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## Seasonal patterns of seston characteristics in Bedford Basin, Nova Scotia, relative to zooplankton feeding: A multivariate approach<sup>1</sup>

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### *Abstract*

Seasonal changes of the characteristics of the particulate organic matter from Bedford Basin were studied at four different depths during 15 months. The data (particle counts in Coulter Counter channels, counts of taxonomic categories, and chemical measurements) are best analyzed as multivariate parameters. Principal component analyses show for each depth the groups of channels responsible for the maximum variability; taxonomic categories and chemical measurements projected onto the graphs as “supplementary” items reveal their potential associations with some channels. Correspondence analysis allows a dual analysis of the size spectra and the sampling dates. In the surface waters, size spectra are influenced by biological productivity, whereas at depth the analyses mostly specify the type of sedimenting material. Regardless of depth, the size spectral diversity is associated with particles ranging from 8 to 25.4  $\mu\text{m}$ . They are responsible for most spring production and some summer and fall production. Several multivariate associations are found (e.g. between flagellates and particles in the 8.0–12.7- $\mu\text{m}$  size range, diatoms and particles in the 16.0–25.4- $\mu\text{m}$  size range, dinoflagellates and particles in the 40.3–50.8- $\mu\text{m}$  size range). Size heterogeneity at depth is related to pulses of sedimenting small and medium size particles, although the particulate standing stock at 30 m consists of large detrital material. The association between microzooplankton and nanoplankton observed at 2.5 and 5 m illustrates a trophic relationship. The grazing pressure by the large population of ciliates limits the growth of small cells, and their distribution, to the surface layer. A summer maximum of ATP without associated chlorophyll is probably related to such feeding activity and to the high growth rate and short division time of protozoans.

An appreciation of the significance of the size of marine particulate matter has been important in defining in situ feeding characteristics of “herbivorous zooplankton” (Parsons et al. 1967; Poulet 1973, 1974; Richman et al. 1977; Conover and Huntley 1980; Chervin et al. 1981). Unfortunately, relating size spectra to conventional measures of primary production is difficult and only a few attempts have been made to consider the biological meaning of the size of particles (Parsons 1969; Sheldon et al. 1972; Valkenberg et al. 1978; Malone and Chervin 1979).

Marine seston is composed of different

kinds of living and nonliving material (Riley 1970) and each kind will have different nutritional potentials and will vary differently in space and time. A population of grazers will therefore face seasonal and cyclic variations of phytoplankton size fractions and biomass, which will have different residence times in the surface layers (Malone and Chervin 1979). This will give rise to great changes in the quality of the food supply.

During the course of feeding studies carried out in Bedford Basin it became obvious that a definition of the natural diet of the so-called herbivorous copepods was necessary. This has normally been done by various methods, such as microscope counts, Coulter counts, chlorophyll *a* measurements, carbon and nitrogen analysis, and radioisotope counts. Each of these methods gives only a partial representation of the

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overall characteristics of the marine particulate matter (Mayzaud and Taguchi 1979). To define seston in a way that is meaningful to a copepod, one needs relevant measurements of both the size and the chemical characteristics of the different components (Nischizawa 1969; Riley 1970; Hobson 1971; Beers *et al.* 1975). Unfortunately because of the overwhelming amount of data generated by such a number of measurements, a comparison of their variation is usually not possible by classical bivariate analysis. This probably explains why so few attempts have been made to relate size measurements and chemical constituents.

The use of multivariate statistical analysis serves a heuristic purpose. It may reveal relationships not otherwise apparent and it can provide an objective evaluation of subjective relationships. The use of vector analysis (Kitchen *et al.* 1975; Eppley *et al.* 1977) and principal component analysis (Chanut and Poulet 1979; Chervin *et al.* 1981) to relate size spectra to spatial heterogeneity has encouraged us to look at the general question of variation of seasonal and depth patterns of seston.

