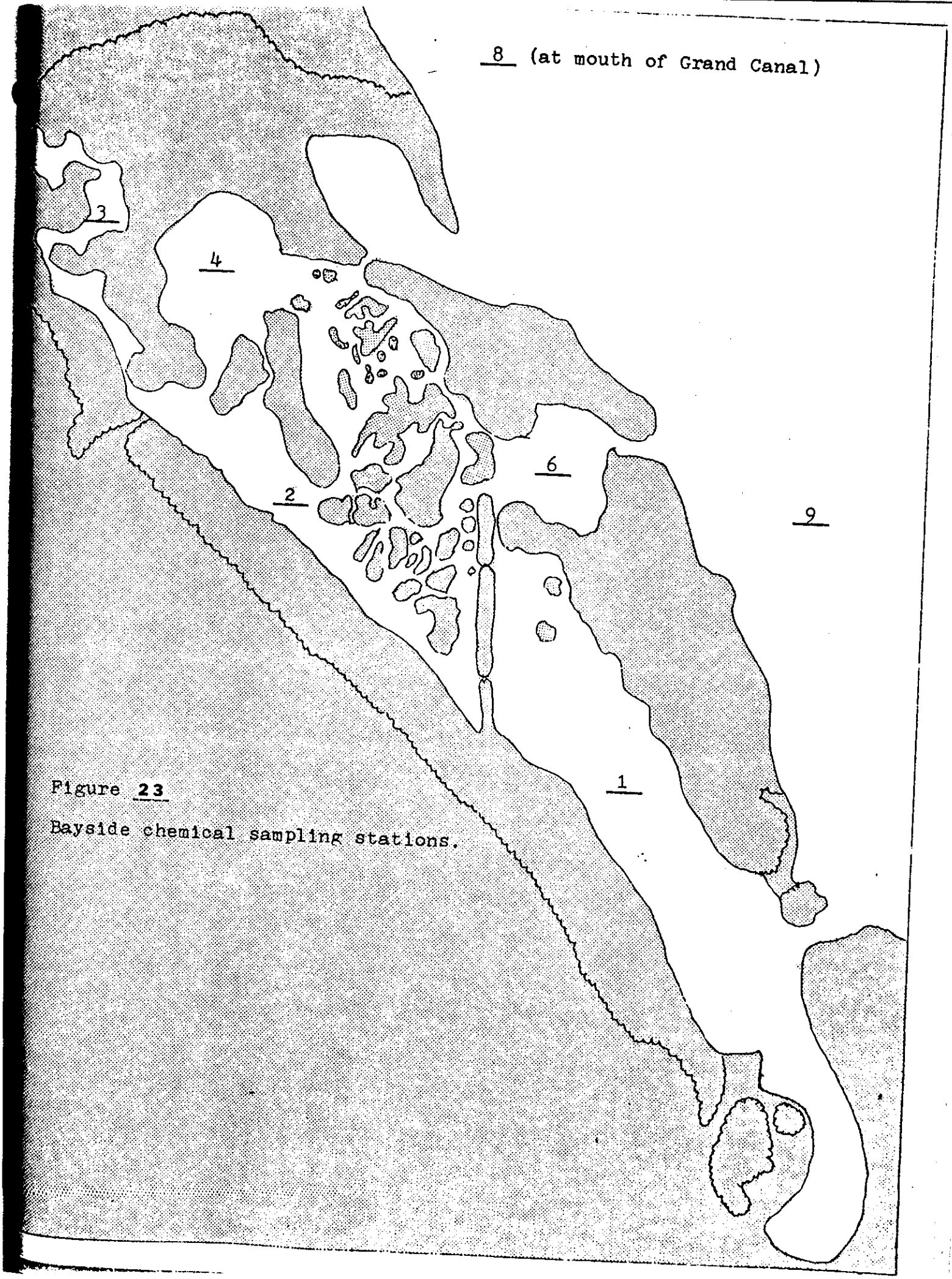


Figure 23

Bayside chemical sampling stations.

