COMPUTER ANALYSES OF PETERSEN'S ORIGINAL DATA ON BOTTOM COMMUNITIES

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Abstract

Petersen-type bottom communities (a concept based on Petersen's 1914 data) are characterized by constant species which are dominant in terms of numbers and weight. Some workers recently have questioned the existence of these communities, in which quantitative data upon very few of the species present have been analyzed subjectively, and other potentially important species have been neglected. Various computer techniques were used to analyze Petersen's data. For the majority of species only presence-absence data can be used; for quantitative data 88 species from 193 stations were processed. The final methods involved transformed data of numbers and weights, respectively, the Canberra metric coefficient, and a combination of flexible and group-average sorting followed by allocation. The presentation of results is difficult because, even after classification, the complexity of the data—for example, the lists of species of different grades of constancy and abundance which characterize site groups—lies beyond human ability to comprehend adequately. Results are compared with Petersen's and with each other. Petersen's classification compares most closely with ours involving binary data. Our "numbers" and "weights" classifications both reveal Petersen-type communities, but they differ markedly from each other and more markedly still from Petersen's results.

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INTRODUCTION

In this paper we shall use the terms "association" and "community" as synonyms and shall accept Mills' (1969:1427) definition of a community as "a group of organisms occurring in a particular environment." We shall avoid the biotype—biocoenosis controversy, of which a balanced account is given in Longhurst (1958).

In benthic work on intertidal rocks descriptions of associations have almost invariably been in terms of the dominant species. The classical work of Petersen (1914, 1915, 1918, 1924) on the shallow-water benthos of soft bottoms involved quantitative data upon the number and weights of species present and led to a designation of communities in terms of dominance and constancy. As more work was done, the criteria of the characterizing species became more precise, and Petersen-type bottom communities were recognized by almost all workers in the field and in most of the seas investigated (Thorson 1957). In the late 1950's and in the 1960's increasing numbers of investigations were carried out in warmer waters where some workers found Petersen-type communities, for example, in Southern California (Hartman and Barnard 1958, 1960, Barnard and Zieshenenne 1961), West Africa (Longhurst 1955, 57, 1958, Buchanan 1958), India (Seshappa 1953), and Madagascar (Plante 1967). Others failed to recognize communities with a few dominant species, for example, in Southern California (Hartman 1955), in the Gulf of Mexico (Parker 1956, 1960), in the Gulf of California (Parker 1964), off Thailand (Thorson 1966), and off South Vietnam (Gallardo briefly quoted by Thorson 1966). The problems in warmer waters could be explained by an increased faunistic diversity (Hessler and Sanders 1967, Sanders 1968, Mills 1969).

Meanwhile some of the more recent workers in cooler waters have failed to find communities of the classical type. Examples are Sanders (1960) on the northeastern coast of the United States, Glemarec (1969) in France, and Mills (1969) at Nova Scotia. The approach of these workers has been to plot populations of different species along a traverse and to note that specific boundaries do not coincide. Eisma (1966) used correlation coefficients in working on Dutch marine molluscs and concluded that each species tended to have its own distributional pattern. Glemarec also (1969) thought that his data best fitted a continuum concept.

Elsewhere (Stephenson, Williams, and Lance 1970) we have noted that marine biologists have lagged behind terrestrial plant ecologists in the methods they have used in analyzing associations. Until recently few species of the total present in any marine situation have had diagnostic value. More-over, as Day, Field, and Montgomery (1971) have noted, they have been at the two extremes of abundance—the dominant species (as mentioned above) and the rare and occasional species which have been used as planktonic indicators if not of associations then at least of water masses.

Whittaker (1962), McIntosh (1967), Mills (1969), and Stephenson, Williams, and Lance (1970) have pointed out that in plant ecology there have been, in rough chronological order, (a) the dominance school, (b) the Braun-Blanquet school of floristic associations characterized by the fidelity and constancy of certain species, (c) the school of individualistic dissenters who deny the existence of associations, and finally (d) the school of numerical analysts who have established associations with different degrees of coherence by mathematical methods. Use of computers has increased the speed and power of these methods. Few such studies have been made on the benthos of shallow waters. G. F. Jones (1969) used computer methods on samples from Southern California and stated (p. 193): "The accurate distribution of organisms lies somewhere between the idea of 'biocoenosis' and the idea of continuum without discontinuities." The difference between this concept and those of other workers in the same area (Hartman and Barnard 1958, 1960, Barnard and Zieshenenne 1961) may well be due to the difference in analytical methods.

We have used computer techniques in the analysis of dredged catches from Moreton Bay, Queensland. Associations were far from definite and each of the site groups revealed by the classification contained many species, but few of high fidelity or constancy (Stephenson, Williams, and Lance 1970). Like G. F. Jones (1969) we presented two clear alternatives: either independent distributions of individual species (implying continuity and no associations), or a complex situation of ill-defined species groups and site groups. In defending the use of objective methods of analysis we stated (p. 486) that "Even in higher latitudes and simpler situations, objective methods of analysis merit trial."

We have also used such methods in analyzing a limited number of grab catches from Sek Harbour, New Guinea, where, because of the warmer conditions, a more complex situation than that existing in Moreton Bay might have been anticipated—in other words, even further deviation from the classical Petersen-type community. The picture which emerged (Stephenson and Williams 1971) was relatively simple: considerable areas were dominated by one or another species of ophiuroid, probably because of adverse hydrographic factors. This work showed that computer methods were capable of con-
firming, as well as throwing doubt upon, the reality of the classical ideas.

It must be admitted that Petersen's sampling methods were unsatisfactory by modern standards. Nevertheless, his data, which were published in full (Petersen 1914), remain of historic importance because so many of the earlier concepts of benthic ecology rest ultimately on his conclusions. It therefore seems desirable to attempt to establish whether the difficulties that later workers have experienced in recognizing "Petersen-type" communities arise from his sampling procedure or from the simple intuitive methods he used for analyzing his data. One approach to this problem is to use objective classificatory programs for re-examining the original data. If the results fail to reveal Petersen-type communities, the conclusions of many later workers may well require revision; if they reveal Petersen-type communities differing only in detail from the original, his intuitive analyses will be vindicated. This is the object of the research here reported.

OUTLINE OF PETERSEN'S WORK

Petersen listed 193 sites from the North Sea to the Eastern Baltic, mostly from discrete situations, but some involving considerable areas (Appendix 1). He gave 294 faunistic entries, but many of these were separate listings of juveniles following adults. Several entries are polyspecific, due to species problems of identification, and these include taxa which later workers have found important in community diagnosis. However, Petersen sometimes based his communities on genera rather than species, for example, with Echinocardium and with Nucula, so the incomplete identifications would not affect his analysis.

Petersen (1914:4-5) selected the species which diagnosed his communities in the following terms: "The animals, which are not seasonal and which compose an important part of the whole mass of the community, owing to number or weight will presumably be best suited for characterizing the community. . . ." Later (p. 7) he repeats: "It is thus seen, that we are able on broad lines to give a vertical characterization of the main quantity of the animals, at least at the places chosen, by means of a few, either very common or very heavy species." Earlier (p. 4) he justified the exclusion of many species for characterizing purposes in these words: "the long lists just obscure the differences especially if not accompanied by [sic] quantitative information, which can emphasize the characteristic species by comparison with the less important." In summary, Petersen's communities are characterized by few species which have high constancy within his site groups (occur at almost all sites) and which are dominant. Dominance is in terms of "number or weight."

Petersen's characterizing species were listed by letters. For example: B.n. (Brissopsis-Nucula); B.T. (Brissopsis-Turritella); E.T. (Echinocardium-Turritella). Only the following 12 taxa were involved:

- A.—Astarte banksii; b.—Abra alba; B.—Brissopsis lyrifera; c.—Macoma calcarea; Cyprina—C. islandica; d.—Macoma baltica; E.—Echinocardium cordatum; Haploops—H. tubicola; n.—Nucula spp.; R.M.—rich molluscs, polyspecific; T.—Turritella terebra; V. and v.—Venus gallina.

Twenty-six site groups were characterized by various combinations of these taxa, with details of species and site groups as follows (numbers of site groups are transformed to our system—see next section and Fig. 1):

- a.b.c. as a rule with Cyprina—111, 118, 152, 158, 173.
- a.b.c. frequently with Cyprina and sometimes d.—181, 182, 184, 185, 186, 187, 188, 189, 190, 191.
- a.b.c. with d.—81, 102.
- a.b.c. frequently with E.—109, 110, 114, 116, 117, 119.
- a.b.c. as a rule without E.—127, 128, 136, 137, 138, 139, 140, 145, 146, 167.
- Poor a.b.c. without E. and without full-grown Cyprina—106, 115, 126, 135, 142, 148.
- a.b.c. influenced by R.M.—120, 123, 124, 125, 149.
- B.n.—23, 25, 30, 36, 40.
- B.T.—21, 22, 27, 42, 43.
- c.—150.
- d.—75, 76, 93, 94, 95, 96, 107, 108, 112, 113, 121, 122, 129, 130, 131, 132, 133, 134, 141, 143, 144, 147, 151, 153, 155, 156, 157, 159, 160, 161, 162, 163, 164, 165, 166, 168, 170, 171, 172, 175, 177, 178, 179, 183, 192, 193.
- d. also a.—174, 176, 180.
- d. also with b.—154, 169.
- d. and allied—52, 78, 83, 84, 91, 105.
- d. and allied poor—32, 39, 63, 74.
- Poor E.a.b.c.—55, 57, 64, 69, 70, 86, 90, 92, 97.
- Rich E.b.c.—61, 73, 85, 98, 99, 100, 101, 103, 104.
- E.T.—20, 26, 28, 31, 48, 59.
- Reduced E.T.—47, 51, 53, 56.
- (E.T.)—88, 89.
- (E.T.) R.M.—62, 65, 66, 68, 71, 72, 77, 79, 82.
- E.v.—19, 24, 29, 33, 37, 38, 67.
- E.(v) —35, 41, 45, 49, 50, 58.
- Haploops—44, 46, 54.
- V.—34, 60.

Very much reduced v.—80, 87.

*Throughout this paper spelling of names of species follows Petersen in omitting specific authors and disregards later name changes.
Fig. 1. Petersen's sites with our numbering, in main sampling area; islands are shaded. Heavy lines show boundary of areas: I, Kattegat; II, Samso Belt; III, Isefjord; IV, Sound; VI, Little Belt; VII, Western Baltic; VIII, True Baltic. For further details of area between Funen and Sealand, see Fig. 3.
In addition 18 sites were not characterized by species but only listed by areas, viz., North Sea, Skagerrak (Kattegat), and Gullmarfjord.

These results will be compared in detail with our classifications. Meanwhile several features should be noted: first, that only 12 taxa are used of over 260 species which were listed; second, that one group (d. group) preponderates, with 46 sites characterized only by \textit{Macoma baltica}; third, that there are many small site groups, one with a single site and six with two sites; and fourth, that the sites with characterizing species can be fused to form seven groups as follows:

1) \textit{Macoma} communities—(d., d. and allied, d. and allied poor, d. also a., d. also with b.).
2) \textit{Brissopsis} communities—(B.n., B.T.).
3) \textit{Echinocardium} communities—(E.T., E.T. (R.M.), (E.T.) R.M., (E.T.), Ev., E. (v), reduced E.T. with rich influence of R.M., rich E.b.c., poor E.a.b.c.).
4) \textit{Astarte}, \textit{Abra}, \textit{Macoma calcarea} communities—(a.b.c. influenced by R.M., a.b.c. frequently with E., a.b.c. as a rule without E., poor a.b.c. without E. and without full-grown \textit{Cyprina}, a.b.c. as a rule without \textit{Cyprina}, a.b.c. frequently with \textit{Cyprina} sometimes with d., a.b.c. with d.).
5) \textit{Venus} communities—(V., very much reduced v.).
6) \textit{Macoma calcarea} community—(c).
7) \textit{Haploops} community.