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#### *Material and methods*

Particulate matter in Bedford Basin was studied at depths of 2.5, 5, 10, and 30 m from October 1973 to December 1974. Both the site and the methods have been described (Mayzaud and Taguchi 1979). Water samples were taken with a 6-liter Van Dorn bottle and prefiltered through Nitex (163- $\mu\text{m}$  mesh size) to eliminate large zooplankters and debris; some large phytoplankton and tintinnids may have been removed by this process (Malone *et al.* 1979). Known volumes were then filtered either on pre-baked 0.8- $\mu\text{m}$  silver filters (Selas Flotronics) for carbon and nitrogen analyses or on Whatman GF/C filters for chlorophyll and ATP analyses. ATP filters were immediately boiled in Tris buffer solution for 5 min. All filters were frozen until analyzed. Particle concentrations at sizes ranging from 2.0 to 161  $\mu\text{m}$  were estimated with a model

Table 1. Correspondence between channel number and equivalent diameter.

| Channel No. | Size ( $\mu\text{m}$ ) | Channel No. | Size ( $\mu\text{m}$ ) |
|-------------|------------------------|-------------|------------------------|
| 1           | 2.00                   | 11          | 20.20                  |
| 2           | 2.52                   | 12          | 25.40                  |
| 3           | 3.17                   | 13          | 32.00                  |
| 4           | 4.00                   | 14          | 40.30                  |
| 5           | 5.04                   | 15          | 50.80                  |
| 6           | 6.35                   | 16          | 64.00                  |
| 7           | 8.00                   | 17          | 80.60                  |
| 8           | 10.08                  | 18          | 101.60                 |
| 9           | 12.70                  | 19          | 128.00                 |
| 10          | 16.00                  | 20          | 161.00                 |

T Coulter Counter having three aperture tubes (100, 280, 400  $\mu\text{m}$ ). After removal of overlaps, 20 channels were defined to cover the entire size range (Sheldon 1973); these are used in the statistical analysis (Table 1). Total volume was obtained from the sum of volumes of each channel (Sheldon 1973). All particle sizes refer to spherical equivalent diameters and equivalences between size and channel number are listed in Table 1. In addition to Coulter counts, we made taxonomic counts and optical size measurements (diatoms, flagellates, dinoflagellates, silicoflagellates, microzooplankton, and fecal pellets) (*see* Mayzaud and Taguchi 1979).

Bivariate statistical analyses were performed with nonparametric Spearman correlations (Tate and Clelland 1957). A multivariate approach was necessary to compare a large number of particle size spectra distributed over more than a year. We considered each size distribution as a random vector and each channel as a variable and then compared size spectra in a space of reduced dimensionality. Correspondence analysis (Benzecri 1969; Hill 1974; Teil 1975) is basically a method of profile analysis and seems particularly well suited for comparing particle spectra. This method is also known as reciprocal averaging (Hill 1973) or reciprocal ordering (Orloci 1978).

Counts in the data matrix (*i.e.* channels  $\times$  samples) are first transformed to relative frequencies and scaled so that each row (or column) can be viewed as a row (or column) profile of conditional probability distribu-

tions. Distances between profiles are then computed with  $\chi^2$  metrics. This distance gives a symmetry to the two sets of data so that each factorial axis of the cloud of channels corresponds to a factorial axis of the cloud of samples. Thus it is possible to represent simultaneously channels and samples on the plane defined by the axes of maximum inertia of the clouds. Samples having similar profiles will be found close together, with the characteristic channels projected onto them. Moreover, the center of gravity of the cloud represents a mean profile.

The factorial axes can be interpreted by using computed quantities known as "contributions." These contributions may be absolute or relative. The absolute contribution of an item (i.e. channel or sample) measures the part it takes in the total variance explained by the axis. The relative contribution is the squared correlation between the item and the axis. The underlying mathematics of correspondence analysis can be found in statistical texts (e.g. Benzecri 1973; Legendre and Legendre 1979).

Once the factorial axes, based on the "active" variables, have been extracted, "supplementary" variables, not used in the determination of the axes, can be added to the analysis. The profile of these can be located on the projections by characteristic vectors derived only from the active ones. Formulations for computing supplementary variable projections are given by Lebart et al. (1977). In this study, we treated counts from the first and last channels which were improperly sampled by the counter as supplementary variables.

