# LARVAL FISH DATA 

# a new approach to analysis 

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and
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## a new approach to analysis

## Sally L Richardson <br> and

William Stephenson

## abstract

The application of numerical classification techniques to ichthyoplankton data is introduced and demonstrated. Data on larval fishes were classified hierarchically using polythetic agglomerative techniques. Bray-Curtis dissimilarity Falues mere cajculated from transformed data and clustered using a group average sorting strategy to obtain site, time, and species groups. This approach provides insight into complex spatial and temporal interrelationships among species of larval fish which are not evident from the traditional species-by-species analysis of data from ichthyoplankton surveys.

## acknowledgment

Sincere thanks are extended to Dr. Michael D. Richardson for thoughtful discussions and helpful comments. Dr. William G. Pearcy reviewed the manuscript.


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## INTRODUCTION

The purpose of this paper is to introduce the techniques of numerical classification to ichthyoplanktologists. It outlines a method of data analysis that will be helpful to interpret distribution and abundance data on fish eggs and larvae. The pattern recognition techniques described here have been used successfully with other forms of data, e.g., benthos (Stephenson et al. 1972, 1974, 1976; Boesch 1973; Richardson 1976) and demersal fishes (Musick 1976; Stephenson and Dredge 1976), but have not been used previously with ichthyoplankton. These "among species" analyses can complement the "single species" analyses commonly used in ichthyoplankton studies (e.g., Ahlstrom 1965, 1971, 1972; Waldron 1972; Richardson 1973; Moser et al. 1974; Smith et al. 1975; and others) by demonstrating broad patterns in data that may not be obvious from the latter approach. These patterns can provide insight into complex temporal and spatial interrelationships anong species of larval fish.

Few attempts have been made to describe "among species" patterns in ichthyoplankton data. Leis and Miller (1976) examined inshore-off shore distribution gradients of Hawaiian fish laryae. They grouped larvae into four types based on adult habitat and mode of spawning. Areas sampled were then categorized according to percent composition in the larval fish catch of each of these four groups and distribution patterns of larvae in each group were compared. No formal numerical techniques were applied to the data. Kendall (1975) used Fager's (1957) recurrent group analysis in a preliminary examination of groupings within northwest Atlantic fish larvae. Results based on this method, which only considers co-occurrences and not abundances, indicated that there were four recurring groups of fish larvae in the Middle Atlantic Bight: a spring, summer, fall, and offshore group. While this technique has been used rather widely in marine ecology, it has some serious disadvantages as discussed by Boesch (1977) in a review of numerical classification techniques. He concluded
that "there remains little value in the continued use of the recurrent group analysis and it is best considered obsolete." Richardson and Pearcy (1977) described "among species" patterns in ichthyoplankton off Oregon using a similarity coefficient matrix based on Sanders (1960) dominance affinity index. They found two assemblages (i.e., station groups) of larval fishes, a coastal and an offshore group. They also categorized species as "coastal" or "offshore" if 80 percent or more of all larvae occurred at the coastal or offshore stations. However, they proceeded to characterize each assemblage with a more traditional species by species approach.

This paper denonstrates the application of more sophisticated methods of numerical classification to temporal and spatial data on species of larval fish. Subsets of Richardson and Pearcy's (1977) data were chosen for demonstration and evaluation of the techniques because of accessibility and patterns known to be contained therein. The approach that was taken for analysis of the data is outlined. The strategies selected for classification, reasons for selection, results of the classifications, and evaluation of the effectiveness of the techniques are presented. The general applicability of these numerical classification techniques to ichthyoplankton data is discussed.

## COLLECTIONS

Details of sampling times, locations, and procedures were given by Richardson (1977) and Richardson and Pearcy (1977). Briefly, bongo net ( 0.7 m mouth diameter, 0.571 mm mesh nets) plankton samples were taken at 12 stations along an east-west transect (lat. $44^{\circ} 39.1^{\prime N}$ ) off the mid-Oregon coast during 30 cruises made over a $1 \frac{1}{2}$ year period from January 1971 to August 1972. Stations were located $2,6,9,18,28,37,46,56,65,74$, 93 , and 111 kna offshore over the continental shelf and slope. A total of 287 station occupancies were made (Table 1). Tows were made obliquely through the water column from 150 m (or just above the bottom in shallower depths) to the surface. A measure of the volume of water filtered was provided by a flowneter in the mouth of each net and depth of tow was given by a time-depth recorder. Samples were preserved in $10 \%$ buffered formalin at sea.