\textbf{OUR UTILIZATION OF PETERSEN'S DATA}

\textbf{Sites}

Petersen grouped sites by areas and numbered within them. We have renumbered (roughly in a clockwise direction) to give a continuous series as shown in Fig. 1, 3, and 4 (Fig. 2 shows depths). Full details of the renumbering are in the Library of the Queensland Museum; some later data are also filed designated “in archives.”

Intensity of sampling was not uniform, data being the mean values of from 5 to 50 grab catches. In addition, variation is considerable in the areas included in each “site.” These inequalities place constraints on the methods we can use. For example, one would expect that the more intensely sampled sites would have more rare species and higher diversities than the remainder. We have avoided numerical techniques based on diversity.

Proximity of sites varies, and most sites are too far apart to suspect, for any a priori reason, that data from adjacent sites are different samples of the same fauna. Hence grouping of sites into clusters prior to analysis, a technique which proved valuable in our work in Moreton Bay (Stephenson, Williams, and Lance 1970) and in New Guinea (Stephenson and Williams 1971), cannot be used in the present case.
Species to consider

At the time these analyses were undertaken, the complete set of 193 sites x 264 taxa was too large for any but divisive monothetic analyses of presence-absence data, and it was essential to reduce the number of species used. We began by deleting the 57 taxa which each occur only at a single station. Such taxa, though they may indicate peculiarities of individual sites, cannot contribute to any larger scale consideration of communities. A presence-absence analysis, which will be reported in detail later, produced a "residual" group of 83 species hardly at all involved in interspecific associations; these were next deleted. (One of Petersen's community indicators, Haploops tubicola, was included in this list.) We then deleted 22 incompletely identified taxa, which should probably have been excluded earlier. Lastly, since the remaining 101 species were still more than we desired for the main analyses, we removed the more infrequent species—those occurring five times or less in the 193 sites; 13 species were so removed. (For a complete accounting of the removal of species by these steps, see Appendix 2.)

The residual 88 species were employed in most of the analyses and are listed in Table 1, with the numbers assigned to them. Twenty-one species were temporarily eliminated and later brought back to the analysis; these are asterisked.

Numbers

Two types of quantitative data were given by Petersen, number of individuals and rough weight. Numbers data contain only three obscurities: "+," "fragments," and "oo." We felt it was reasonable to replace the first two by 0.1, the lowest value given by Petersen. The third is more difficult because in some analyses considerable bias is given to occasional very high values. For this reason, although the highest value in Petersen's data is 3,960 (Mytilus edulis, sta. 130), we thought it advisable to err by possible understatement and arbitrarily chose 1,000 for infinity values. Only five stated values exceeded 1,000, viz., 3,960, 3,000, 1,350, 1,254, and 1,140.

Weights

Data on weights involved more uncertainties. When species were small and infrequent, two or more were often weighed together. If sizes were believed to be similar and numbers of individuals were given, the weights were proportioned between them. A few weights given by Petersen are less than 0.01 g, but enter our tables as 0.01 g since it is the lowest value we quote. In a few cases two species
of suspectedly similar size and with “infinity” individuals were weighed together, and in these cases each weight is taken as half the total. Four stations (12, 14, 17, and 115) must be eliminated from the weight data; specific weights were not given and are impossible to deduce.

**Methods of Analysis**

**Data**

We possess two basic sets of data. The first consists of 193 sites defined by the numbers (i.e., counts) of about 260 species. For four of these sites no weights are available, and our second set therefore consists of 189 sites defined by the weights of about 260 species. The “numbers” set can be dichotomized into binary (presence-or-absence) data, and we shall regard this as a third data-set. The methods used for reducing the number of species have been outlined in the previous section; there remains the possible desirability of transforming the “weights” and “numbers” sets. It is characteristic of most marine data-matrices that they contain many zeros and a small number of very large outlying values.

Few numerical models are insensitive to both zeros and outliers, and we have therefore thought it desirable to reduce the extreme asymmetry of distribution by the conventional transformations. For the “numbers” set, which are likely to be approximately Poissonian, we have replaced the values by their square roots; for the “weights” set, where the distribution is likely to approach the lognormal, we have used the $\ln(1 + w)$ transformation.

**Measures of dissimilarity**

**Binary set.—**For this we have used a conventional Shannon-type information statistic. If a group of $n$ sites is defined by the presence-or-absence of $s$ species, and if $a_j$ of the sites contain the $j$th species, we define the information-content of the group, $I$, as

$$I = s \ln n - \sum_j (a_j \ln a_j + (n - a_j) \ln (n - a_j)).$$

We dichotomize on each species in turn, calculate and add the information-contents of the two resulting subgroups, and subtract this from the original group information-content. Division is then on that species which produces the largest fall in information-content. The process is carried out automatically by the Canberra program DIVINF (Lance and Williams 1967).

**Numerical sets.—**We reject the use of a Euclidean measure; without standardization of variances a small number of abundant species can completely dominate the results, and after standardization to unit variance the system becomes unduly sensitive to the absence of common species or the presence of rare ones. Two measures based on the “Manhattan metric” call for more serious consideration.

If $x_{ij}$ and $x_{ij}$ are the numbers or weights of the $j$th species in two sites, the first measure to consider is

$$\sum |x_{ij} - x_{ij}|$$

This is often known as the “Bray-Curtis measure,” since its complement was used by Bray and Curtis (1957) in a well-known study. It was, however, certainly used by Motyka, Dobrzanski, and Zawadzki (1950). A closely related measure was used by

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**Table 1.** The 88 species used in most of the analyses, with their arbitrary numbers (species excluded from some analyses are indicated with an asterisk)

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---------|---|---|---|---|---|---|---|---|---|----|
| A. abbrev | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. affinis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. brevis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. chinensis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. concava | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. coriacea | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. denticulata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. echinata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. expansa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. fusiformis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. globosa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. gouldi | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. hirsuta | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. japonica | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. knausiana | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. lanceolata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. latissima | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. longirostris | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. marginata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. matsui | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. neglecta | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. nitida | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. obtusata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. parvula | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. perspicax | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. plicata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. profunda | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. quinqueloba | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. radiata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. reniformis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. robusta | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. rostrata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. setosa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. simplex | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. subterranea | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. subulata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. truncata | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. vulgaris | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. ventricosa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| A. vitrea | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |

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Gleason (1920), and it is the quantitative extension of a presence-absence measure originally proposed by Czekanowski (1913). It is therefore sometimes known as the "Czekanowski measure." It has been used by Field (1969) and by Day, Field, and Montgomery (1971), and we ourselves used it in a previous study (Stephenson and Williams 1971). It ignores double-zero matches, but is easily dominated by outlying values, so that species of low frequency contribute little.

The second measure is the "Canberra metric":

$$\sum \frac{|x_{ij} - x_{kj}|}{(x_{ij} + x_{kj})}.$$  

Double-zero matches can be ignored by incorporating only other matches and averaging, though it is then no longer a metric. It possesses a troublesome singularity at zero. If $x_{ij}$ is zero, the contribution of that species takes its maximum possible value of 1, irrespective of the value of $x_{kj}$. It is usual to counter this by replacing $x_{ij}$ for that comparison only, by a value somewhat smaller than the smallest value appearing in the data-matrix. After several trials we used the value 0.1 for the "numbers" data, and for the "weights" data, 1/n(1.01).

**Classificatory strategies**

We have chosen to use hierarchical strategies, since we have previous experience of their use and appropriate programs are available; and we require an agglomerative fusion strategy such that, given the interelement dissimilarity matrix, all subsequent measures can be calculated without further reference to the original data. The general problem of such *combinatorial* strategies has been discussed by Lance and Williams (1967). Given two groups or individuals $(i)$ and $(j)$ which we are to fuse into a composite group $(k)$, and which we have fused into a further individual or group $(h)$, we need to be able to calculate the distance from $(h)$ to $(k)$, which we shall denote by $d_{hk}$, in terms of the pre-existing distances $d_{hi}$, $d_{hj}$, and $d_{ij}$. Most fusion strategies can be accommodated within the linear model

$$d_{hk} = \alpha d_{hi} + \beta d_{hj} + \gamma |d_{ij} - d_{hi}|,$$

where the parameters $\alpha$, $\beta$, $\gamma$ determine the nature of the strategy.

Fusion strategies fall into one of two main types. They may be *space-dilating*, i.e., they cluster intensely, sharpening and emphasizing weak boundaries; such strategies are indicated when it is desired to obtain an overall view of a complex population. However, all such strategies exhibit the phenomenon of "group-size dependence" (Williams, Clifford, and Lance 1971), in that it becomes more difficult to join the group as the group grows during the fusion process. This commonly produces a small degree of misclassification. The other strategies are *space-conserving*; they impose no enhanced clustering on the data and are consequently not liable to misclassification. However, they provide little assistance if the groups inherent in the population are diffuse and ill defined. It has therefore become usual to use two strategies, one space-dilating whose results are then checked by the use of a space-conserving strategy. In this study we have, we believe for the first time, attempted to combine the results from two such opposed strategies. We have considered three strategies, two space-dilating and one space-conserving.

**Flexible.**—This is defined by the quadruple constraint: $\alpha + \beta = 1; \alpha = \beta; \beta < 1; \gamma = 0$. It is applicable to any dissimilarity measure and has the unusual advantage that the intensity of clustering is variable, depending only on $\beta$; increasingly negative values of $\beta$ produce increasingly intense clustering. We have used the now conventional value of $\beta = -0.25$.

**Furthest neighbor.**—This is defined by the condition:

$$\alpha_i = \alpha_j = +\frac{1}{2}; \beta = 0; \gamma = +\frac{1}{2}.$$  

The distance between two groups becomes, in this model, the distance between that pair of individuals, one in each group, that are furthest apart. It, like "flexible", clusters fairly intensely; our reason for investigating its use lies in the fact that there is some evidence (e.g., Jardine and Sibson 1968) that so-called "single-link" strategies of this type are more stable than the group-strategies under small changes and errors in data.

**Group average.**—If there are $n_i$ members in group $(i)$ and $n_j$ members in group $(j)$, so that in the fused group $(k)$ there are $n_k = n_i + n_j$ members, this strategy is defined by $\alpha_i = n_i/n_k; \alpha_j = n_j/n_k; \beta = \gamma = 0$. It is a generalization of a measure originally proposed by Sokal and Michener (1958), and in effect defines the intergroup distance as the mean of all the between-group interindividual distances. It clusters only weakly.

**Allocation procedures**

When two classificatory strategies are used, there will result two alternative classifications, with some groups of elements common to both. Such groups are extracted, but leave a residue which need to be allocated to one of the extracted groups or, if necessary, retained as isolated elements. Since we propose to classify both stations ("normal analyses") and species ("inverse analyses"), two allocation processes will be necessary. The method for stations was to define, for any reference group, a group vector whose $j$th element was the mean of the transformed counts or weights for that species in
that group. This vector could then be compared with a disputed station by means of whichever measure (Bray-Curtis or Canberra metric) had been used for the initial classifications. If there was still ambiguity, appeal was made to geographical proximity. The station groups now being complete, the data could now be compressed to provide a vector of means, each corresponding to a site group, and disputed species allocated by means of the measure in use. Since Bray-Curtis and Canberra metric are both dissimilarity measures, allocation was to that group for which the measure was minimum.

Criteria for assessment

There is no completely satisfactory way of deciding how many groups to accept in a classificatory process. As applied to site grouping, too few groups reduces the homogeneity as regards species-group distribution, whereas too many groups results in topographic fragmentation.

When a single strategy has been used, a hierarchy (dendrogram) exists, and the point of optimum clarity can be obtained by moving up or down the hierarchy; this facility is not available when strategies have been combined. Three criteria were used.