Normality of the data is not required for correspondence analysis. Attempts to use a logarithmic transformation did not lead to meaningful interpretations of the results, probably because of too much distortion of the profiles. Binet et al. (1972), working with plankton counts, also observed that a log-transformation preceding the analysis was detrimental.

We also investigated the structure of the correlation matrix between channels. Simple examination showed that groups of adjacent channels were highly correlated. These were easily separated by a cluster analysis, carried out by transforming the correlation

matrix to a distance matrix and then computing the minimum spanning tree from which a single linkage clustering was derived (Gower and Ross 1969).

It would be interesting to project, as supplementary variables, the taxonomic and chemical data on the Coulter channels. Unfortunately these data are not commensurate, because correspondence analysis requires homogeneity of the data (Benzecri 1973). Rather than recoding all values in a few classes, which could result in a loss of information, we preferred to subject all the data to a principal component analysis, using the correlation matrix. Thus all variables are centered and reduced to unit variance. Data transformation was not found necessary, as observed by Chanut et al. (1977). Only the active variables (channels 2–19) were used to compute the eigenvectors. The other variables were projected as supplementary items on the factorial planes.

All computations were made on a Hewlett-Packard 9835A computer, using programs developed by Ph. Laval.

### Results

*Seasonal variation of the total volume, carbon, and nitrogen of particulate matter*—The seasonal variability of total particle volume was characterized by pulses which became less important with depth (Fig. 1). At 2.5 and 5 m, six peaks of high concentration occurred with two pulses in January–February and in April. The winter peak was mainly composed of large detrital particles (80–128  $\mu\text{m}$ ) and these were mainly phytoplankton and microzooplankton. The small cells were accounted for as flagellates, diatoms (*Chaetoceros borealis*, *Thalassionema nitzschioides*, *Thalassiosira nordenskiöldi*), and dinoflagellates (*Ceratium lineatum*), whereas medium size cells were mostly *Thalassionema* sp. and *Gymnodinium* sp. Pulses of lower amplitude occurred in June, July, September, and November. The November peak was made up exclusively of large dinoflagellates (*Ceratium fusus*, *Ceratium longipes*, *Dinophysis* sp., *Gymnodinium* sp., *Peridinium* sp.), while the summer peaks generally contained varying proportions of small and medium size particles. The small phytoplankton cells were