The 71 observations from the four areas were used to calculate a product-moment correlation coefficient matrix, from which the principal components were generated. Analysis was performed both on the raw data and log transformed data. A log transformation, in addition to the properties discussed in Part 1, will change a multiplicative or exponential model to the additive one required by correlation. For example, the model presented in numerous basic texts of ecology lists

$$c = Ae^{Bx}E,$$

where c is an estimate of the abundance of an organism and x is an environmental variable, and A and B are constants, while E is the error term. This is equivalent to the transformed model

$$\log c = \log A + Bx + E,$$

which satisfies additive requirements. Unfortunately, we have no real evidence it applies to our situation.

The complete correlation matrices and the first five vectors of the facture structure matrix for raw and transformed data are shown by Tables 12, 13, 14, and 15.

The most obvious relationships exist among alkalinity, pH, dissolved oxygen and carbon dioxide: inverse functions between alkalinity and CO_2 and pH and O_2. Of interest is the extremely high correlation (.95) of the log of pH with the log of CO_2. Almost as high (-.83) is the correlation of O_2 with CO_2. Correlations are only slightly lower for raw data. From a purely pragmatic standpoint, pH and DO, which are easily measured in the field, seem to be excellent predictors of carbon dioxide concentrations, which require more elaborate procedures

Table 12 - Factor Structure Vectors: Chemical data, untransformed

	1	2	3	4	5
Salinity	.09	.86	-.03	.08	.27
Alkalinity	.64	-.45	-.43	.20	.21
pH	-.84	.39	-.20	.16	-.07
CO_2	.80	-.47	.00	-.10	.17
O_2	-.87	.11	-.14	.22	.19
Inorganic PO_4	-.47	-.74	.39	-.12	-.18
Organic PO_4	-.12	-.61	-.32	.65	.00
$NO_2 + NO_3$	-.28	-.42	.74	.26	.31
Chlorophyll a	-.50	-.59	-.40	-.28	-.24
Particulate matter	-.52	-.34	-.25	-.42	.58

TABLE 13 - Correlations, untransformed data: Chemical stations

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. Salinity	1.00									
2. Alkalinity	-.26	1.00								
3. pH	.24	-.58	1.00							
4. CO_2	-.28	.69	-.87	1.00						
5. O_2	.04	-.45	.81	-.68	1.00					
6. Inorganic PO_4	-.70	-.19	.03	-.03	.20	1.00				
7. Organic PO_4	-.44	.39	0.00	.13	.17	.31	1.00			
8. NO_2 + NO_3	-.28	-.15	-.04	-.02	.19	.63	.20	1.00		
9. Chlorophyll a	-.52	.03	.22	-.13	.31	.60	.37	-.01	1.00	
10. Particulte matter	-.23	-.07	.25	-.14	.43	.35	.11	.16	.51	1.00

TABLE 14 - Factor Structure Vectors: Chemical data, log transformed.

	1	2	3	4	5
Salinity	-.47	.72	.17	.19	.19
Alkalinity	.72	-.03	.21	.49	.10
pH	-.93	-.23	.08	.03	-.11
CO_2	.96	.16	.00	-.01	.10
O_2	-.83	-.30	.15	-.05	.01
Inorganic PO_4	.38	-.68	-.35	-.42	-.05
Organic PO_4	.23	-.47	.65	.28	-.41
$NO_2 + NO_3$	.22	-.03	.65	-.69	.10
Chlorophyll a	-.01	-.87	-.20	.21	-.04
Particulate matter	-.13	-.71	.21	.16	.60