Constancy and fidelity of species.—These concepts have been extensively discussed by Stephenson, Williams, and Lance (1970). We have used, as a simple measure of constancy of a given species in a given site group, the percentage of sites in that group in which the species occurs. For a corresponding measure of fidelity we have used the percentage of individuals of each species which occurs in a given site group. As the number of site groups is increased, the constancy of the species is increased at the expense of fidelity. Throughout these analyses we have used four reference grades for both constancy and fidelity: very high (VH) 100-95%, high (H) 94-66%, medium (M) 65-33%, and low (32-0%).

Using the "numbers" data, we derived 28 site groups and explored the possibility of reducing this number. Scrutiny of two-way coincidence tables indicated the groups with closest affinities, and further indicated that constancy and fidelity would be sacrificed by fusion.

We then investigated the possibilities of fusion by an ordination procedure. Following the discussion of general problems of ordination of groups by Williams, Dale, and Lance (1971) we used the "principle coordinate analysis" of Gower (1966, 1967). This showed that only two site groups are in close proximity. These (site-groups 18 and 19—see later) are quite separately diagnosed, and fusion is unwarranted.

Prior considerations.—We have been concerned to obtain as close a comparison with Petersen's results as is practicable by the use of substantially objective methods. Since Petersen recognized 26 site groups, and since there is no known rigorous means of mapping one classification into another, we have attempted to use a number of groups of approximately the same order. Similarly, since Petersen stressed constancy and dominance, we have placed less stress on fidelity than might otherwise have been the case.

Choice of measure and strategies

The sequence of operations was as follows:

1) Preliminary classification. 193 X 88 "numbers" set, Bray-Curtis measure, flexible sorting. The degree of concentration was disappointing, producing only nine cells with medium densities; 31 species attained a constancy of less than 25% in any site group, and these (marked with an asterisk in Table 1) were temporarily eliminated.

2) Bray-Curtis/Canberra metric comparison. The resulting 193 X 57 "numbers" set was now run with both measures and flexible sorting with $\beta = -0.25$. The normal and inverse classifications were truncated at the level of 20 site groups and 10 species groups, respectively. Examination of the constancy and cell-density results gave, for Bray-Curtis, 43 species with VH constancy, seven cells with H density, and 27 cells with M density; for the Canberra metric, 56 species with VH constancy, 12 cells with H density, and 20 cells with M density. It is clear that the Canberra metric provides sharper sorting and more discrete entities in terms of constancy. Comparison with Petersen's original groups showed that there were approximately 110 stations in groups common to Bray-Curtis and Petersen, but approximately 123 common to Canberra metric and Petersen. Since the approximate retrieval of Petersen's classification (if this is possible) is one of our aims, this is additional evidence in favor of the Canberra metric, which was used in all subsequent analyses.

3) Comparison of fusion strategies. Using the "numbers" set with the square-root transformation, we carried out normal and inverse analyses by flexible ($\beta = -0.25$), group-average, and furthest-neighbor strategies, and two-way tables were constructed. It was intended to work at the 20-group site level, but since the weakly clustering group-average strategy produced many small site groups, it was taken to the 30-group level, and then reduced (to 18 groups) by elimination of those groups containing only one or two sites. In each case species classification was taken to the 10-group level. Four comparisons were examined: (a) for site groups only, the number of species attaining VH or H...
TABLE 2. Comparison of sorting strategies; (a), (b), (c), and (d) refer to listing in text

| Single strategies | (a) | (b) |
|-------------------|-----|-----|
|                   | Site groups | Two-way tables |
|                   | Number of species | Number of cells |
|                   | in upper grades | with grades of |
|                   | constancy | cell density |
|                   | VH | H | | M |
| Flexible          | 22 | 56 | 12 | 20 |
| Group average     | 32 | 58 | 7  | 28 |
| Furthest neighbor | 19 | 59 | 7  | 27 |

| Strategies in pairs | (c) | (d) |
|---------------------|-----|-----|
|                     | Sites | Species |
|                     | No. ex. 193 | No. ex. 107 |
|                     | associated in | associated in |
|                     | similar groups | similar groups |
| Group average cf. furthest neighbor | 130 | 47 |
| Group average cf. flexible | 163 | 50 |
| Flexible cf. furthest neighbor | 158 | 48 |

Grades of constancy; (b) for two-way tables, the number of cells attaining H or M grades of cell density; (c) for strategies in pairs, the numbers of sites (out of 193) which remained associated in similar groups; and (d) for strategies in pairs, the number of species similarly associated. The results are summarized in Table 2. The results of (a) suggest a preference for group average, (b) favors flexible, (c) and (d) both favor the combination of group average and flexible. The single-link strategy furthest-neighbor was therefore abandoned.

**Combination of strategies**

**Numbers.**—The preliminary classifications (flexible and group average) used the 193 X 57 data set; we obtained 26 site groups in common, with 163 of the 193 sites accommodated. For allocation of the remaining 30 disputed sites, the data-set was extended to the 193 X 88 case, and the allocation procedures as outlined earlier were undertaken. All but two sites (71 and 93) could thus be allocated. The corresponding inverse classifications of the 193 X 57 set gave 13 groups comprising 50 species, leaving seven in dispute. We now have a set of 28 site groups (two with single sites) by 13 species groups accounting for 50 of the species; the remaining 38 of the 88 species were then duly allocated.

Examination of the final table from the point of view of the degree of constancy of each of the 88 species to one or more of the 28 site groups disclosed 41 VH, 60 H, and 173 M entries, considerably better than either of the strategies achieved alone. Although our, frankly somewhat primitive, method of using paired strategies has been computationally extremely cumbersome, its success in this regard suggests that the methodology of combined strategies might well repay further attention.

The 28 site groups X 13 species groups represents the final result of our numbers classification.

**Weights.**—The matrix used was the 189 X 88 log-transformed data-set. As with the numbers analyses, we used the Canberra metric with combined flexible (β = -0.25) and group-average sorting, followed by allocation procedures, exactly as before. The details of the intermediate steps are of no special interest, since they closely parallel those of the numbers set; the final result was of 28 site groups (three of which contained only a single site) and 15 species groups. The results are discussed later.

**Presence-Absence Classification**

Because we believe later classifications to be more meaningful, the results of the present one are not detailed at length. We took the classification only to the level of 15 site groups and 12 species groups and in Table 3 give a condensed two-way coincidence table which includes all cell densities > 10%.

In this table site groups are characterized by species groups, not by individual species, and from the table plus the data from which it was condensed it is evident that (a) no site groups were uniquely characterized by the presence of one species group to the exclusion of all others (in Table 3 this appears to be true for site-group 4 only because small percentages are eliminated); (b) no species groups are restricted to any particular site group; in other words, there is no completely faithful species group (again species-group 10 appears so because of elimination of low percentages); (c) species-group 12 does not characterize any of the site groups.

Most of the infrequently occurring species were concentrated in group 12, where most species were recorded from two to five times. The 83 species involved were excluded from further analyses.

Characterization of site groups in terms of individual species is relatively easy (Fig. 5). The first dichotomy in the site classification separates sites with *Macoma baltica* from those without it. The former include site-groups 1-4. These are subdivided on the presence or absence of *Abra alba*, and site-group 1 is thus a *Macoma baltica–Abra alba* community. The remainder are subdivided on the presence or absence of *Modiolaria discors*, site-group 2 becoming a *Macoma baltica–Modiolaria discors* community. Similarly site-group 3 is a *Macoma baltica–Mytilus edulis* community, and site-group 4 is *Macoma baltica* alone.

Similarly sites without *Macoma baltica* are subdivided on the presence or absence of *Turritella terebra*. Site-group 5 is a *Turritella terebra–Brisseopsis*
TABLE 3. Site-group/species-group coincidence table from DIVINF analysis, showing cell densities when they exceed 10% (number of sites in each group and number of species in each group in brackets)

| Species groups | Site groups |
|----------------|-------------|
|                | 1 (20)      | 2 (7) | 3 (23) | 4 (19) | 5 (13) | 6 (6) | 7 (9) | 8 (10) | 9 (15) | 10 (16) | 11 (12) | 13 (5) | 14 (11) | 15 (16) |
| 1 (7)          | -          | -     | -      | -      | -      | 48    | 57    | 79    | 90    | 72      | 50      | 51      | -       | -       | 36      | 35      |
| 2 (7)          | -          | 26    | -      | -      | -      | -     | 70    | 31    | 29    | 35      | -       | -       | -       | -       | -       | -       |
| 3 (6)          | -          | -     | 54     | -      | -      | -     | 60    | -     | 51    | -       | 40      | -       | -       | -       | -       | -       |
| 4 (9)          | 17         | -     | -      | -      | -      | -     | -     | -     | -     | 37      | 18      | 16      | 21      | -       | -       | -       |
| 5 (13)         | 31         | 51    | 23     | 22     | -      | -     | 35    | -     | -     | -       | -       | -       | -       | -       | -       | -       |
| 6 (16)         | 16         | 58    | 24     | -      | -      | -     | -     | -     | -     | -       | -       | -       | -       | -       | -       | -       |
| 7 (25)         | -          | -     | -      | 40     | 29     | 26    | 31    | -     | -     | -       | -       | -       | -       | -       | -       | -       |
| 8 (23)         | -          | -     | -      | -      | 16     | 25    | -     | -     | -     | 14      | 14      | 22      | -       | -       | -       | -       |
| 9 (15)         | -          | -     | 27     | -      | -      | -     | -     | -     | -     | -       | -       | -       | 49      | -       | -       | 16      |
| 10 (6)         | -          | -     | -      | -      | 16     | -     | -     | -     | -     | -       | -       | -       | -       | -       | -       | -       |
| 11 (7)         | -          | -     | -      | -      | -      | -     | -     | -     | -     | -       | -       | -       | -       | -       | -       | -       |
| 12 (83)        | -          | -     | -      | -      | -      | -     | -     | -     | -     | -       | -       | -       | -       | -       | -       | -       |

**Fig. 5.** Dendrogram of site classification by DIVINF, taken to the 15 site-group level. Site-group numbers in larger lettering; numbers of species on which dichotomies are based in small lettering (refer to Table 1).

_in summary we have the following communities:

Macoma baltica–Abra alba Site-group 1
M. baltica–Modiolaria discors Site-group 2
M. baltica–Mytilus edulis Site-group 3
M. baltica alone Site-group 4
Turritella terebra–Brissopsis lyrifera Site-group 5
T. terebra–Venus gallina Site-group 6
T. terebra alone Site-group 7
Abra alba–Lepidonotus squamatus Site-group 8
A. alba–Nucula tenuis Site-group 9
A. alba alone Site-group 10
Ophioglypha robusta Site-group 11
Natica pulchella Site-group 12

lyrifera community. Site-group 6 is a Turritella terebra–Venus gallina community, and site-group 7 is Turritella terebra only.

Sites without Macoma or Turritella are subdivided by Abra alba. There is an Abra alba–Lepidonotus squamatus association (site-group 8), an Abra alba–Nucula tenuis association (site-group 9), and Abra alba alone (site-group 10). Sites without Macoma, Turritella, or Abra are subdivided by Ophioglypha robusta, giving a community based on this species (site-group 11) and several in which it is absent. These are subdivided by Natica pulchella with one community based on the species (site-group 12) and three on its absence. These are an Axinus flexuosus community (site-group 13), a Buccinum undatum community (site-group 14), and a community diagnosed by none of the above-mentioned species (site-group 15).
Axinus flexuosus Site-group 13

Buccinum undatum Site-group 14

Negatively diagnosed Site-group 15

The 12 species above have 100% constancy in the site groups they characterize. By taking the site-group classification further, the array of 100% constant species is maintained, but fidelity is lost.

The first separation of sites by the present divisive information statistic is usually on neither the most nor the least frequently occurring species, but instead one of intermediate frequency. In the present case the first dichotomy is by the most ubiquitous species, Macoma baltica.

NUMBERS CLASSIFICATION

Tabular results

Table 4 shows the site composition of the 26 + 2 site groups finally adopted, and Table 5 the 13 species groups.

Characterization of site groups

Although the species groups can be used to characterize site groups via two-way coincidence tables, it is more meaningful to use individual species, which vary in both constancy and abundance between the site groups they characterize.