All fish larvae were sorted, identified, and enumerated from one side of each bongo pair. The number of larvae in each sample was adjusted to the number under $10 \mathrm{~m}^{2}$ sea surface.

Of the 90 taxa identified in the samples, 78 were at the species level; the others were multispecies groups (see Richardson 1977; Richardson and Pearcy 1977). In the analyses here we refer to all taxa as "species" regardless of the polyspecific nature of some of them.

## DATA SETS SELECTED FOR ANALYSIS

Data from the original 287 samples (Table 1) formed an incomplete three dimensional matrix of 90 species $x 12$ sites ( $=$ stations) $\times 30$ times (= sampling or cruise dates). Some stations were not sampled on cach cruise. For this data set, two criteria were used to select samples for analysis: (1) only daytime samples were selected and
(2) only those that formed conplete data matrices were considered. These criteria allowed for selection of the most complete data series available in the original data set, and the selection of only daytime samples elininated the day-night avoidance problem discussed by Richardson and Pearcy (1977). Two subsets of data were chosen: Subset 1 , in which species $x$ sites were of prime interest, consisted of 24 samples from 12 sites (stations 2 to 111 ) and two times (2-3 August 1971 and 28-29 June 1972) and contained 33 species; Subset 2, in which species $x$ times were of prime interest, consisted of 96 samples from four sites (stations 2 to 18 ) and 24 times ( 6 January 1971 to 5 August 1972) and contained 65 species. Only 112 of the original 287 samples were thus considered and eight samples were common to both subsets.

## APPROACH TO ANALYSIS

Each of the two data sets were threedimensional, consisting of species (s) $x$ sites ( $q$ for quadrats) $x$ times ( $t$ ). Data were sumed over a given dimension and the resultant two dimensional matrix was analyzed. First, species were sumed overall. Resultant values, set in a $q \times x$ matrix, were then examined for general trends to provide an overview of the data. The original matrices were then summed over the remaining dimensions and classified to examine patterns of occurrence of individual species in sites and in times.

## Data Summed Over Speaies

The $q x$ matrices gave the number of individuals ( $N$ ) and the number of species (S) from site to site (Subset 1 primarily) and from time to time (Subset 2). Mean values of $N$ and $S$ were plotted for each of the 12 sites (two times combined) in Subset 1 and each of the four sites (24
times combined) in Subset 2 (Figure 1) and for each of the 24 times (four sites combined) in Subset 2 (Figure 2). Each subset was also examined for variability in sites and times using variance of the mean values of $S$ and $N$ (Table 2).

The sites means in the Subset 1 data showed obvious trends (Fig. 1). The inshore sites had relatively high numbers of individuals and many species, the middle sites had few individuals and species, and the numbers of both individuals and species increased at the offshore sites. The means of the first four sites from the Subset 2 data showed the same tendencies.

The times means from the Subset 2 data were more difficult to interpret, partly because of gaps in the data at April 1971 and January-February 1972 (Fig. 2). Both S and N values were relatively low in January, increased to highs from February into July and then decreased to lower values from August through December 1971. S values were again high March through June 1972. N values were an order of magnitude lower in 1972 than in 1971 and exceeded $50 / 10 \mathrm{~m}^{2}$ only once in 1972 in May. Peak values of $S$ occurred in March and May 1971 while peak values of $N$ occurred in March and June 1971. The high $N$ value in June was due to large numbers of one "species" (Osmeridae). Whether the decrease in $S$ and $N$ values in late March 1971, between the two highest peaks, was part of a trend cannot be determined because of the missing April data. The high variability in the times data may be related, in part, to the seasonal nature of meroplanktonic animals.

In both subsets variance in $S$ means was much lower than in $N$ means (Table 2), partly because of the occasional very high abundance of a particular species. In Subset 1 data, variance was higher in site means than in time means, while in Subset 2 , variance was higher in time means than site means. This lends support to the chosen approach of examining site differences (lumping times) in Subset 1 and time differences (lumping sites) in Subset 2 . The highest variance was in N means over times in Subset 2 . This high variance in times means could indicate the potential within the data for "nonsense" groupings in the classification analyses due to random variability.