TABLE 15 - Correlations, log transformed data: Chemical stations

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. Salinity	1.00									
2. Alkalinity	-.24	1.00								
3. pH	.23	-.57	1.00							
4. CO_2	-.31	.68	-.95	1.00						
5. O_2	.16	-.48	.83	-.79	1.00					
6. Inorganic PO_4	-.73	.05	-.22	.25	-.12	1.00				
7. Organic PO_4	-.31	.32	-.03	.10	-.02	.10	1.00			
8. $NO_2 + NO_3$	-.11	.01	-.16	.21	-.05	.14	.21	1.00		
9. Chlorophyll a	-.53	.06	.19	-.16	.20	.55	.33	-.20	1.00	
10. Particulate matter	-.28	.03	.23	-.19	.30	.25	.28	.05	.54	1.00

to measure. Ecologically, the apparently stable relationship of the two gases should permit small changes in their ratio, if sufficiently characterized, to distinguish differences in the quality and productivity of a station.

Salinity and inorganic phosphate show a significant tendency to vary inversely. When data from the separate areas are considered individually, the relationship always holds, even though sources may be different. For instance, the Skua sewage treatment plant on the Grand Canal (near station 15) is an obvious source of low salinity, high phosphate water. At Heron Lagoon it may be due to runoff from fertilized lawns, and Bayside may represent some natural condition, though its proximity to the Grand Canal might lead to some underground seepage. Although our data are from summer months only, analysis of data from the Bradenton County Health Department collected throughout several years from a variety of locations in the Bradenton area tends to support the existence of the relationship. There is, however, an extremely strong seasonal effect, coinciding perhaps with changes in rainfall. Nevertheless, the inverse function of salinity and phosphate exists, and much useful work might be done in distinguishing the various sources.

Another apparently valid relationship exists between chlorophyll and particulate matter, which are seen to vary for the most part in a direct manner: increases in one marked by increases in the other. Still, judging from components of data from the separate areas, there also exists an inverse relationship which might be expected on grounds

of turbidity. There might exist statistical methods for distinguishing the functions, but this seems premature. The author feels that no intelligent use of mathematical models of this situation can be made until the sources of chlorophyll and their significance have been identified, at least by qualitative microscopic examination.

By combining data from all areas studied, we limit ourselves to those relationships among the variables which are fairly constant in different situations. Although we did attempt an analysis of single areas, we felt that differences in sampling time and tidal conditions, for example, made comparisons between areas unwarranted. These analyses do suggest that functions described for the whole may not exist or may exist in varying degree when considered for limited areas. The quantitative relationships among water quality parameters have been explored for many years. Principal components, though we do not think it has ever been applied to such data, probably represents a method best used in only preliminary stages of investigation. It is, however, an excellent method of mapping areas based on measured parameters; Figs. 24, 25, 26, 27, and 28 show the distances between stations of the various areas based on the first two principal components. We leave it to the interested to explore the significance of the plots.

Positive values on the horizontal axis indicate a predominance of carbon dioxide in the sample, negative indicates oxygen predominates. On the vertical axis positive values occur in high salinity, low PO_4--chlorophyll samples, negative scores indicative of the inverse situation.