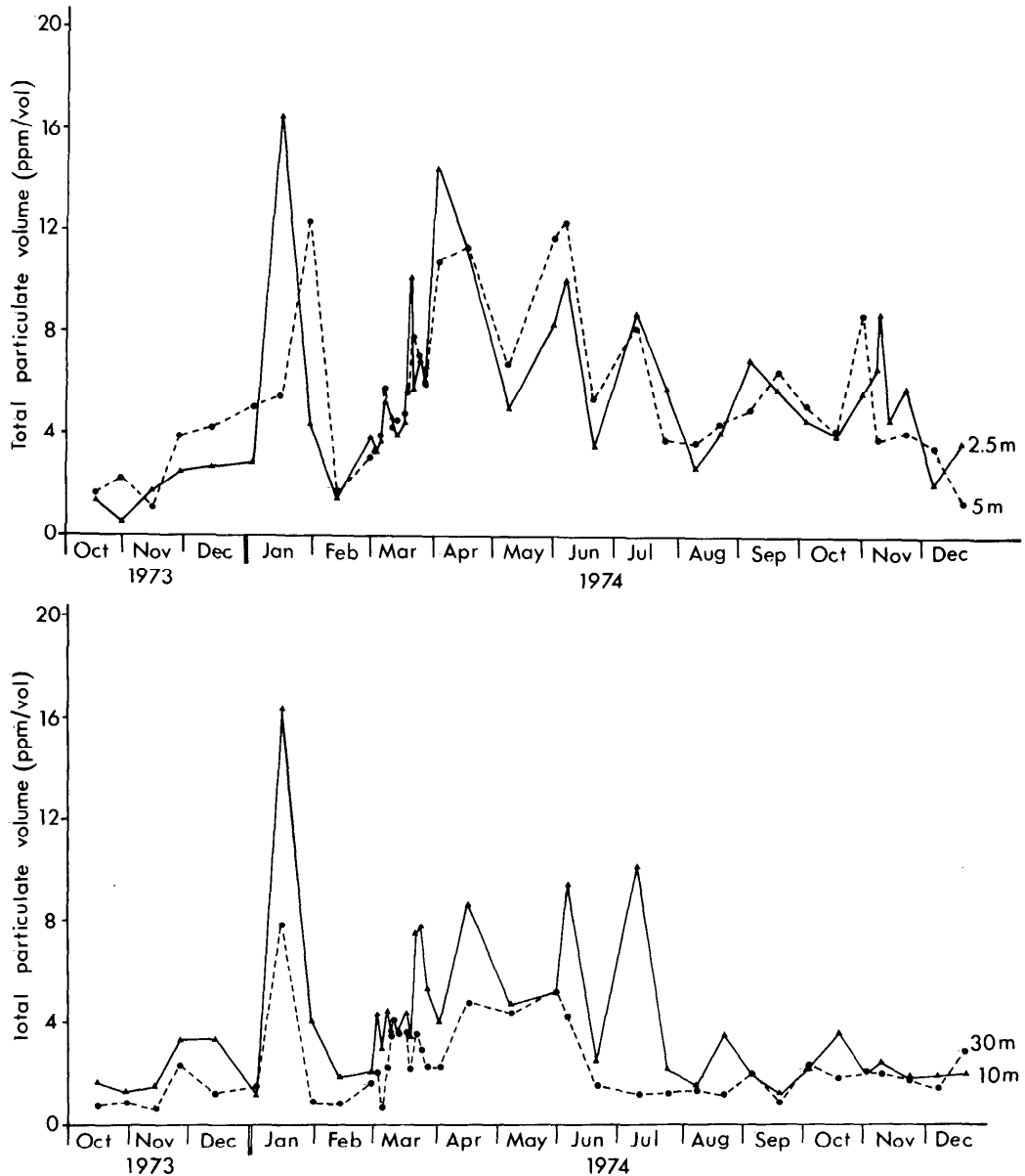


Fig. 1. Seasonal variations of total particulate volume.

most often represented by *Skeletonema costatum*, *Nitzschia seriata*, and *T. nitzschoides* and different species of flagellates, whereas the medium size and large particles were mainly tintinnids with small numbers of diatoms and dinoflagellates (*Rhizosolenia hebetat*, *Gymnodinium* spp., *Dinophysis* spp., *C. longipes*, *Peridinium* spp.). It is

noteworthy that the spring bloom of phytoplankton did not coincide with a large increase in particle volume but as a succession of small peaks, each due to different kinds of particles (see Taguchi and Platt 1978). A similar pattern of variation was obtained at 10 m (Fig. 1), although this was strongly attenuated during spring and fall. At 30 m,

only winter and spring changes were still apparent, probably because of temperature stratification during summer and fall. Microscope observations of 30-m samples showed a dramatic decrease both in the number of species and in the number of individuals per species.

Changes in particulate organic carbon (POC) and nitrogen (PON) (Fig. 2) only loosely followed those of total volume. At shallow depths the spring bloom and summer peaks of particulate volume are associated with carbon and nitrogen concentrations. However at 2.5 m the spring peaks of carbon and nitrogen are shifted relative to those of particulate volume by one sampling interval (3–17 April). Such changes in the carbon-to-volume and nitrogen-to-volume ratios resulted from a decrease in the volume of small particles and an increase of the large ones on 17 April. The lack of correlation between the high January peaks of volume and the POC and PON concentrations is not really surprising since, as indicated earlier, the particles present at that time were large (80–160  $\mu\text{m}$ ). More puzzling is the lack of correspondence between the fall 1973 peaks of POC or PON and the particulate volume. Microscopic observations of these samples showed a great dominance of dinoflagellates (*C. longipes*, *Dinophysis* spp., *Gymnodinium* sp., and *Peridinium* spp.) which apparently were not recorded by the counter to the extent of their carbon content.