## Classification. Methods

For Subset I, where the main interest was in species $x$ sites, data were sumed over times giving an $s \times q$ matrix. For Subset 2, where the main interest was in species $x$
times, data were summed over sites giving an $s x$ matrix. Data in these matrices were then classified hierarchically using polythetic agglomerative techniques. Refer to C1ifford and Stephenson (1975) and Boesch (1977) for descriptions of these terms and justification of these choices. The objectives were to obtain site groups and species groups in Subset 1 and time groups and species groups in Subset 2.

Before classifying the data, rare species were eliminated, in this case species occurring at a single site in Subset 1 and species occurring at a single time in Subset 2 , provided that abundance values in the single site or time were less than $6.0 / 10 \mathrm{~mm}^{2}$. The criteria for eliminating rare species were somewhat arbitrary, based in part on knowledge of the data set and the fact that a single occurrence of a species has little classificatory meaning (Boesch 1977).

Because we considered abundance to be important, we chose to use the Bray-Curtis dissimilarity coefficient, which is sensitive to abundance:

$$
D_{12}=\frac{\sum_{i}^{n}\left|x_{1 j}-x_{2 j}\right|}{\sum_{1}^{\sum}\left(x_{1 j}+x_{2 j}\right)}
$$

where $D_{12}$ is a measure of dissimilarity between site (or time) 1 and $2 ; X_{1}$ and $X_{2}$ are values for the $j$ th species at each site (or time) and $n$ is the number of species found at the two sites (or times) (Clifford and Stephenson 1975). A Bray-Curtis value of 0 means complete similarity and a value of 1 means complete dissimilarity.

Before classification, the data were transformed to reduce the effects of dominant species. Since 7 of the 68 nonzero entries in the $s \times \mathrm{q}$ matrix of Subset 1 and 118 of the 408 nonzero entries in the $s x$ matrix of Subset 2 were less than unity, all values were first multiplied by 10 to eliminate values between 0 and 1 . Because of the differences in the heterogeneity of the two data sets values ranged from 0.46 to 47.10 in Subset 1 and from 0.29 to 1892.92 in Subset 2) differeni transformations were applied--a square root to Subset 1 and a $\log _{10}(\pi+1)$ to Subset 2. Ratios of highest to lowest values were 102.39 and 6527.31 before transformation and 10.12 and 7.24 after transformation in Subsets 1 and 2 respectively.

After traneformation, the data were classified following methods of Stephenson et a1. (1976). For sites (or times) classification, species $x$ sites (or species $x$ times) matrices were used, and Bray-Curtis dissimilarity measures were calculated and clustered by group average sorting. This clustering strategy was chosen because it is monotonic (no reversals), space conserving, and little prone to misclassification (lance and Williams 1967). For species classification, the transpose of the species $x$ site (or species $x$ times) matrix was used. The same procedures were followed as for the sites (or times) classification, except that after transfomation species were standardized so that proportionalities of species were considered. Thus species were grouped together primarily on the basis of similar patterns of relative distribution. Selection of acceptable fusion levels for site, tine, and species groups was somewhat subjective, based in part on intuitive knowledge of the data and experience with other data sets.

Site and time groups were then characterized by dominant species, i.e., those having a Biological Index (BI) value $>1$. This value, which takes into account both abundance and frequency, was determined by a ranking procedure modified from Fager (1957) in which the most abundant species in a site or time is given five points, the next four, etc. Scores for each species are summed for each site or time and divided by the number of sites or times. Species groups were described in tems of most frequently occurring species. Relationships between species groups and site or time groups were demonstrated by two-way coincidence tables calculated from the site $x$ species classification analysis in Subset 1 and the time $x$ species classification analysis in Subset 2. These tables show the percentage of species group constancy at each site or time group, i.e., the frequency with which species within a species group occur at sites or times within a site or time group, i.e., "cell density" (Stephenson et al. 1972).