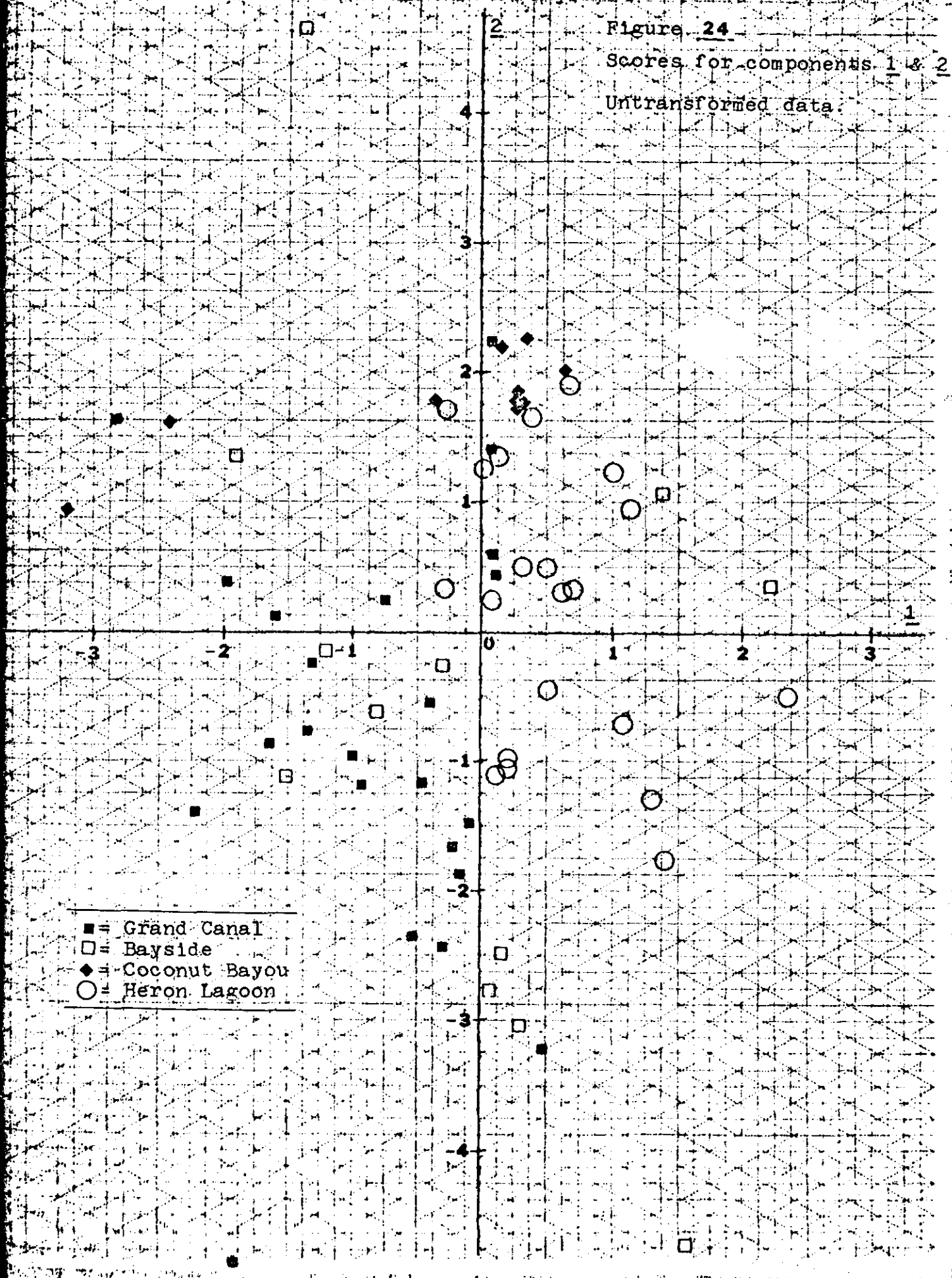