The average levels of POC and PON decreased with depth as did the height of the maxima. Concentrations were usually high in the surface waters (2.5 and 5 m), except during February. At 10 m the pattern of variation was similar to that at the surface, except that the spring maximum was not present. Hardly any significant changes were recorded at 30 m, where concentrations of POC and PON oscillated most of the time around 200  $\text{mg C}\cdot\text{m}^{-3}$  and 25  $\text{mg N}\cdot\text{m}^{-3}$ .

*Seasonal variations in particulate chlorophyll a and adenosine triphosphate*—The changes in Chl *a* in the surface waters were associated with periods of phytoplankton blooms (Fig. 3). Concentrations were maximal during spring and fall and minimal during winter. Variations at intermediate

depths (5 and 10 m) were similar except that the influence of the fall bloom on the chlorophyll vertical gradient seemed limited to the first 3 m of the water column (Taguchi 1981). The low levels from July to October are associated with thermal stratification (Mayzaud and Taguchi 1979). Very little chlorophyll could be detected at 30 m and only the sedimentation of the spring bloom produced high concentrations (2–5  $\text{mg}\cdot\text{m}^{-3}$ ). Interestingly such pulses were not associated with corresponding ones in POC or PON.

Surprisingly, the distribution of particulate ATP (Fig. 4) was not similar to any of the patterns described above. Levels were low at all depths during fall 1973 and winter 1974, even though a vertical gradient of POC, PON, and chlorophyll was present. The surface waters (2.5 and 5 m) showed increasing ATP concentrations during the spring bloom and these remained at relatively high levels during most of summer and fall 1974. The pattern of variation at 10 m was quite strange since it seemed to show a maximum level of accumulation of living organic matter early in summer. In June and July concentrations were  $>2.0 \text{ mg}\cdot\text{m}^{-3}$  with a maximum of 4.4 on 10 July. As expected, at 30 m, values higher than 0.2  $\text{mg}\cdot\text{m}^{-3}$  did not occur, confirming the non-living detrital character of the particles.

*Relationships among the particulate parameters*—When compared to taxonomic or biochemical parameters the amount of information contained in a single channel of the Coulter Counter is too small to be meaningful. Nevertheless certain groups of channels show similar seasonal variations and these probably represent the changes in biomass concentration of the most productive groups of particles. The relationships can best be defined by using statistical groupings of the Coulter Counter data. To do so, we used a cluster analysis derived from the correlation matrix between channels (1–20), based on 39 observations. It was possible to distinguish four groups at 2.5 and 5 m, five groups at 10 and 30 m (Fig. 5). The two groups representing the two ends of the spectrum were found at all depths. It is clear that it is within the groups of particles of intermediate size that vari-