Seventy-six of the 88 species are found in one or another of the 26 major site groups at medium constancy or higher. Because they reappear in different site groups, an embarrassingly large number of species is available for characterization; there are 41 at the VH level, 61 at H, and 155 at M (Appendix 3). A full list is filed in the Library of the Queensland Museum.

A fraction of the apparently constant species may owe something to random distribution, and this particularly applies to small site groups—a single-recording gives 50% constancy in a site group of two, and as such may mean very little. Although use of a chi-squared test indicated that all species were highly nonrandom in their site groupings, we also undertook a “commonsense” analysis which showed that possibly a minority of the medium constancies were questionable. Since none of these is used in the presentation below, the problem disappears.

The main abundance of each species in each site group was estimated from summation of $\sqrt{n}$ values, which were readily available. For the sake of compression, data on the more abundant species were expressed in three grades: 1, 20 and greater; 2, 19.9-10; and 3, 9.9-5. Again there was a super-abundance of characterizing species; for example, 72 instances of grade 1 species (Appendix 4) (full list in archives).

Table 4. Site composition of the 28 site groups adopted in the numbers classification

| Site group | Sites in group |
|-----------|----------------|
| 1         | 15, 107, 160, 163, 174, 176, 177, 183, 193 |
| 2         | 94, 171, 192 |
| 3         | 131, 132, 133, 143, 144, 164, 165 |
| 4         | 80, 87, 95, 129 |
| 5         | 14, 190, 191 |
| 6         | 151, 159, 170 |
| 7         | 42, 162, 166, 168 |
| 8         | 91, 102, 154, 186 |
| 9         | 55, 97, 115, 118, 119, 126, 127, 135, 145 |
| 10        | 142, 152, 158, 173, 181 |
| 11        | 134, 148, 150, 161 |
| 12        | 3, 4, 32, 34, 39, 74, 84, 105 |
| 13        | 10, 63 |
| 14        | 13, 60 |
| 15        | 1, 2, 5, 6, 7, 8, 9, 29 |
| 16        | 17, 40, 62, 68 |
| 17        | 44, 54, 65, 66, 72, 79, 82, 86 |
| 18        | 18, 19, 20, 21, 22, 24, 26, 28, 31, 33, 35, 41, 42, 43, 45, 47, 59 |
| 19        | 37, 38, 48, 49, 50, 51, 53, 56, 58, 67 |
| 20        | 11, 12, 23, 25, 30, 36, 46 |
| 21        | 16, 27 |
| 22        | 92, 106, 109, 111, 113, 120, 123, 124, 125, 126, 127, 138, 139, 167, 180, 182, 184, 185, 187, 188, 189 |
| 23        | 31, 108, 128, 140, 149 |
| 24        | 57, 61, 64, 69, 70, 73, 77, 85, 88, 89, 90, 98, 99, 100, 101, 103, 104, 110, 114, 116, 117, 146 |
| 25        | 75, 76, 83, 130, 141, 147, 155, 156, 169, 172, 175, 179 |
| 26        | 78, 96, 112, 121, 122, 153, 157, 178 |
| 27        | 71 |
| 28        | 93 |

Table 5. Species composition of the 13 species groups (numbers classification)

| Species group | Species in group |
|---------------|-----------------|
| 1             | 17, 29, 30, 37, 41, 49, 55, 59, 66, 70, 72, 75, 78, 88 |
| 2             | 16, 26, 31, 52 |
| 3             | 34, 54, 69, 79, 82 |
| 4             | 22, 44, 50, 51, 57 |
| 5             | 35, 65, 85 |
| 6             | 29, 42, 45, 68, 80, 83 |
| 7             | 14, 15, 40 |
| 8             | 4, 5, 9, 10, 12, 38, 46, 74 |
| 9             | 8, 32, 71, 87 |
| 10            | 2, 19, 43, 63 |
| 11            | 7, 21, 27, 62 |
| 12            | 1, 48, 67 |
| 13            | 3, 6, 11, 13, 18, 20, 23, 24, 25, 28, 33, 36, 39, 47, 53, 56, 59, 60, 61, 64, 73, 75, 76, 77, 81, 84, 86 |

*Equal values for two species groups.

Complete characterization of site groups would involve numerical values of constancy and abundance of every species; zero values would have particular importance in cases of ubiquitous species. Omitting zeros and scaling higher values still gives...
a mass of data almost beyond human comprehension, so we have only used the two upper grades of constancy and abundance below.

The data revealed that sometimes a species characterized a site group in terms of both constancy and abundance, and in these cases we have a Petersen-type association. The following associations are of this type:

Site-group 1. Species 47 (Macoma baltica) VH constant and grade 1 abundance; species 12 (Aricia armiger) highly constant.

Site-group 2. Species 47 (M. baltica) VH constant and grade 2 abundance; species 13 (Artacama proboscidea) grade 2 abundance.

Site-group 3. Species 47 (M. baltica) and species 17 (Asterias rubens) both VH constant and grade 1 abundance.

Site-group 6. Species 47 (M. baltica) and species 82 (Terebellides strømi) both VH constant and grade 1 abundance.

Site-group 7. Species 47 (M. baltica) VH constant and grade 1 abundance; species 72 (Pectinaria koreni) VH constant and grade 2 abundance.

Site-group 8. Species 47 (M. baltica) and species 1 (Abra alba) both VH constant and grade 1 abundance; species 28 (Corbula gibba) VH constant and grade 2 abundance.

Site-group 25. Species 47 (M. baltica) VH constant and grade 1 abundance; three other species highly constant and grade 1 abundance (24-Cardium edule, 40-Hydrobia ulvae, and 56-Mylitus edulis).

Site-group 26. Species 47 (M. baltica) and species 24 (Cardium edule) both VH constant and grade 1 abundance.

Site-group 5. Species 82 (Terebellides strømi) VH constant and grade 1 abundance; species 67 (Ophioglypha albida) highly constant and grade 1 abundance.

Site-group 9. Species 67 (Ophioglypha albida) VH constant and grade 4 abundance; species 1 (Abra alba) and 48 (Macoma calcarea) of high constancy and grade 1 abundance.

Site-group 10. Species 1 (Abra alba) VH constant and grade 1 abundance; species 72 (Pectinaria koreni) VH constant and grade 2 abundance.

Four other species of grade 4 abundance.

Site-group 11. Species 48 (M. calcarea) VH constant and grade 1 abundance; species 72 (Pectinaria koreni) VH constant and grade 2 abundance.

Site-group 13. Species 49 (Mactra subtruncata) VH constant and grade 1 abundance; species 12 (Aricia armiger) grade 2 abundance.

Site-group 14. Species 31 (Cyprina islandica) and species 88 (Venus gallina) both VH constant and grade 1 abundance.

Site-group 15. Species 66 (Ophioglypha affinis) and species 78 (Solen ensis) both VH constant and grade 1 abundance.

Site-group 16. Species 42 (Leda minuta) VH constant and grade 1 abundance; species 52 (Modiolaria nigra) VH constant and grade 2 abundance.

Site-group 17. Species 42 (Leda minuta) and species 68 (Ophioglypha robusta) both highly constant and grade 1 abundance.

Site-group 18. Species 33 (Echinocardium cordatum) highly constant and grade 1 abundance; species 71 (Pectinaria auricoma) also highly constant and grade 2 abundance.

Site-group 19. Species 31 (Cyprina islandica) VH constant and grade 1 abundance; species 33 (Echinocardium cordatum) and species 63 (Nucula tenuis) highly constant and grade 1 abundance.

Site-group 20. Species 62 (Nucula sulcata) VH constant and grade 1 abundance; species 7 (Amphiura chiajei) and species 19 (Axinus flexuosus) highly constant and grade 1 abundance.

Site-group 21. Five species all VH constant and grade 1 abundance: 2 (Abra nitida), 19 (Axinus flexuosus), 21 (Brissopsis lyrifera), 43 (Leda pernula), and 71 (Pectinaria auricoma).

Site-group 22. Six species all highly constant and grade 1 abundance: 1 (Abra alba), 14 (Astarte banskii), 15 (A. borealis), 16 (A. elliptica), 48 (Macoma calcarea), and 67 (Ophioglypha albida).

Site-group 23. Species 26 (Cardium fasciatum) and species 48 (M. calcarea) both VH constant and grade 1 abundance; species 35 (Echinocyamus pusillus) also VH constant.

Site-group 24. Species 33 (Echinocardium cordatum) VH constant and grade 1 abundance; species 48 (M. calcarea) and species 63 (Nucula tenuis) also VH constant.

Thus 24 out of 26 “larger” associations are characterized by constant and abundant species. The two aberrant site groups (excluding the two with single sites) are:

Site-group 4. The VH constant species 17 (Asterias rubens) is only of grade 2 abundance, below the abundance of four other species.

Site-group 12. There are no species of very high or high constancy or of grade 1 abundance. Three are of grade 2 abundance: 65 (Opelis limacina), 67 (Ophioglypha albida), and 85 (Travisia forbesi).

Topographical distribution of site groups

On Fig. 6 and 7 site groups are plotted within
Fig. 6. Distribution of our numbered site groups ("numbers" classification) in Petersen's main sampling area. Inset area is given in Fig. 7.
the main area of Petersen's investigation. On Fig.
8 and 9 groups having most in common have been
fused and replotted, i.e., site-groups 1, 2, 3, 6, 7, 8,
25, 26 (Macoma baltica groups), site-groups 10, 22
(Abra alba groups), site-groups 16, 17 (Leda minuta
groups), site-groups 18, 24 (Echinocardium cor-
datum groups), and site-groups 14, 19 (Cyprina
islandica groups). Plotting of the separate site groups
gives a far from coherent topographical pattern,
even in the area of densest sampling. The plots of
the fused site groups give a more meaningful pattern
in the more sparsely sampled areas but not in the
area of densest sampling. This suggests either that
the classification has been taken to too fine a level
(which is contrary to the indications of the coinci-
dence table) or that denser sampling would be
needed to give more acceptable topographic patterns.

WEIGHTS CLASSIFICATION

Tabular results

Table 6 shows the site composition of the 25 + 3
site groups adopted and Table 7 the 15 species
groups.

Characterization of site groups

Constancy and weightiness of individual species
are used. Mean weightiness was calculated from
summatd $1n$ values and expressed as three grades:
1 for values $> 2$, 2 for 1-2, and 3 for 0.5-0.99.
(Appendices 5 and 6). (Full relevant data in
archives.)

When the same species are diagnostically im-
portant in both constancy and weightiness we have a
Petersen-type association, and these are listed first.
Site-group 3. Species 11 (Arenicola marina) VH
constant and grade 1 weight; species 47 (Macoma
baltica) VH constant and grade 2 weight.

| Site group | Sites |
|------------|-------|
| 1          | 1, 2, 3, 5, 6, 7, 9 |
| 2          | 78, 94, 112, 155, 171, 192, 193 |
| 3          | 52, 161, 162 |
| 4          | 159, 168, 169 |
| 5          | 103, 113, 147 |
| 6          | 4, 39, 105 |
| 7          | 29, 32, 34, 60, 63, 74, 80, 81, 84, 87, 91, 93 |
| 8          | 134, 144 |
| 9          | 107, 160, 163, 174, 176, 180, 183 |
| 10         | 73, 76, 83, 121, 122, 129, 130, 131, 132, 133, 143, 153, 156, 157, 164, 165, 175, 177 |
| 11         | 95, 96, 141, 172, 178, 179 |
| 12         | 151, 170, 190, 191 |
| 13         | 108, 109, 111, 136, 137, 138, 139, 140, 167, 173, 184, 185, 187, 188, 189 |
| 14         | 55, 97, 102 |
| 15         | 106, 118, 126, 135, 142, 145, 148, 150, 152, 154, 166, 181, 182, 186 |
| 16         | 57, 61, 69, 158 |
| 17         | 73, 85, 88, 89, 90, 98, 99, 100, 101, 104, 110, 114, 116, 117, 119, 127, 128, 146 |
| 18         | 44, 54, 92 |
| 19         | 65, 68, 79 |
| 20         | 8, 19, 24, 33, 35, 37, 38 |
| 21         | 41, 45, 48, 49, 50, 53, 58, 59, 64, 67, 70 |
| 22         | 18, 20, 21, 26, 28, 31, 42, 43, 47, 51, 56 |
| 23         | 11, 16, 22, 23, 25, 27, 30, 36, 40, 46 |
| 24         | 62, 66, 71, 77, 82 |
| 25         | 72, 86, 120, 123, 124, 125, 149 |
| 26         | 13 |
| 27         | 15 |
| 28         | 10 |

Site-group 5. Species 17 (Asterias rubens), species
47 (M. baltica), and species 49 (Mactra sub-
truncata) VH constant and grade 3 weight; spe-
cies 12 (Aricia armiger), species 24 (Cardium
edule), and species 72 (Pectinaria koreni) VH
constant.