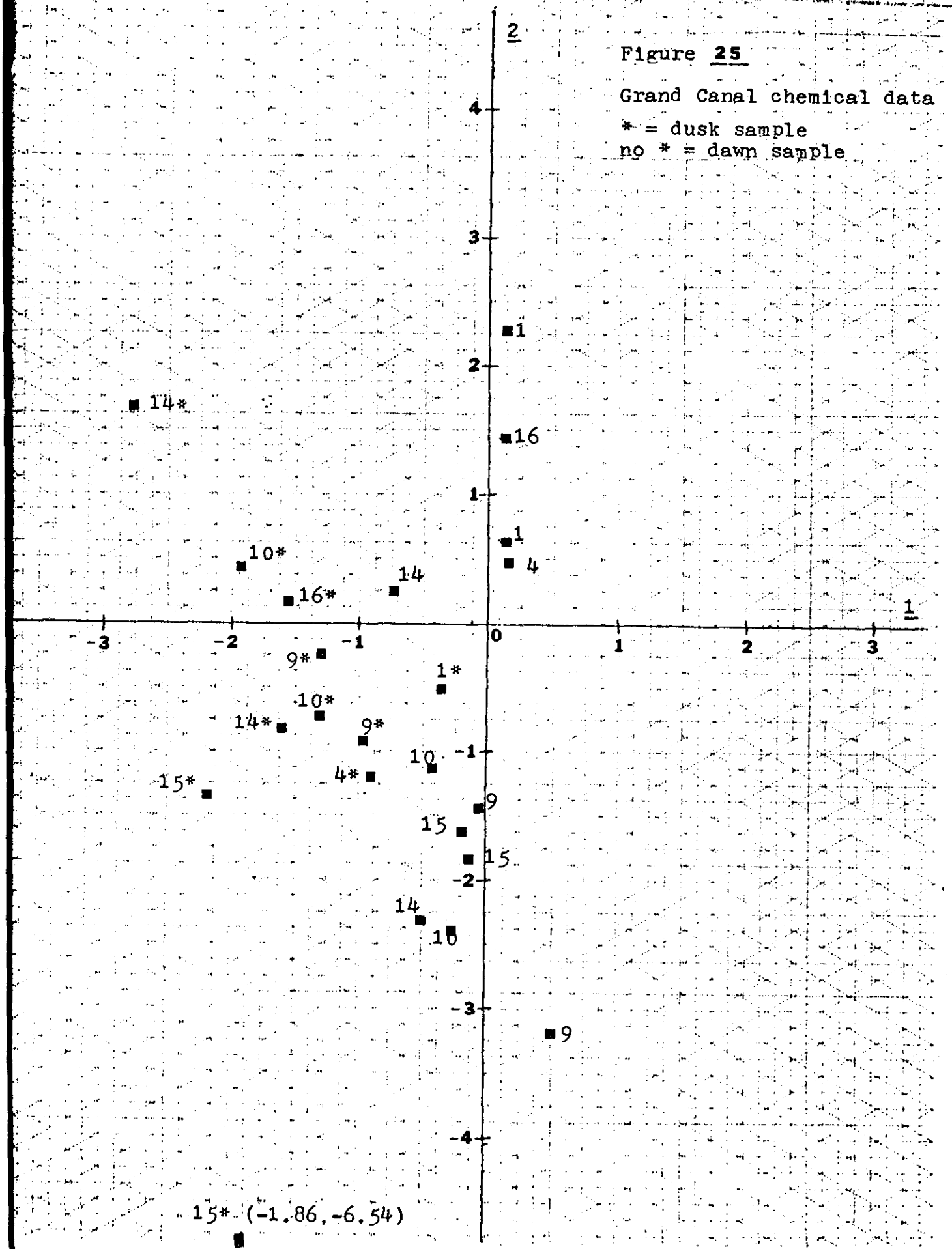