## Classifioation Results

In the Subset 1 data, two main site groups fused at Bray-Curtis values between 0.50 and 0.55 (Fig. 3). Site Group A consisted of four inshore stations, $2,6,9$, and 18. Site Group B consisted of six offshore stations, $46,56,65,74,93$, and 111. Stations 28 and 37 , not included in either site group, were intermediate to these two site groups in geographic location and contained relatively few species and individuals. Dominant species that charac-
terized Site Group A were Osmeridae (BI = 5.00), Psettichthys melanostiotue (1.75), Sebastes spp. (1.50), Miorogadus proximus (1.25), Isopsetta isotepts (1.25), Artedius sp. 1 (1.25), and Artedius sp. 2 (1.00) and Site Group B were Sebastes spp. (4.50), Engraulis mordax (3.25), and Stenobranchius Zeисорsams (3.25).

Two major species groups fused at BrayCurtis values of 0.63 and 0.74 in Subset 1 (Fig. 3). Although these values were relatively high, they were accepted because groupings below these levels did not appear to be more meaningful. Species Group 1 contained nine species. Those occurring at more than two sites were Artedius sp. 1 (frequency out of $12=5$ ), Osmeridae (4), Isopsetta isolepis (3), and Icelinus sp. 1 (3). Species Group 2 consisted of eight species. Those occurring at more than two sites were Sebastes spp. (11), Engraulis mordaw (8), Stenobraonius leucopsarus (5), Lyopsetta exilis (5), Cyclopteridae spp. 1 (5), and Protomyctophum thompsoni (5).

A cell density diagran (Fig. 3) showed that, in the Subset 1 data, Species Group 1 occurred primarily in Site Group A and Species Group 2 occurred primarily at Site Group B. Thus inshore species were concentrated at inshore stations and offshore species at offshore stations in sumer months.

In the Subset 2 data, three major time groups fused at Bray-Curtis values of 0.43, 0.52 , and 0.63 (Fig. 4). Time Group A could have been subdivided into two groups if a fusion level of 0.52 rather than 0.63 had been chosen, but the larger grouping was considered to be more appropriate based on the sampling dates involved and knowledge of ichthyoplankton seasonality in the area. Tine Group A contained six times, mainly fall and winter months, September through January. Time Group B contained eight times, primarily winter through spring, February through April plus May of 1971. Time Group C contained nine times, primarily summer, May through August. The 19 August 1971 time period was not included in any time group because of low numbers of species and individuals. Dominant species that characterized Time Group A were Parophrys vetulus ( $\mathrm{BI}=4.83$ ), Fsettichthys melanostiotus (2.33), Osmeridae (2.17), and Sebastes spp. Characterizing species of Time Group B were Isopsetta isolepis (3.00), Parophrys vetulus (2.88), Osmeridae (2.75), Anmodytes hexapterus (1.62), and Microgadus proximus ( 1.00 ), and those of Time Group C were Osmeridae (4.89), Isopsetta isolepts
(2.33), Microgadus proximus (2.33), and Psettichthys melanostiotus (2.00).

In Subset 2, two main species groups fused at Bray-Curtis values of 0.51 and 0.55 (Fig. 4). Other species groups chained on to these at higher fusion levels. All species involved with these chain groups occurred less than six times and generally had low abundances. Species Group 1 contained 12 species, the most frequent (occurring more than 14 times) being Sebastes spp. (18) and Parophrys vetulus (15). Species Group 2 contained 16 species, the most frequent being Osmeridae (23), Psettichthys melanostictus (20), Isopsetta isolepis (19), Artedius sp. 1 (19), Microgadus proximus (18), and Artedius sp. 2 (16).

The cell density diagram (Fig. 4) showed that Species Group 1 began to appear in fall and winter, Time Group $A$, and peaked in the winter-spring period, Time Group B. Species Group 2 occurred mainly in the winter-spring and sumer periods, Time Groups $B$ and $C$. There was a gradual shift in density from Species Group 1 to Species Group 2, probabiy reflecting winter and spring spawnings, which may also have been related to the abundance peaks discussed earlier. Although broad trends were evident, there was also considerable overlap among time groups and species groups.