Site-group 6. Species 65 (Ophelia limacina) VH
constant and grade 3 weight; species 85 (Travista
forbesi) highly constant and grade 3 weight.
Fig. 9. Distribution of fusions of our site groups ("numbers" classification) in Petersen's main sampling area. Inset area is given in Fig. 8. Macoma baltica groups—closed square; Echinocardium cordatum—closed circle; Cyprina islandica groups—open circle.
ANALYSIS OF BOTTOM-COMMUNITY DATA

Table 7. Species groups (weight classification)

| Species group | Species                        |
|---------------|--------------------------------|
| 1             | 12, 17, 57, 72, 82             |
| 2             | 11, 55                         |
| 3             | 8, 10, 87                      |
| 4             | 5, 9, 32, 38, 61, 71, 79       |
| 5             | 6, 33, 54, 59, 65, 74, 75, 81, 83, 85, 88 |
| 6             | 34                             |
| 7             | 24, 45, 47, 56                 |
| 8             | 50, 69, 70, 80                 |
| 9             | 22, 26, 44, 52, 68, 86         |
| 10            | 1, 31, 33, 48, 67              |
| 11            | 14, 15, 16                     |
| 12            | 3, 4, 13, 20, 23, 25, 27, 28, 29, 37, 39, 40, 41, 49, 51, 53, 58, 60, 66, 73, 76, 77, 78, 84 |
| 13            | 18, 30, 36, 64                 |
| 14            | 2, 19, 42, 43, 46, 63          |
| 15            | 7, 21, 62                      |

Site-group 8. Species 57 (Nassa reticulata) and species 77 (Rissoa membranacea) VH constant and grade 2 weight; species 25 (Cardium exiguum), species 26 (C. fasciatum), and species 39 (Harmothoe imbricata) VH constant.

Site-group 9. Species 47 (Macoma baltica) VH constant and grade 2 weight; species 12 (Arctica armigera) and species 56 (Mytilus edulis) VH constant.

Site-group 10. Species 56 (M. edulis) VH constant and grade 1 weight; species 47 (Macoma baltica) VH constant and grade 2 weight; species 45 (Littorina littorea) highly constant and grade 2 weight.

Site-group 11. Species 47 (Macoma baltica) and species 56 (M. edulis) VH constant and grade 1 weight; species 55 (Mya arenaria) VH constant.

Site-group 12. Species 12 (Arctica armigera) VH constant and grade 1 weight.

Site-group 13. Species 14 (Astarte banksii), species 15 (A. borealis), and species 31 (Cyprina islandica) highly constant and grade 1 weight.

Site-group 14. Species 1 (Abra alba) and species 48 (Macoma calcarea) VH constant and grade 1 weight; species 47 (M. baltica) VH constant.

Site-group 15. Species 67 (Ophioglypha albida) VH constant and grade 2 weight; species 1 (Abra alba) and species 48 (M. calcarea) highly constant and grade 2 weight.

Site-group 16. Species 1 (A. alba), species 48 (M. calcarea), and species 67 (O. albida) VH constant and grade 2 weight.

Site-group 17. Species 67 (O. albida) VH constant and grade 2 weight; species 33 (Echinocardium cordatum) and species 48 (M. calcarea) highly constant and grade 1 weight.

Site-group 18. Species 80 (Strongylocentrotus droebachiensis) VH constant and grade 1 weight; species 26 (Cardium fasciatum) and species 67 (O. albida) VH constant.

Site-group 19. Species 33 (Echinocardium cordatum) and species 76 (Psolus phantapus) VH constant and grade 1 weight; species 80 (S. droebachiensis) highly constant and grade 1 weight.

Site-group 20. Species 33 (E. cordatum) VH constant and grade 1 weight; species 88 (Venus gallina) VH constant and grade 2 weight.

Site-group 21. Species 31 (Cyprina islandica) and species 33 (E. cordatum) highly constant and grade 1 weight; species 48 (Macoma calcarea) highly constant and grade 2 weight.

Site-group 22. Species 87 (Turritella terebra) VH constant and grade 1 weight; species 8 (Amphitrite filiformis) and species 33 (E. cordatum) highly constant and grade 1 weight.

Site-group 23. Species 21 (Brissopsis lyrifera) VH constant and grade 1 weight; species 7 (Amphitrite chiajei) highly constant and grade 1 weight.

Site-group 24. Species 50 (Modiola modiolus) and species 70 (Ophiopholis aculeata) VH constant and grade 1 weight; species 68 (Ophioglypha robusta) VH constant and grade 2 weight.

Site-group 25. Species 48 (Macoma calcarea) VH constant and grade 1 weight; species 14 (Astarte banksii), species 67 (O. albida), and species 68 (O. robusta) VH constant and grade 2 weight.

Site-group 1. Species 34 (Echinocardium flavescens) highly constant and grade 2 weight; species 35 (Echinocyamus pusillus), species 67 (O. albida), and species 78 (Solen ensis) VH constant.

Site-group 2. Species 47 (Macoma balitica) VH constant; species 3 (Acera bullata) highly constant; species 24 (Cardium edule) grade 2 weight.

Site-group 4. Species 12 (Arctica armigera), species 34 (Echinocardium flavescens), species 45 (Littorina littorea), and species 82 (Terebellides strémii) VH constant.

Site-group 7. Medium constancy for nine species, none at even grade 3 weight.

Site-groups 26, 27, and 28 are single sites.

Of the 25 site groups which contain more than one site, in 21 cases the constant species are also the weighty ones, giving Petersen-type communities (site-groups 3, 5, 6, 8-25). In three cases the constant species are not the weightiest (site-groups 1, 2, 4), and in one case (site-group 7) there is only medium constancy and low weights throughout; this approximates to a "nil-return" group.

Comparison of Classifications

Four classifications are to be considered: (a) Petersen's original, (b) presence-absence data, (c)
### Table 8. Site correspondences between Petersen site groups and those of our numbers classification (A) and weights classification (B)

#### (A) Numbers classification

| Petersen site groups | Number of sites in group | Number of site group | Number of sites in group | Number of sites corresponding |
|----------------------|--------------------------|----------------------|--------------------------|------------------------------|
| B. T.                | 5                        | (18)                 | 17                       | 4                            |
| B. n.                | 5                        | (20)                 | 7                        | 4                            |
| Rich E. b. c.        | 9                        | (24)                 | 22                       | 9                            |
| (E. T.) R. M.        | 9                        | (17)                 | 8                        | 5                            |
| a. b. c. influenced by R. M. | 5                  | (22)                 | 21                       | 4                            |
| a. b. c. frequently with *Cyprina* and sometimes d. | 10                  | (22)                 | 21                       | 6                            |

#### (B) Weights classification

| E. v.                | 7                        | (20)                 | 7                        | 5                            |
| B. T.                | 5                        | (22)                 | 11                       | 3                            |
| B. n.                | 5                        | (23)                 | 10                       | 5                            |
| E. (v.)              | 6                        | (21)                 | 11                       | 5                            |
| Haploops             | 3                        | (18)                 | 3                        | 2                            |
| Rich E. b. c.        | 9                        | (17)                 | 18                       | 7                            |
| (E. T.) R. M.        | 9                        | (19)                 | 3                        | 3                            |
| (E. T.) R. M.        | 9                        | (24)                 | 5                        | 5                            |
| Poor a. b. c. without E./without full grown *Cyprina*, shallow water, a. b. c. as a rule without E., a. b. c. frequently with *Cyprina* and sometimes d. | 6                  | (15)                 | 14                       | 5                            |
| a. b. c. influenced by R. M. | 5                  | (25)                 | 7                        | 5                            |

| Approximate corresponding “numbers” site groups |
|-----------------------------------------------|
| Number of sites in group | Number of site group |
|--------------------------|----------------------|
| 5                        | (18)                 |
| 5                        | (20)                 |
| 9                        | (24)                 |
| 9                        | (17)                 |
| 5                        | (22)                 |
| 10                       | (22)                 |

#### Site classifications

The first difficulty in comparisons is that one of Petersen’s site groups (d) characterized by *Macoma baltica* alone is much larger (46 sites) than any of our site groups. To effect a meaningful comparison, we must move to higher levels of classification of those site groups which involve *M. baltica* as the most important species. In Petersen’s analysis this involves fusion of site groups designated d, d. also a., d. also with b., d. and allied, and d. and allied poor. This enlarged group contains 61 sites; non-designated sites would increase it to 62.

In our presence-absence classification 69 sites are characterized by the presence of *M. baltica* (site-groups 1-4). The main difference is, first, that a few Petersen sites with *M. baltica* were placed in two of his a.b.c. groupings (a.b.c. with *Cyprina* and sometimes with d., and a.b.c. with d.), and second, that his broad d. grouping contained some sites without *M. baltica* (e.g., 39, 74, 84, 95, 108).

In our numbers classification 57 sites are characterized by *M. baltica* as the “prime” species (site-groups 1-8, 25, 26). Compared with Petersen, additional sites containing *M. baltica*, but dominated by other species, have been transferred to other site groups.

In our weights classification 23 sites are characterized by *M. baltica* as the “prime” species (site-groups 2, 5, 9, 11). Clearly many more occurrences of this species have been transferred to site groups better designated by other species.

Summarizing, Petersen’s d. groups of sites lie roughly between the two *M. baltica* groups of sites which appear in the presence-absence and numbers analyses, respectively. They bear scant relationship to those derived in our weights classification. It appears that Petersen’s classification had some unconscious bias towards ubiquity (hence the large number of sites characterized by *M. baltica* alone), some conscious bias towards numbers, but hardly any towards weights.

Correspondences were sought between the constituent units of the enlarged d. site group of Petersen and our various groups. There was only one reasonable correspondence; by fusing Petersen’s d. and allied, and his d. and allied poor we obtain the following sites: 32, 39, 52, 63, 74, 78, 83, 84, 91, 105. Half of these correspond with the eight sites...
in our numbers site-group 12 which comprises sites 3, 4, 32, 34, 39, 74, 84, 105.

The remaining comparisons exclude the presence-absence results, and involve the "non-d." Petersen site groups and the comparable groups in our numbers and weights classifications respectively. Correspondences are listed in Table 8. It is evident that Petersen's "non-d." groups of sites correspond better with our weights than our numbers classification, although this is only at a low level.

Our numbers and weights classifications of sites were compared in similar fashion, with details in archives. There were reasonably high correspondences between many of the site groups with 121 out of 193 sites in common. Nevertheless, some site groups in one classification had no counterpart in the other, and there were no cases of identical groups.

| Petersen Designation | Species | Numbers Designation | Species |
|----------------------|---------|---------------------|---------|
| B.n.                 | 21,62   |                     | 11      |
| Five groups          |         | 1, 14, 31, 33, 48   | 12      |

The Petersen groups bear a slightly greater resemblance to the weights groups. More significant is the fact that only two of our species groupings, numbers or weights, carry seven of Petersen's diagnostic species.