Figure 24

Scores for components 1 & 2

Untransformed data


2
1
Figure 25
Grand Canal chemical data
* = dusk sample
no * = dawn sample
4
3
2
1
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
14*
10*
16*
14
16
1
1
4
9*
1*
10*
14*
9*
10
4*
15*
9
15
15
14
10
9
15* (-1.86, -6.54)

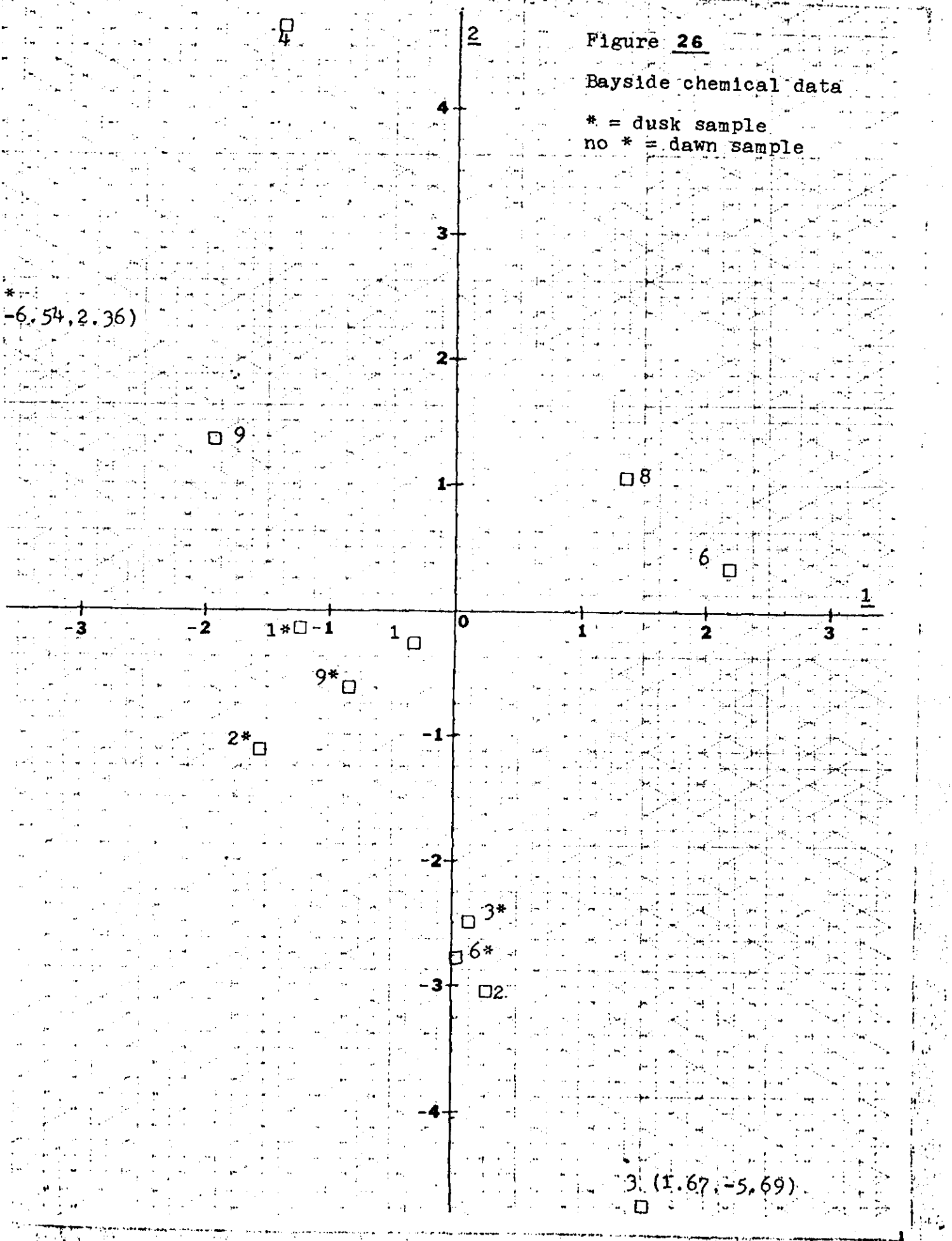


Figure 26
Bayside chemical data
* = dusk sample
no * = dawn sample
4
2
4
3
*
-6.54, 2.36)
2
9
8
1
6
1
-3
-2
1*
-1
1
0
1
2
3
9*
2*
-1
-2
3*
6*
-3
2
-4
3 (1.67, -5.69)