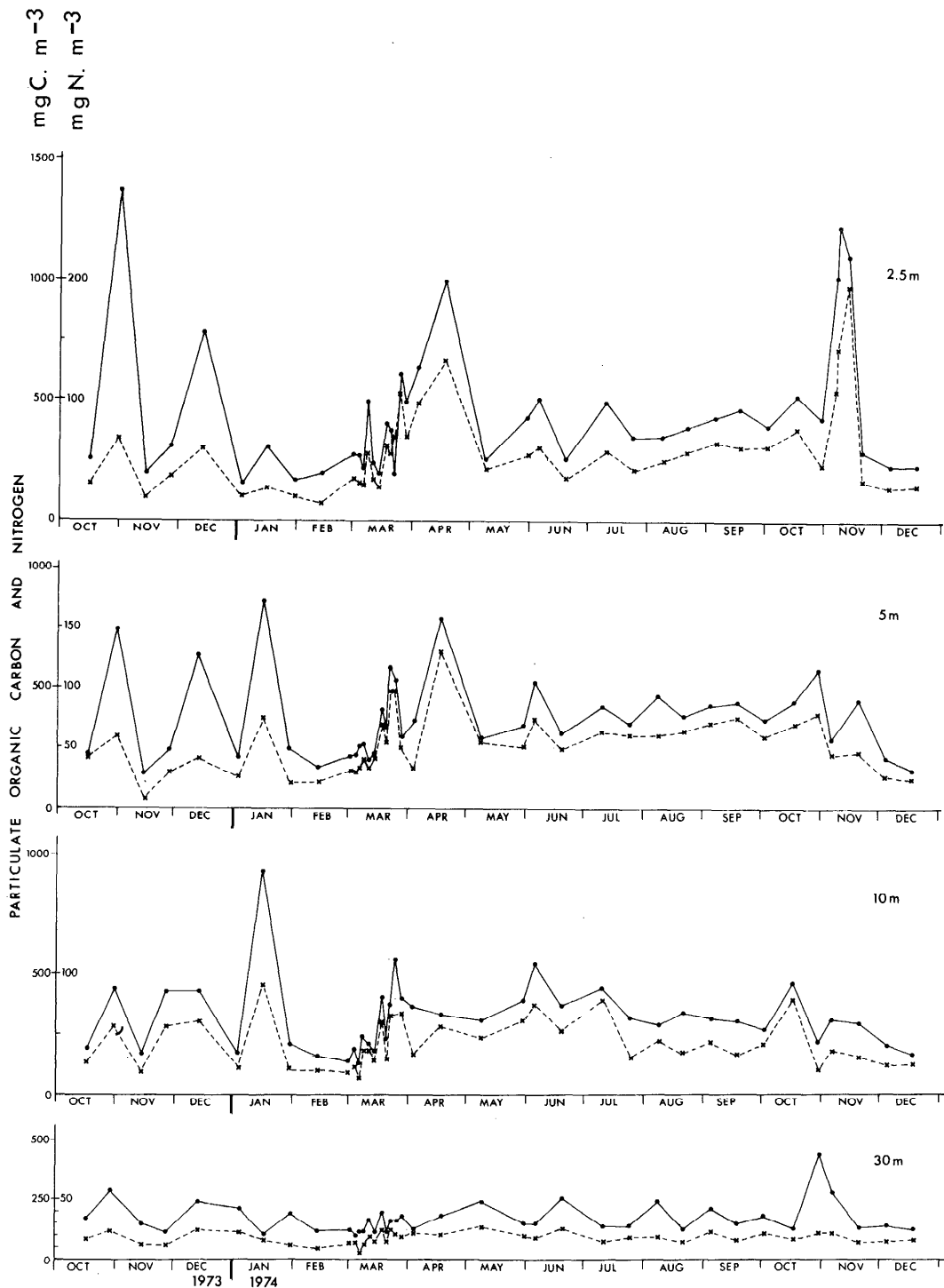


Fig. 2. Seasonal variations of particulate organic carbon (●) and nitrogen (×).