## DISCUSSION OF THE TECHNIQUES

The results obtained by the numerical classification techniques used here are similar to those obtained by Richardson and Pearcy (1977), even though only subsets of their data were analyzed. We found coastal and offshore site groups at 2 to 18 km and 46 to 111 km offshore in sumer months. These were similar to the coastal and offshore assemblages found by Richardson and Pearcy at 2 to 28 and 37 to 111 knl offshore for both the 1971 and 1972 sampling periods. The classification techniques showed more clearly the transitional rature of the 28 and 37 km stations. Species groups probably were defined better by classification than by the abundance criteria used by Richardson and Pearcy, and relationships between species groups and site groups were demonstrated more clearly by the two-way coincidence tables than by simple description.

The three time groups we found in the $1 \frac{1}{2}$ years of data, i.e., August to January, February to May, May to July, were similar to the periods of peak and low abundances described by Richardson and Pearcy for the 1971 data with peaks fron February to March and from May to July, and lows in January
and from August through Decenber. The mumerical classification techniques clearly showed the transition of species from one time period to the next. Although May of 1971 joined with the winter-spring period, it was transitional between the winterspring period and the summer period in tems of dominant species. May of 1972 joined with the summer months, indicating reduced presence of "winter" species, possibly a result of earlier spawning that year. The cell density diagram showed transition and overlap between species groups and time groups more directly than the approach used by Richardson and Pearcy (1977) of comparing dominant taxa in the two periods of peak abundance.

After site, time, and species groups have been determined, each could be described in more detail, e.g., in terms of relative abundance of species in site or time groups, constancy and fidelity of species in species groups within site or time groups, etc. Groups could be compared with each other and with enviromental parameters. This was done in some detail by Richardson and Pearcy (1977) and will not be repeated here.

The effectiveness of classificatory techniques is limited by a number of factors and precautions are necessary. The taxonomic level to which fish larvae (and eggs) have been identified will strongly influence results, with the best information being derived from data in which all specimens have been identified to species or "species types." Patterns may not emerge if sampling has been inadequate in terms of seasonal or areal coverage. High variances in species and particularly in numbers could lead to nonsense groupings.

Even with these problems, we believe the pattern recognition techniques demonstrated in this paper are useful tools for analyzing ichthyoplankton data. Their main value is that they allow reduction of large volumes of data to a comprehensible level in a relatively short tine, compared to more cumbersone "single species" approaches. They are primarily descriptive tools that can be used effectively to sumarize data on distribution and abundance of ichthyoplankton. The patterns they describe may lead to a better understanding of the complexities and interactions of the system being studied, which in turn may lead to additional studies --more specific, more directed--to determine causal mechanisms.

LITERATURE CITED
Ahlstrom, E. H. 1965. Kinds and abundance of fishes in the California current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10:31-52.

Ah1strom, E. H. 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific based on collections made on EASTROPAC I. Fish Bull. 69:3-77.

Ah1strom, E. H. 1972. Kinds and aburdance of fish larvae in the eastern tropical Pacific on the multivessel EASTROPAC survey, and observations on the anmual cycle of Iarval abundance. Fish. Bull. 70:1153-1242.

Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21:226-244.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Environmental Protection Agency, Ecol. Res. Ser. EPA-600/3-77-033. 115 p .

Clifford, H. T., and w. Stephenson. 1975. An introduction to numerical classification. Academic Press, N.Y. 229 p.

Fager, E. W. 1957. Detemination and analysis of recurrent groups. Ecology 38:586-595.

Kendall, A. W., Jr. 1975. Patterns of larval fish distributions in the Middle Atlantic Bight. Effects of Energy Related Activities on the Atlantic Continental Shelf Conf., Brookhaven National Laboratory, Upton, NY, November 10-12, 1975:126-145.

Lance, G. N., and W. T. Williams. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. Computer J. 9:373-380.

Leis, J. M., and J. M. Miller. 1976. Offshore distributional patterns of Hawailan fish larvae. Mar. Biol. 36: 359-367.

Moser, H. G.; E. H. Ah1strom; D. Kraner; and E. G. Stevens. 1974. Distribution and aburdance of fish eggs and larvae in the Gulf of California. Calif. Coop. Oceanic Fish. Invest. Rep. 17:112-128.

Musick, J. A. 1976. Commanity structure of fishes on the continental slope and rise off the middle Atlantic coast of the U.S. Paper read at Joint Int. Oceanogr. Assembly, 15 Sept. 1976, at Edinburgh, Scotland. 132 p . Manuser.