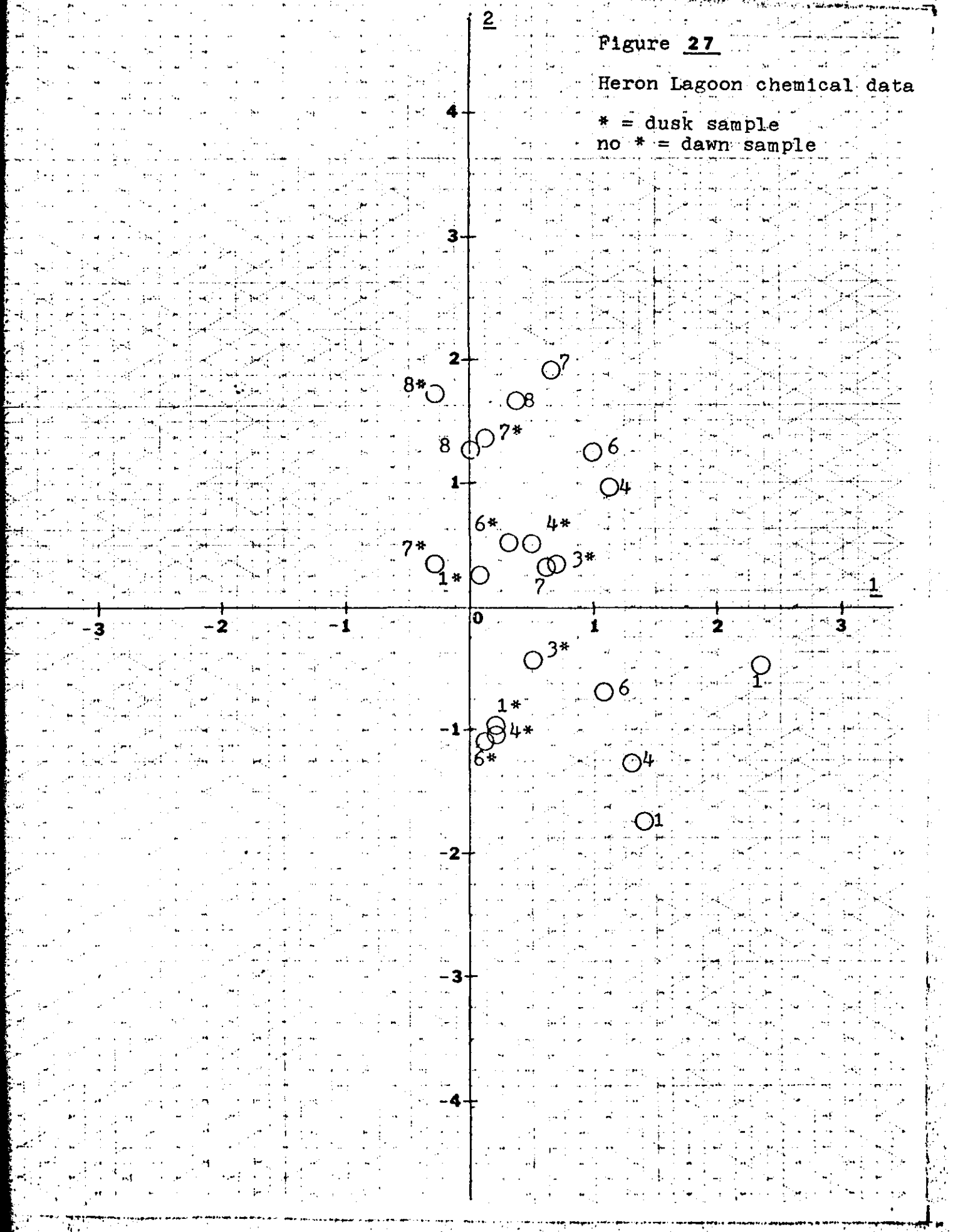


Figure 27

Heron Lagoon chemical data

* = dusk sample
no * = dawn sample

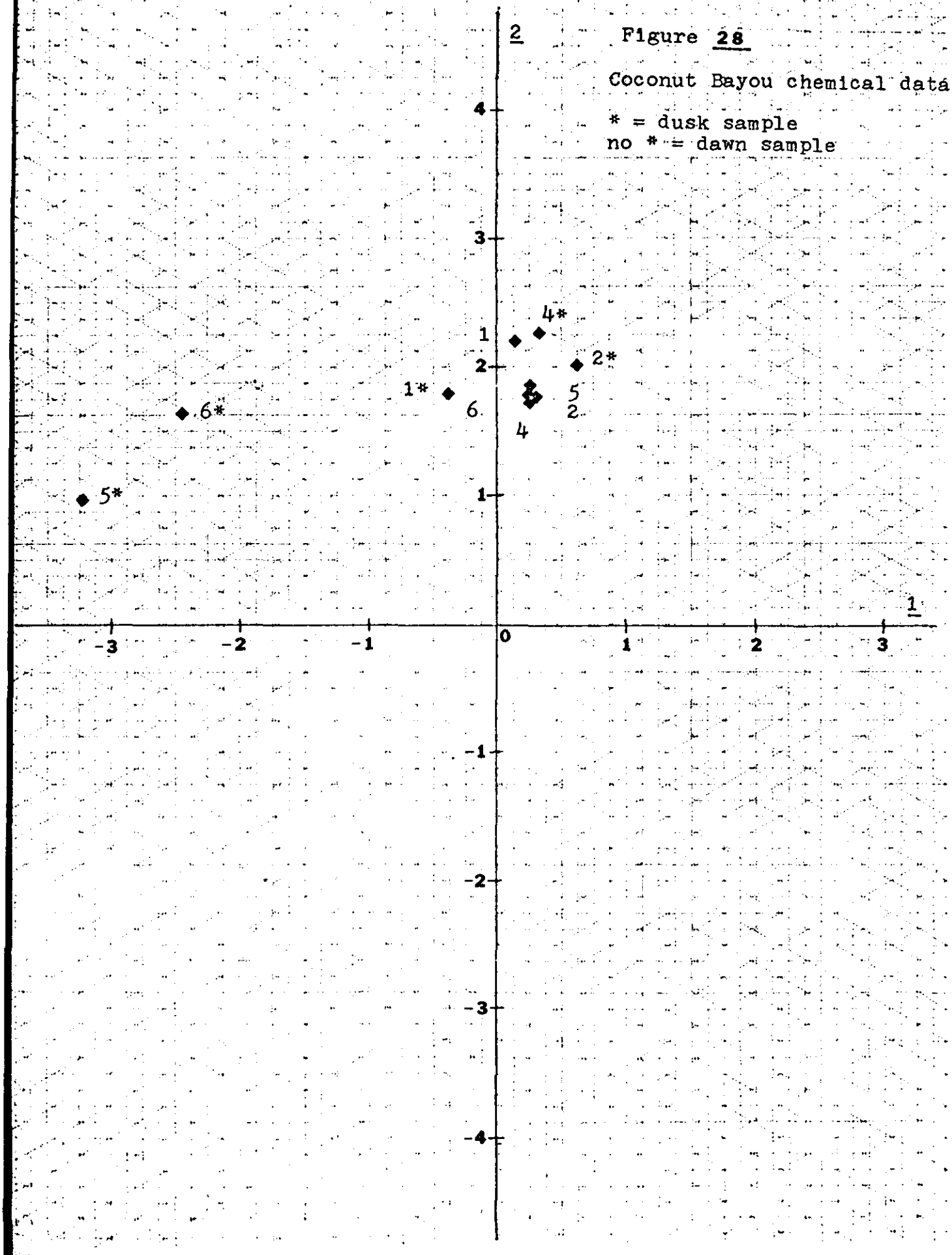


Figure 28

Coconut Bayou chemical data

* = dusk sample
no * = dawn sample

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