Our numbers and weights classification of species were then compared (details in archives). Correspondences were low between most of the species groups with only 40 out of 88 species showing rough correspondence in their groupings.

The above data concern all 88 species in the analysis; we now consider only the more constant species. There were 26 species of VH constancy in the numbers classification and 42 in the weights classification. This disparity is surprising; evidently the latter classification is somewhat "tighter" as regards high constancy. Of the 26 and 42 species, only 17 were common.

Comparisons of diagnostic species in terms of highest abundance and highest weight categories are not affected because arbitrary levels were selected in each case.

**Summary**

The comparison of classifications may be summarized as follows:

1) The results of the classifications differ considerably from each other.

2) Petersen's site groupings are more unequal than ours and suggest an unconscious bias towards giving diagnostic importance to the most ubiquitous species, *Macoma baltica*. In this his site groupings bear some resemblance to those derived from our DIVINF analysis.

3) Differences between our numbers and weights classifications are very evident. It is difficult to see how a numbers-and-weights-combined classification could be carried out by objective techniques. It is thus of interest to know whether Petersen's intuitive methods lay closer to our numbers or to our weights results.

4) In his various *Macoma baltica* site groups Petersen's results are closer to our numbers results, but in his site groups without *M. baltica* the correspondence with our weights method is closer.

5) In the species-group classifications there is only very slight correspondence between Petersen's groups and ours, slightly greater in the case of the weights.

6) The site groups of our numbers and weights classifications have more in common than our species groups.

7) The highly constant species revealed by our numbers and weights methods are markedly different in the numbers of species as well as the actual species involved.

**DISCUSSION**

The results of analyses of grab samples from New Guinea with computer techniques (Stephenson and Williams 1971) led us to expect that the analyses of Petersen's data might confirm the
existence of “Petersen-type” communities. This has proven to be so in the majority of cases. Petersen designated his communities by species which were dominant by numbers and weights. The disparities between our classifications imply that a compromise involving numbers and weights is not possible, but instead a decision must be made between communities based upon numbers and communities based on weights. Field and McFarlane (1968) have also compared numbers and weights classifications with computer methods. They obtain the same main groupings with the two methods, but obtained “differences in fine structure of the groupings” (p. 132). Comparison of the dendrograms (their Fig. 5 and 7) shows that the differences in “fine structure” are appreciable. They also compared the results of presence-absence analyses and analyses using numbers and weights. Their conclusions, with which we agree, are that analyses using quantities are necessary, and that it is far from obvious whether the extra labor in obtaining weight data for analysis is worthwhile.

Inherent in many concepts of the community is the idea that a group of species will have similar ecological requirements and hence act as a unit in pattern of site distribution. No such groups were revealed in Petersen’s original work. He sometimes listed a single species as characterizing a group of sites, sometimes it combined with one or more others, and elsewhere with yet others. Our analyses show much the same, except that we have dealt in detail with many more species (88 vs. 12) and so the “confusion” is compounded. We feel the confusion is a real phenomenon and to that extent the community concept is weakened.

The lack of correspondence between species occurrences has already been documented in a North Sea locale by Eisma (1966), who worked on molluscs only and used correlation coefficient matrices between pairs of the 16 most important species. Two matrices were used, based upon presence-absence data and upon abundance data. Surprisingly they led to very similar conclusions: that although he confirmed “the reliability of the community concept of Petersen” (p. 150), he could only distinguish with difficulty the bottom communities described by others in the North Sea. In this his conclusions are identical with our own. Eisma thought the difference was due to the small scale of his operations, but it seems almost equally likely that it was due to his different analytical approach. The communities he derived do not compare closely to those obtained in the present paper, although it is possibly significant that he obtained high correlations between _Abra alba_ and _Macoma baltica_.

In carrying out the present analyses we have not been able to allow for seasonality of occurrences, although Petersen has given the dates of his collections which might enable this to be done. In this respect Petersen’s intuitive analyses may have advantages over our own because he states (1914: 4) “... every single species ... is not of the same importance, either for characterization of the community as such or for characterization of the outer conditions on which the existence of the community is dependent; many animals only occur in quantity at certain times of the year, hence called seasonal animals; from the different quantities in which they occur on the lists we are, therefore, in general not able to draw any conclusions as to the composition of the community.” In spite of this statement it is not obvious which, if any, species Petersen excluded, and it seemed desirable for us not to exclude any for this reason.

Problems of analysis and interpretation arise if variations of communities in terms of area and also of time are to be considered. Hailstone (1970) has faced these problems in a survey of the fauna at the mouth of the Brisbane River, which leads into Moreton Bay. For each month of the year the data reveal site groups and species groups related through coincidence tables. But from month to month the site groups alter their composition and so do the species groups. Current grab work in Moreton Bay (Stephenson, Williams, and Cook, unpublished data) reveals that there are few species whose numbers remain constant from one season to another or from one area to another. We are uncertain how we shall analyze and define somewhat indefinite communities in such a context, but have noted the effective use of analyses of variance by Green and Hobson (1970). Until this has been done we must select whether area or time seems the more important variable. In the present work we have been forced to neglect time and restrict the analyses to areas.

Based upon a given sampling program, a decision is needed upon how many site groups to recognize. In the present work it seemed that the optimal number to obtain “tight” groupings in the two-way coincidence tables was approximately 25. Petersen designated approximately this number, but comparisons show that the groupings are conspicuously different. When our site groups are map-plotted, the results show as much topographical confusion as topographical pattern, and this is only slightly reduced when faunistically similar site groups are fused (Fig. 6, 7, 8, and 9).

Workers since Petersen have spaced their grab stations at very different distances apart, ranging
from about 30 miles apart (Zenkewitch, Brotzky, and Idelson 1928) to about seven per square mile (Davis 1923, 1925). Spacing ought to relate, first, to the heterogeneity of the area investigated and, second, to whether macropatterns or micropatterns are sought. This in turn will be related to the smallest size of the organisms under consideration, and with smaller sieve sizes and more refined sorting techniques the scale of patterning will become smaller. The existence of small-scale heterogeneity even in the macrofauna was recorded by Ford (1923) in the English Channel, who noted that on several occasions a slight change in the position of the ship gave striking changes in fauna and substratum. Holme (1953) further investigated this “patchiness” by obtaining double samples at a known distance apart. In current work in Moreton Bay we have obtained “communities” which differ noticeably within a 20-m distance.

Until the micropatterns in an area have been investigated, the reality of macropatterns as revealed by grab sampling may remain uncertain. Petersen’s multiple sampling allows patterns on a very small scale to be neglected, but the wide spacing of most of his sites suggests that the area was undersampled from the aspect of large-scale patterns. This would explain the sort of topographical results we have obtained by analysis of his data.

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## Appendix 1. Descriptive data for Petersen’s sites and station numbers used in this study