Richardson, M. D. 1976. The classification and structure of marine macrobenthic assemblages at Arthur Harbor, Anvers Island, Antarctica. Ph.D. Dissertation. Oregon State University, Corvallis, Oreg. 142 p .

Richardson, S. L. 1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, Engraulis mordax. Fish. Bull. 71:697711 .

Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution and seasonality January 1971 to August 1972. Oregon State University Sea Grant College Program Publ. ORESU-T-77-003. 73 p .

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. 75:125-145.

Sanders, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the softbottom community. Limnol. Oceanogr. 5:138-153.

Smith, W. G.; J. D. Sibunka; and A. Wells. 1975. Seasonal distributions of larval flatfishes (Pleuronectiformes) on the continental shelf between Cape Cod, Massachusetts, and Cape Lookout, North Carolina, 1965-66. U.S. Dept. Comulerce, NOAA Tech. Rep. NMFS S5RF-691. 68 p .

Stephenson, W., and M. C. L. Dredge. 1976. Nunerical analysis of fish catches from Serpentine Creek. Proc. Royal Soc. Queensland 87:33-43.

Stephenson, W.; W. T. Williams; and S. D. Cook. 1972. Computer analysis of Petersen's original data on bottom commurities. Ecol. Monogr. 42:387-415.

Stephenson, W. ; W. T. Williams; and S. D. Cook. 1974. The benthic fauna of soft bottons, southern Moreton Bay. Mem. Queensland Mus. 17:73-123.

Stephenson, W.; Y. I. Raphael; and S. D. Cook. 1976. The macrobenthos of Bramble Bay, Moreton Bay, Queensland. Mem. Queensiand Mus. 17:425-427.

Waldron, K. D. 1972. Fish larvae collected from the northeastern Pacific Ocean and Puget Sound during April and May 1967. U.S. Dep. Commerce, NOAA Tech. Rep. NMFS SSRF-663. 16 p .

LIST OF TABLES

Table 1. Original data set considered for classification analyses. + , daytime samples used in analyses; 0 , daytime sanples not used in analyses; $D$, dawn, dusk, or night samples not used in analyses.

Table 2. Variance of site means and times means for number of species (S) and number of individuals ( $N$ ) in Subset 1 and Subset 2 data.

LIST OF FIGURES
Fig. 1. Mean number of individuals/ $10 \mathrm{~m}^{2}$ (N) at each site (upper) and mean number of species at each site (lower). Bars are Subset 1 data; circles are Subset 2 data. Numbers above bars are site codes.

Fig. 2. Mean number of individuals/l0 $\mathrm{m}^{2}$ (N) at each time (upper) and mean number of species ( $S$ ) at each tine (lower) in Subset 2 data. Numbers above bars are times codes.

Fig. 3. Results of classification of Subset 1 data. (a), dendrogram of site groups; (b), dendrogram of species groups; (c), two-way coincidence table showing species group constancy (\%) at each site group.

Fig. 4. Results of classification of Subset 2 data. (a), dendrogram of times groups; (b), cendrogram of species groups; (c), two-way coincidence table showing species group constancy (\%) within each time group.