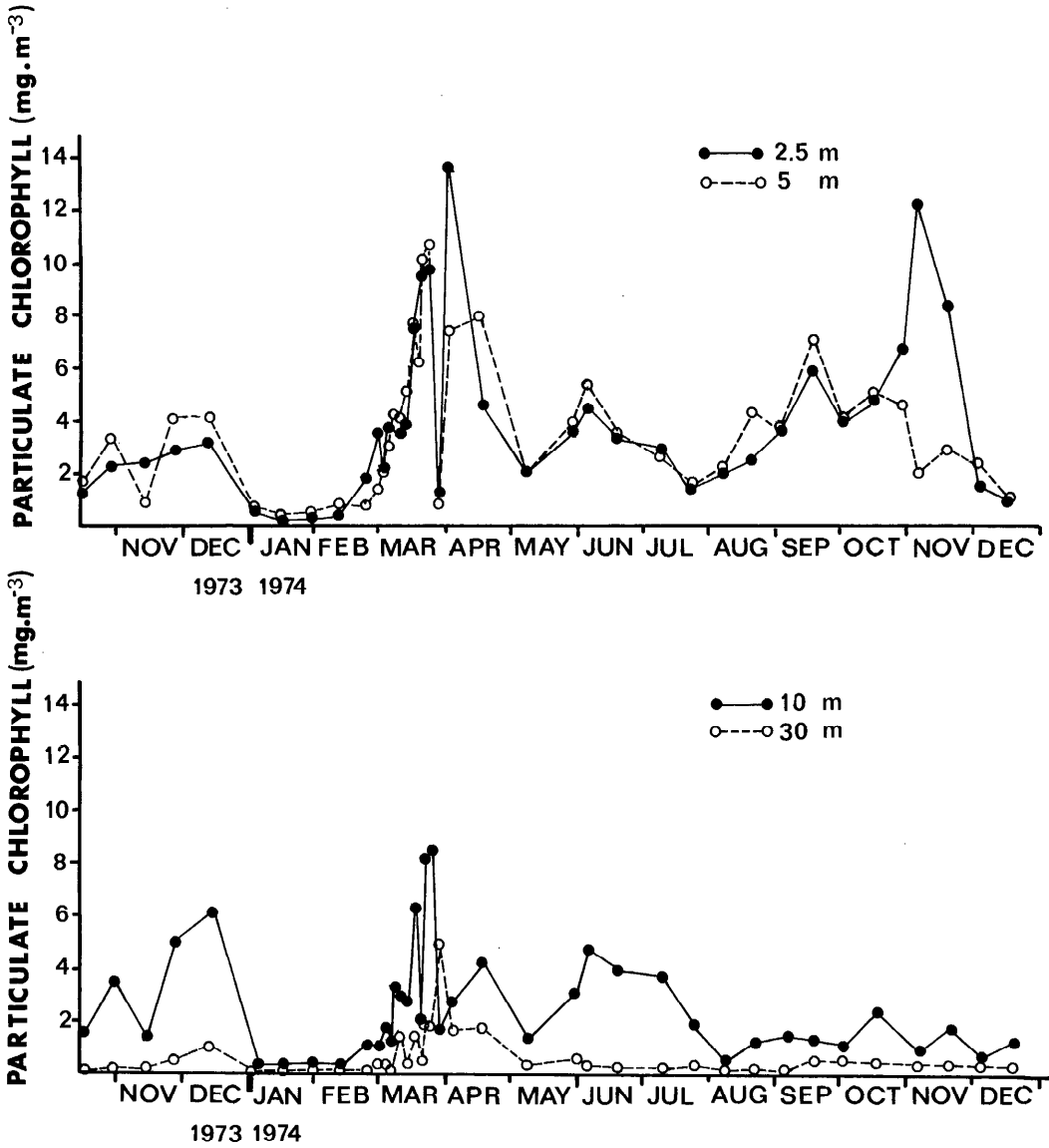


Fig. 3. Seasonal variations of particulate chlorophyll *a*.

ations and diversity in particle production are most apparent.

We compared values of POC, PON, Chl *a*, ATP, total particle volume per group of channels, and the volume occupied by each taxonomic assemblage by using Spearman nonparametric rank correlation coefficients. The results (Fig. 6) showed that for the sur-

face samples (2.5 m) most parameters were significantly intercorrelated ( $P < 0.01$ ). Small particle concentrations (channels 2–5) were correlated with nitrogen and ATP, while large size groups (channels 7–15) were correlated with carbon, chlorophyll, and to a minor extent with nitrogen. Phytoplankton components were associated with dif-