| Our station number | Locality          | Petersen’s station number | Communities | Number of samples |
|--------------------|-------------------|---------------------------|-------------|------------------|
| 1                  | North Sea         | 1                         | E. v.       | 25               |
| 2                  |                   | 2                         | E. T.       | 25               |
| 3                  |                   | 3                         | B. T.       | 25               |
| 4                  |                   | 4                         | B. n.       | 25               |
| 5                  |                   | 5                         | E. v.       | 5                |
| 6                  |                   | 6                         | B. n.       | 10               |
| 7                  |                   | 7                         | B. T.       | 10               |
| 8                  |                   | 8                         | E. T.       | 10               |
| 9                  |                   | 9                         | E. v.       | 10               |
| 10                 |                   | 10                        | B. n.       | 20               |
| 11                 |                   | 11                        | E. T.       | 20               |
| 12                 |                   | 12                        | d. and allied poor | 25 |
| 13                 |                   | 13                        | E. v.       | 20               |
| 14                 |                   | 14                        | E. T.       | 50               |
| 15                 |                   | 15                        | E. (v.)     | 10               |
| 16                 |                   | 16                        | B. n.       | 50               |
| 17                 |                   | 17                        | B. v.       | 20               |
| 18                 |                   | 18                        | B. (v.)     | 10               |
| 19                 |                   | 19                        | B. T.       | 10               |
| 20                 |                   | 20                        | E. (v.)     | 10               |
| 21                 |                   | 21                        | E. v.       | 20               |
| 22                 |                   | 22                        | E. (v.)     | 10               |
| 23                 |                   | 23                        | Haploops    | 25               |
| 24                 |                   | 24                        | E. (v.)     | 10               |
| 25                 |                   | 25                        | Haploops    | 10               |
| 26                 |                   | 26                        | Reduced E. T. | 20 |
| 27                 |                   | 27                        | E. T.       | 10               |
| 28                 |                   | 28                        | E. (v.)     | 10               |
| 29                 |                   | 29                        | Reduced E. T. | 10 |
| 30                 |                   | 30                        | E. T.       | 10               |
| 31                 |                   | 31                        | E. (v.)     | 10               |
| 32                 |                   | 32                        | Reduced E. T. | 10 |
| 33                 |                   | 33                        | d. and allied poor | 10 |
| 34                 |                   | 34                        | Reduced E. T. | 10 |
| 35                 |                   | 35                        | Haploops    | 10               |
| 36                 |                   | 36                        | Reduced E. T. | 10 |
| 37                 |                   | 37                        | Reduced E. T. | 10 |
| 38                 |                   | 38                        | Reduced E. T. | 10 |
| 39                 |                   | 39                        | Reduced E. T. | 10 |
| 40                 |                   | 40                        | Reduced E. T. | 10 |
| 41                 |                   | 41                        | Reduced E. T. | 10 |
| 42                 |                   | 42                        | Reduced E. T. | 10 |
| 43                 |                   | 43                        | Reduced E. T. | 10 |
| 44                 |                   | 44                        | Reduced E. T. | 10 |
| 45                 |                   | 45                        | Reduced E. T. | 10 |
| 46                 |                   | 46                        | Reduced E. T. | 10 |
| 47                 |                   | 47                        | Reduced E. T. | 10 |
| 48                 |                   | 48                        | Reduced E. T. | 10 |
| 49                 |                   | 49                        | Reduced E. T. | 10 |
| 50                 |                   | 50                        | Reduced E. T. | 10 |
| 51                 |                   | 51                        | Reduced E. T. | 10 |
| 52                 |                   | 52                        | Reduced E. T. | 10 |
| 53                 |                   | 53                        | Reduced E. T. | 10 |
| 54                 |                   | 54                        | Reduced E. T. | 10 |
| 55                 |                   | 55                        | Reduced E. T. | 10 |
| 56                 |                   | 56                        | Reduced E. T. | 10 |
| 57                 |                   | 57                        | Reduced E. T. | 10 |
| 58                 |                   | 58                        | Reduced E. T. | 10 |
| 59                 |                   | 59                        | Reduced E. T. | 10 |
| 60                 |                   | 60                        | Reduced E. T. | 10 |
| 61                 |                   | 61                        | Reduced E. T. | 10 |
| 62                 |                   | 62                        | Reduced E. T. | 10 |
| 63                 |                   | 63                        | Reduced E. T. | 10 |
| 64                 |                   | 64                        | Reduced E. T. | 10 |
| 65                 |                   | 65                        | Reduced E. T. | 10 |
| 66                 |                   | 66                        | Reduced E. T. | 10 |
| 67                 |                   | 67                        | Reduced E. T. | 10 |
| 68                 |                   | 68                        | Reduced E. T. | 10 |
Our station number | Locality         | Petersen's station number | Communities                                                   | Number of samples |
|-------------------|-----------------|---------------------------|---------------------------------------------------------------|-------------------|
| 69                | "               | 16                       | Poor E. a.b. c.                                               | 10                |
| 70                | "               | 24                       |                                                                  | 10                |
| 71                | Sound           | 4                        | (E.T.) R. M.                                                  | 10                |
| 72                | Samsø-Belt      | 21                       | Reduced (E.T.) with rich influence of R. M.                   | 10                |
| 73                | "               | 20                       | Rich E. b. c.                                                 | 10                |
| 74                | Kattegat        | 39                       | d. and allied poor                                            | 5                 |
| 75                | Sound           | 6                        | d.                                                            | 50                |
| 76                | "               | 5                        | d.                                                            | 50                |
| 77                | Samsø-Belt      | 1                        | (E.T.) R. M.                                                  | 50                |
| 78                | "               | 1                        | d. and allied                                                 | 10                |
| 79                | Samsø-Belt      | 6                        | Reduced (E.T.) with rich influence of R. M.                   | 10                |
| 80                | Isefjord        | 2                        | Very much reduced v.                                          | 10                |
| 81                | Sound           | 3                        | a. b. c. with d.                                              | 25                |
| 82                | Samsø-Belt      | 5                        | Reduced (E.T.) with rich influence of R. M.                   | 10                |
| 83                | "               | 19                       | d. and allied                                                 | 20                |
| 84                | "               | 8                        | Rich E. b. c.                                                 | 10                |
| 85                | "               | 7                        | Poor E. a. b. c.                                              | 25                |
| 86                | Isefjord        | 1                        | Very much reduced v.                                          | 50                |
| 87                | Sound           | 2                        | (E.T.)                                                        | 10                |
| 88                | "               | 9                        |                                                                  | 10                |
| 89                | Samsø-Belt      | 17                       | Poor E. a. b. c.                                              | 10                |
| 90                | "               | 18                       | d. and allied                                                 | 20                |
| 91                | Isefjord        | 2                        | Poor E. a. b. c.                                              | 10                |
| 92                | "               | 4                        | d.                                                            | 25                |
| 93                | Isefjord        | 4                        | d.                                                            | 20                |
| 94                | "               | 6                        | d.                                                            | 20                |
| 95                | "               | 3                        | d.                                                            | 20                |
| 96                | Samsø-Belt      | 30                       | Poor E. a. b. c.                                              | 10                |
| 97                | "               | 25                       | Rich E. b. c.                                                 | 20                |
| 98                | "               | 27a                      | "                                                            | 20                |
| 99                | "               | 27b                      | "                                                            | 10                |
| 100               | "               | 3                        | Rich E. b. c.                                                 | 20                |
| 101               | Sound           | 1                        | a. b. c. with d.                                              | 25                |
| 102               | Samsø-Belt      | 4                        | Rich E. b. c.                                                 | 20                |
| 103               | "               | 26                       | d.                                                            | 20                |
| 104               | "               | 29                       | d. and allied                                                 | 5                 |
| 105               | Great Belt      | 28                       | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 5                |
| 106               | Great Belt N. of Sprogø | 12                | d.                                                            | 20                |
| 107               | "               | 14                       | d.                                                            | 10                |
| 108               | "               | 13                       | a. b. c. frequently with E.                                    | 10                |
| 109               | "               | 26                       | a. b. c. as a rule with Cyprina.                               | 12                |
| 110               | "               | 29a                      | d.                                                            | 5                 |
| 111               | Little Belt     | 9                        | d.                                                            | 5                 |
| 112               | Great Belt N. of Sprogø | 29b                | a. b. c. frequently with E.                                    | 22                |
| 113               | "               | 11                       | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 22                |
| 114               | "               | 27                       | a. b. c. frequently with E.                                    | 20                |
| 115               | Great Belt      | 27                       | a. b. c. as a rule with Cyprina.                               | 8                 |
| 116               | Great Belt N. of Sprogø | 15                | a. b. c. frequently with E.                                    | 50                |
| 117               | "               | 25                       | a. b. c. as a rule with Cyprina.                               | 25                |
| 118               | Little Belt     | 4                        | a. b. c. frequently with E.                                    | 50                |
| 119               | Great Belt N. of Sprogø | 9                        | a. b. c. as a rule with Cyprina.                               | 25                |
| 120               | Great Belt      | 24                       | a. b. c. frequently with E.                                    | 50                |
| 121               | True Baltic     | 6                        | a. b. c. frequently with E.                                    | 10                |
| 122               | Great Belt      | 31                       | a. b. c. frequently with E.                                    | 10                |
| 123               | "               | 2a                       | a. b. c. influenced by R. M.                                  | 11                |
| 124               | "               | 2b                       | "                                                            | 15                |
| 125               | "               | 2c                       | "                                                            | 14                |
| 126               | "               | 5                        | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 50                |
| 127               | Great Belt S. of Sprogø | 4a                        | a. b. c. as a rule without E.                                 | 50                |
| 128               | "               | 4b                       | "                                                            | 25                |
| 129               | Great Belt      | 16a                      | d.                                                            | 10                |
| 130               | "               | 16b                      | d.                                                            | 10                |
| 131               | "               | 19                       | d.                                                            | 10                |
| Our station number | Locality                          | Petersen's station number | Communities                                      | Number of samples |
|--------------------|-----------------------------------|---------------------------|-------------------------------------------------|------------------|
| 132                | Great Belt Nyborg Fjord           | 1a                        | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 50               |
| 137                | "                                 | 1b                        | "                                               | 25               |
| 138                | "                                 | 1c                        | "                                               | 10               |
| 136                | Great Belt S. of Sprogø            | 17                        | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 20               |
| 137                | "                                 | 6a                        | a. b. c. as a rule without E.                   | 50               |
| 138                | "                                 | 6b                        | "                                               | 50               |
| 139                | "                                 | 6c                        | "                                               | 25               |
| 140                | "                                 | 6d                        | "                                               | 10               |
| 141                | True Baltic                       | 7                         | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 10               |
| 142                | Great Belt S. of Sprogø            | 8                         | "                                               | 50               |
| 143                | "                                 | 3a                        | a. b. c. influenced by R. M.                    | 10               |
| 144                | "                                 | 3b                        | "                                               | 10               |
| 145                | "                                 | 8a                        | a. b. c. as a rule without E.                   | 50               |
| 146                | "                                 | 8b                        | "                                               | 50               |
| 147                | "                                 | 30                        | d.                                              | 5                |
| 148                | Great Belt                        | 7                         | Poor a. b. c. without E. and without fullgrown Cyprina, shallow water | 50               |
| 149                | "                                 | 22                        | a. b. c. influenced by R. M.                    | 10               |
| 150                | Sealand Archipelago               | 7                         | c.                                              | 10               |
| 151                | True Baltic                       | 8                         | d.                                              | 10               |
| 152                | Little Belt                       | 5                         | a. b. c. as a rule with Cyprina.                | 25               |
| 153                | Great Belt S. of Sprogø            | 23                        | d.                                              | 10               |
| 154                | Sealand Archipelago               | 6                         | d. also with b.                                | 40               |
| 155                | True Baltic                       | 1                         | d.                                              | 20               |
| 156                | Sound                             | 8                         | d.                                              | 10               |
| 157                | Sealand Archipelago               | 8                         | d.                                              | 10               |
| 158                | Little Belt                       | 2                         | a. b. c. as a rule with Cyprina.                | 25               |
| 159                | True Baltic                       | 2                         | d.                                              | 8                |
| 160                | "                                 | 3                         | d.                                              | 10               |
| 161                | "                                 | 6a                        | d.                                              | 50               |
| 162                | "                                 | 6b                        | d.                                              | 8                |
| 163                | "                                 | 10                        | d.                                              | 10               |
| 164                | "                                 | 8a                        | d.                                              | 10               |
| 165                | "                                 | 8b                        | d.                                              | 10               |
| 166                | Great Belt S. of Sprogø            | 10                        | d.                                              | 25               |
| 167                | "                                 | 21                        | a. b. c. as a rule without E.                   | 10               |
| 168                | "                                 | 20                        | d.                                              | 10               |
| 169                | Sealand Archipelago               | 5                         | d. also with b.                                | 40               |
| 170                | True Baltic                       | 9                         | d.                                              | 10               |
| 171                | Little Belt                       | 7                         | d.                                              | 10               |
| 172                | Sealand Archipelago               | 4                         | d.                                              | 10               |
| 173                | Little Belt                       | 1                         | a. b. c. as a rule with Cyprina.                | 25               |
| 174                | True Baltic                       | 4                         | d. also a.                                      | 25               |
| 175                | Sealand Archipelago               | 2                         | d.                                              | 20               |
| 176                | True Baltic                       | 5                         | d. also a.                                      | 20               |
| 177                | Sealand Archipelago               | 1                         | d.                                              | 10               |
| 178                | "                                 | 3a                        | d.                                              | 10               |
| 179                | "                                 | 3b                        | d.                                              | 10               |
| 180                | True Baltic                       | 10                        | d. also a.                                      | 10               |
| 181                | Western Baltic                    | 1                         | a. b. c. frequently with Cyprina and sometimes d. | 25               |
| 182                | "                                 | 2                         | a. b. c. frequently with Cyprina and sometimes d. | 20               |
| 183                | "                                 | 13                        | a. b. c. frequently with Cyprina and sometimes d. | 10               |
| 184                | "                                 | 3                         | a. b. c. frequently with Cyprina and sometimes d. | 20               |
| 185                | "                                 | 5                         | a. b. c. frequently with Cyprina and sometimes d. | 10               |
| 186                | "                                 | 4                         | "                                               | 25               |
| 187                | "                                 | 12                        | "                                               | 15               |
| 188                | "                                 | 11                        | "                                               | 15               |
| 189                | "                                 | 10                        | "                                               | 10               |
| 190                | "                                 | 6                         | "                                               | 10               |
| 191                | "                                 | 7                         | "                                               | 10               |
| 192                | "                                 | 8                         | "                                               | 10               |
| 193                | "                                 | 9                         | "                                               | 10               |
### Appendix 2 (Continued)

| Species | Original number | After eliminating species occurring once | After eliminating incomplete identifications | After being eliminated by DIVIMP | After being eliminated by DIVIMP five or less times | Fall 1972 |
|---------|----------------|-----------------------------------------|---------------------------------------------|-----------------------------|------------------------------------------------|----------|
| Halcryctys spinulosus | 112 | 88 | 53 | 43 | --- | --- |
| Haloplos tubicolora | 113 | 89 | --- | --- | --- | --- |
| Harmothoe glabra | 114 | --- | --- | --- | --- | --- |
| H.投机ica | 115 | 90 | 54 | 44 | 39 | --- |
| Harmothoe sp. | 116 | 91 | --- | --- | --- | --- |
| H. variegata | 117 | 92 | --- | --- | --- | --- |
| Hydrobia ulvae | 118 | 93 | 55 | 45 | 40 | --- |
| L. disputa | 119 | --- | --- | --- | --- | --- |
| L. variegata | 120 | --- | --- | --- | --- | --- |
| L. variegata | 121 | 94 | 56 | --- | --- | --- |
| L. variegata | 122 | 95 | 57 | 46 | 41 | --- |
| L. variegata | 123 | 96 | --- | --- | --- | --- |
| L. variegata | 124 | 97 | --- | --- | --- | --- |
| L. variegata | 125 | --- | --- | --- | --- | --- |
| L. variegata | 126 | 98 | --- | --- | --- | --- |
| L. variegata | 127 | 99 | --- | --- | --- | --- |
| L. variegata | 128 | 100 | 58 | 47 | 42 | 28 |
| L. variegata | 129 | 101 | 59 | 48 | 43 | 29 |
| L. variegata | 130 | 102 | --- | --- | --- | --- |
| L. variegata | 131 | 103 | 60 | 49 | 44 | 30 |
| L. variegata | 132 | 104 | --- | --- | --- | --- |
| L. variegata | 133 | 105 | 61 | 50 | 45 | --- |
| L. variegata | 134 | 106 | --- | --- | --- | --- |
| L. variegata | 135 | 107 | --- | --- | --- | --- |
| L. variegata | 136 | 108 | --- | --- | --- | --- |
| L. variegata | 137 | --- | --- | --- | --- | --- |
| L. variegata | 138 | 109 | 62 | 51 | 46 | 31 |
| L. variegata | 139 | --- | --- | --- | --- | --- |
| L. variegata | 140 | 110 | 63 | 52 | 47 | 32 |
| L. variegata | 141 | 111 | 64 | 53 | 48 | 33 |
| L. variegata | 142 | 112 | --- | --- | --- | --- |
| L. variegata | 143 | 113 | --- | --- | --- | --- |
| L. variegata | 144 | 114 | 65 | 54 | 49 | 34 |
| L. variegata | 145 | 115 | 66 | --- | --- | --- |
| L. variegata | 146 | 116 | --- | --- | --- | --- |
| L. variegata | 147 | 117 | 67 | 55 | 50 | 35 |
| L. variegata | 148 | 118 | 68 | 56 | 51 | --- |
| L. variegata | 149 | 119 | 69 | 57 | 52 | 36 |
| L. variegata | 150 | 120 | --- | --- | --- | --- |
| L. variegata | 151 | --- | --- | --- | --- | --- |
| L. variegata | 152 | --- | --- | --- | --- | --- |
| L. variegata | 153 | 121 | 70 | 58 | 53 | --- |
| L. variegata | 154 | 122 | 71 | 59 | 54 | 37 |
| L. variegata | 155 | 123 | --- | --- | --- | --- |
| L. variegata | 156 | 124 | 72 | 60 | 55 | --- |
| L. variegata | 157 | 125 | 73 | --- | --- | --- |
| L. variegata | 158 | 126 | --- | --- | --- | --- |
| L. variegata | 159 | 127 | --- | --- | --- | --- |
| L. variegata | 160 | 128 | 74 | --- | --- | --- |
| L. variegata | 161 | 129 | 75 | 61 | 56 | 38 |
| L. variegata | 162 | 130 | --- | --- | --- | --- |
### APPENDIX 2 (Continued)