| TIMES |  |  | SITES |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Code |  | number of | (Code number above, km. from coast below) |  |  |  |  |  |  |  |  |  |  |  |
| number of | Sampling sa | ling dates | $\overline{1}$ | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| sampling dates | Date uthe | in analyses | 2 | 6 | 9 | 18 | 28 | 37 | 46 | 56 | 65 | 74 | 93 | 111 |
| 1 | 6 Jan 71 | 1 | + | + | + | + |  |  |  |  |  |  |  |  |
| 2 | 18 Jan 71 | 2 | + | + | + | + |  |  |  |  |  |  |  |  |
| 3 | 3 Feb 71 | 3 | + | + | + | + |  | 0 |  | 0 |  |  |  |  |
| 4 | 16-17 Feb 71 | 4 | + | + | + | + |  | 0 |  | ¢ |  | 0 | 0 | 0 |
| 5 | 1 Mar 71 | 5 | + | + | + | + |  | 0 |  | 9 |  | ¢ | $\emptyset$ | $\square$ |
| 6 | 20 Mar 71 | 6 | + | + | + | + | 0 | 0 |  | $p$ | $\varnothing$ | 0 | $\varnothing$ | 0 |
| 7 | 22-26 Apr 71 |  |  |  | 0 | 0 | 0 | $g$ | $\varnothing$ | 9 |  | $\square$ | 0 |  |
| 8 | 3-4 May 71 | 7 | + | $+$ | + | + | 0 | 0 | 0 | 0 | 0 | $\$$ | $g$ | $\emptyset$ |
| 9 | 14-20 May 71 | 8 | + | + | + | + | 0 | 0 | $\emptyset$ | 0 |  |  |  |  |
| 10 | 29 May-2 Jun 71 |  | 0 | 0 | 0 | $\not 0$ | 0 | 0 | 0 | 0 | Ø | $\square$ | $\emptyset$ | $\varnothing$ |
| 11 | 12-13 Jun 71 | 9 | + | + | + | + | 0 | 0 | 0 | 0 | $g$ | $\emptyset$ | $\emptyset$ | $\varphi$ |
| 12 | 28-30 Jun 71 |  | 0 | 0 | 0 | $\varnothing$ | $\emptyset$ | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 6 Jul 71 | 10 | + | + | + | $+$ |  |  |  |  |  |  |  |  |
| 14 | 21-22 Jul 71 | 11 | + | + | + | + | 0 | 0 | 0 | 0 | 0 | 0 | $\emptyset$ | $\emptyset$ |
| 15 | 2-3 Aug 71 | 12 | + | + | + | + | + | + | + | + | + | + | + | + |
| 16 | 19-20 Aug 71 | 13 | + | + | $+$ | + | 0 | ¢ | 0 | 0 | 0 | 0 | 0 |  |
| 17 | 23-24 Sept 71 | 14 | + | + | + | + | 0 | 0 | 0 | 0 | $\emptyset$ | 0 | 0 | 0 |
| 18 | 11-12 Oct 71 | 15 | + | + | + | + | 0 | 0 | 0 | 0 | $\emptyset$ | $g$ | 0 | 0 |
| 19 | 6 Nov 71 | 16 | + | + | + | + | 0 | 0 | 0 | $\square$ | 0 | $\square$ | 0 | 0 |
| 20 | 7 Dec 71 | 17 | + | + | $+$ | + | 0 | $\emptyset$ | $\phi$ | $\varnothing$ | 0 | $\emptyset$ |  |  |
| 21 | 3-4 Mar 72 |  | 0 | 0 | 0 | 0 | $\emptyset$ | 0 | ¢ | $\emptyset$ | 9 | 9 | $g$ | 0 |
| 22 | 15-16 Mar 72 | 18 | + | + | + | + | 0 | 0 | $\varnothing$ | $\square$ | 0 | $\bigcirc$ | 0 | 0 |
| 23 | 29-30 Mar 72 |  | 0 |  | 9 | 0 | 0 | 0 | 0 | 0 |  |  |  |  |
| 24 | 11 Apr 72 | 19 | + | + | + | + |  |  |  |  |  |  |  |  |
| 25 | 20-21 Apr 72 |  | $\emptyset$ |  | 6 | $\bigcirc$ | 0 | 0 | 0 | 0 |  |  |  |  |
| 26 | 20-21 May 72 | 20 | + | + | + | + | 0 | 0 | 9 | $\emptyset$ | 0 | 0 | 0 | 0 |
| 27 | 11-12 Jun 72 | 21 | + | + | + | + | 0 | 0 | 0 | $\emptyset$ | 0 | 0 | 0 | 0 |



Fig. 2. Mean number of individuals $/ 10 \mathrm{~m}^{2}$ (N) at each time (upper) and mean number of species (S) at each time (lower) in Subset 2
data. Numbers above bars are time codes.


Fig. 3. Results of classification of Subset 1 data. (a), dendrogram of site groups; (b), dendrogram of species groups; (c), twoway coincidence table showing species group constancy (q) at each site group.

Fig. 4. Results of classification of Subset 2 data. (a), dendrogram of times groups; (b), dendrogram of species groups; (c), twoway coincidence table showing species group constancy $(\%)$ within each time group.