| Species | (Original number) | (After eliminating species occurring once) | (After eliminating species occurring once by DIVINE) | (After eliminating species occurring five or six times) | (After being through Bray-Curtis (2/70)) | (1) | (2) | (3) | (4) | (5) | (6) |
|---------|------------------|------------------------------------------|-----------------------------------------------|--------------------------------------------------|------------------------------------------|-----|-----|-----|-----|-----|-----|
| *Psolus phantasmus* | 224 177 | 107 86 | 76 |  |  |  |  |  |  |  |  |
| *Rissoa inconspicua* | 225 178 | 108 87 |  |  |  |  |  |  |  |  |  |
| *R. membranacea* | 226 199 | 109 88 | 77 |  |  |  |  |  |  |  |  |
| *R. rapflavus* | 227 |  |  |  |  |  |  |  |  |  |  |
| *Rissoa sp.* | 228 180 | 110 |  |  |  |  |  |  |  |  |  |
| *Sabellidae* | 229 181 | 111 |  |  |  |  |  |  |  |  |  |
| *Saxicava rugosa* | 230 182 |  |  |  |  |  |  |  |  |  |  |
| *Scalibregma bifarium* | 231 183 |  |  |  |  |  |  |  |  |  |  |
| *Scalpellum sp.* | 232 |  |  |  |  |  |  |  |  |  |  |
| *Scrobicularia plana* | 233 | 184 |  |  |  |  |  |  |  |  |  |
| *S. plana juv.* | 234 |  |  |  |  |  |  |  |  |  |  |
| *Serpulidae* | 235 |  |  |  |  |  |  |  |  |  |  |
| *Sigalion mathildae* | 236 |  |  |  |  |  |  |  |  |  |  |
| *Sipunculidae* | 237 |  |  |  |  |  |  |  |  |  |  |
| *Solen ensis* | 238 155 | 112 | 89 | 78 | 51 |  |  |  |  |  |  |
| *S. ensis juv.* | 239 156 | 113 | 90 | 79 | 52 |  |  |  |  |  |  |
| *S. pellucidus* | 240 |  |  |  |  |  |  |  |  |  |  |
| *Solen sp.* | 241 |  |  |  |  |  |  |  |  |  |  |
| *Spatangus purpurascens* | 242 187 | 114 | 91 |  |  |  |  |  |  |  |  |
| *Strongylocentrotus droebachiensis* | 243 188 | 115 | 92 | 80 | 53 |  |  |  |  |  |  |
| *Syringa inaequerr* | 244 189 |  |  |  |  |  |  |  |  |  |  |
| *Tapes sp.* | 245 |  |  |  |  |  |  |  |  |  |  |
| *Tectura virginica* | 246 190 |  |  |  |  |  |  |  |  |  |  |
| *Tellina fabula* | 247 191 | 116 | 93 | 81 |  |  |  |  |  |  |  |
| *T. psitex* | 248 192 |  |  |  |  |  |  |  |  |  |  |
| *T. tenus* | 249 193 |  |  |  |  |  |  |  |  |  |  |
| *Terebellides stromi* | 250 194 | 117 | 94 | 82 | 54 |  |  |  |  |  |  |
| *Thraulida papyracca* | 251 195 | 118 | 95 | 83 |  |  |  |  |  |  |  |
| *T. praecestans* | 252 |  |  |  |  |  |  |  |  |  |  |
| *Thynaria thalas* | 253 |  |  |  |  |  |  |  |  |  |  |
| *Tipula - larvae* | 254 197 | 119 | 96 | 84 |  |  |  |  |  |  |  |
| *Travisia forbes* | 255 198 | 120 | 97 | 85 | 55 |  |  |  |  |  |  |
| *Trochus cincturus* | 256 199 | 121 | 98 |  |  |  |  |  |  |  |  |
| *Trochus obstreperos* | 257 200 | 122 | 99 | 86 |  |  |  |  |  |  |  |
| *Troponia sp.* | 258 201 |  |  |  |  |  |  |  |  |  |  |
| *Trophon troncolus* | 259 202 |  |  |  |  |  |  |  |  |  |  |
| *Turritella steebow* | 260 203 | 123 | 100 | 87 | 56 |  |  |  |  |  |  |
| *Uriculus obtusus* | 261 204 |  |  |  |  |  |  |  |  |  |  |
| *Urticula sp.* | 262 |  |  |  |  |  |  |  |  |  |  |
| *Vestris gallina* | 263 205 | 124 | 101 | 88 | 57 |  |  |  |  |  |  |
| *V. gallina* | 264 206 |  |  |  |  |  |  |  |  |  |  |
| *V. omar* | 265 207 |  |  |  |  |  |  |  |  |  |  |

*Number 150 deleted, double entry* Modiolus modiolus—*Modiola modiola* (147).

### APPENDIX 3 (Continued)

**APPENDIX 4. Grades of abundance of species in site groups**

| Site group | VH | H | M |
|------------|----|---|---|
| 1 | 14 | 12 | 17 | 12, 67 |
| 2 | 12 | 21 | 35 | 52, 51, 82 |
| 3 | 19 | 24 | 37 | 48, 43, 84 |
| 4 | 28 | 35 | 42 | 49, 51, 82 |
| 5 | 37 | 39 | 13 | 67, 51, 82 |
| 6 | 22 | 24 | 35 | 48, 43, 84 |
| 7 | 26 | 32 | 37 | 49, 51, 82 |
| 8 | 17 | 19 | 21 | 26, 43, 82 |
| 9 | 12 | 26 | 38 | 49, 51, 82 |

*For derivation, see text. Arrangement is in numerical order within grades.*

### APPENDIX 3. Grades of constancy of species in each site group of the “final numbers” analysis

| Site group | VH | H | M |
|------------|----|---|---|
| 1 | 47 | 12 | 56 |
| 2 | 47 | 12 | 56 |
| 3 | 47 | 12 | 56 |
| 4 | 47 | 12 | 56 |
| 5 | 47 | 12 | 56 |
| 6 | 47 | 12 | 56 |
| 7 | 47 | 12 | 56 |
| 8 | 47 | 12 | 56 |
| 9 | 47 | 12 | 56 |
| 10 | 47 | 12 | 56 |

*Grades of constancy are VH, very high (100–95%); H, high (94–66%); and M, medium (65–33%). Within grades, species are in numerical order. Numbering of species as in Appendix 2, column 5 (88 species).*
### Appendix 5. Weights classification\(a\)

| Site group | Grade of constancy* |
|------------|---------------------|
| VH         | H                   |
| 1          | 35, 67, 78          | 34, 37, 59, 65, 66 |
| 2          | 47                  | 3                        |
| 3          | 11, 47, 72          | —                        |
| 4          | 12, 34, 45, 82      | 17, 72                   |
| 5          | 12, 17, 24, 47, 49, | —                        |
|            | 72                  | —                        |
| 6          | 65                  | 12, 46, 85               |
| 7          | —                   | b                        |
| 8          | 25, 26, 39, 57, 77  | —                        |
| 9          | 47                  | 12, 56                   |
| 10         | 47, 56              | 45                       |
| 11         | —                   | 24, 47, 56               |
| 12         | 82                  | —                        |
| 13         | 6                   | 1, 14, 15, 16, 26, 31, 48, 67 |
| 14         | 1, 47, 48           | 33, 67                   |
| 15         | 67                  | 1, 48                    |
| 16         | 1, 48, 67           | 10, 33                   |
| 17         | 67                  | 1, 26, 28, 31, 33, 43, 48, 63 |
| 18         | 26, 67, 80          | 9, 42, 68, 71            |
| 19         | 8, 33, 42, 67, 76   | 2, 9, 31, 43, 80         |
| 20         | 33, 88              | 54, 59, 63, 65, 81       |
| 21         | —                   | 31, 33, 48, 67, 71       |
| 22         | 87                  | 2, 8, 10, 19, 33, 63     |
| 23         | 21                  | 2, 7, 62, 87             |
| 24         | 50, 63, 68, 70      | 8, 31, 33, 42, 44, 46    |
| 25         | 14, 26, 48, 67, 68  | 15, 16, 22, 44, 50, 52, 70, 76, 80 |
| 26         | 8, 10, 13, 31, 38,  | —                        |
|            | 61, 74, 88          | —                        |
| 27         | 11, 47, 57          | —                        |
| 28         | 29, 49              | —                        |

*Species of two uppermost grades of constancy in each site group. Within grades species are in numerical order.
*Medium constancy for species: 12, 17, 28, 35, 47, 49, 56, 57, 65.

### Appendix 6. Weightiness of species in site groups

| Site group | Upper grades of weightiness* |
|------------|------------------------------|
|            | 1 | 2 |
| 1          | — | 34 |
| 2          | — | 24 |
| 3          | 11 | 47 |
| 4          | 47 | 24 |
| 5          | — | b |
| 6          | — | — |
| 7          | — | — |
| 8          | — | 17, 57, 77 |
| 9          | — | 15, 47 |
| 10         | 56 | 45, 47 |
| 11         | 47, 55, 56 | 11, 24 |
| 12         | 82 | — |
| 13         | 14, 15, 31 | 16, 48, 67 |
| 14         | 1, 48 | — |
| 15         | — | 1, 48, 67 |
| 16         | 1, 33, 69 | 10, 31, 48 |
| 17         | 33, 48 | 1, 31, 67 |
| 18         | 80 | 9, 31 |
| 19         | 33, 50, 76, 80 | 8, 9, 31, 67, 70 |
| 20         | 33 | 49, 81, 88 |
| 21         | 31, 33 | 48 |
| 22         | 8, 33, 87 | 10 |
| 23         | 7, 21 | 8, 62 |
| 24         | 31, 33, 50, 70, 80 | 8, 44, 68, 76 |
| 25         | 48, 50, 70, 80 | 14, 15, 16, 17, 22, 31, 33, 44, 67, 68, 76 |
| 26         | 10, 31 | 8, 13, 61 |
| 27         | — | 47, 57 |
| 28         | 49 | — |

*Within grades arrangement is in numerical order.
*bNext grade (3), 0.5–1 for species 11, 17, 47, 49.
*cNext grade (3), 0.5–1 for species 65, 85.
*dAlmost next grade (3), 0.45–0.5 for species 17, 57.