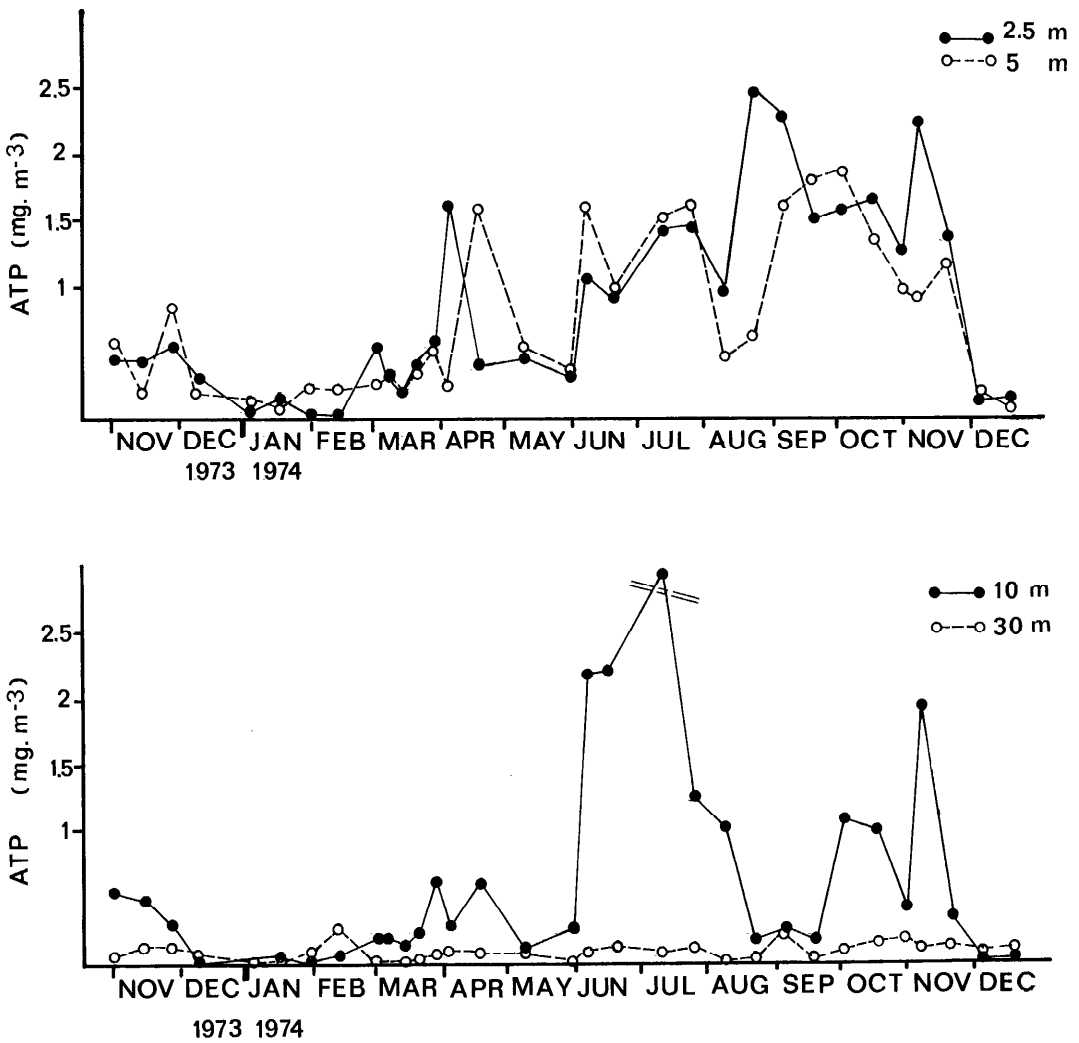


Fig. 4. Seasonal variations of adenosine triphosphate.

ferent size classes and chemical components (e.g. flagellates with ATP, diatoms with channels 7–13 and with nitrogen, dinoflagellates with channels 14–15 and ATP), while microzooplankton was associated with both small and medium size particles as well as nitrogen and ATP. The number of significant correlations ( $P < 0.05$ ) decreased with depth. The repackaging of chlorophyll into large particles, observed at 30 m, suggests an intensive assimilatory metabolism by the surface zooplankton grazers. Only

diatoms retained some degree of correlation at all depths either with the small size groups (2.5 and 5 m) or all size groups (10 and 30 m) though they were not generally responsible for the variations in particle volume.

Covariation of so many parameters cannot be fully described by bivariate correlation analysis. Therefore, we used principal component analysis to further refine our results. Regardless of the depth considered, three factorial axes were needed to explain 70–80% of the total variance. The first axis

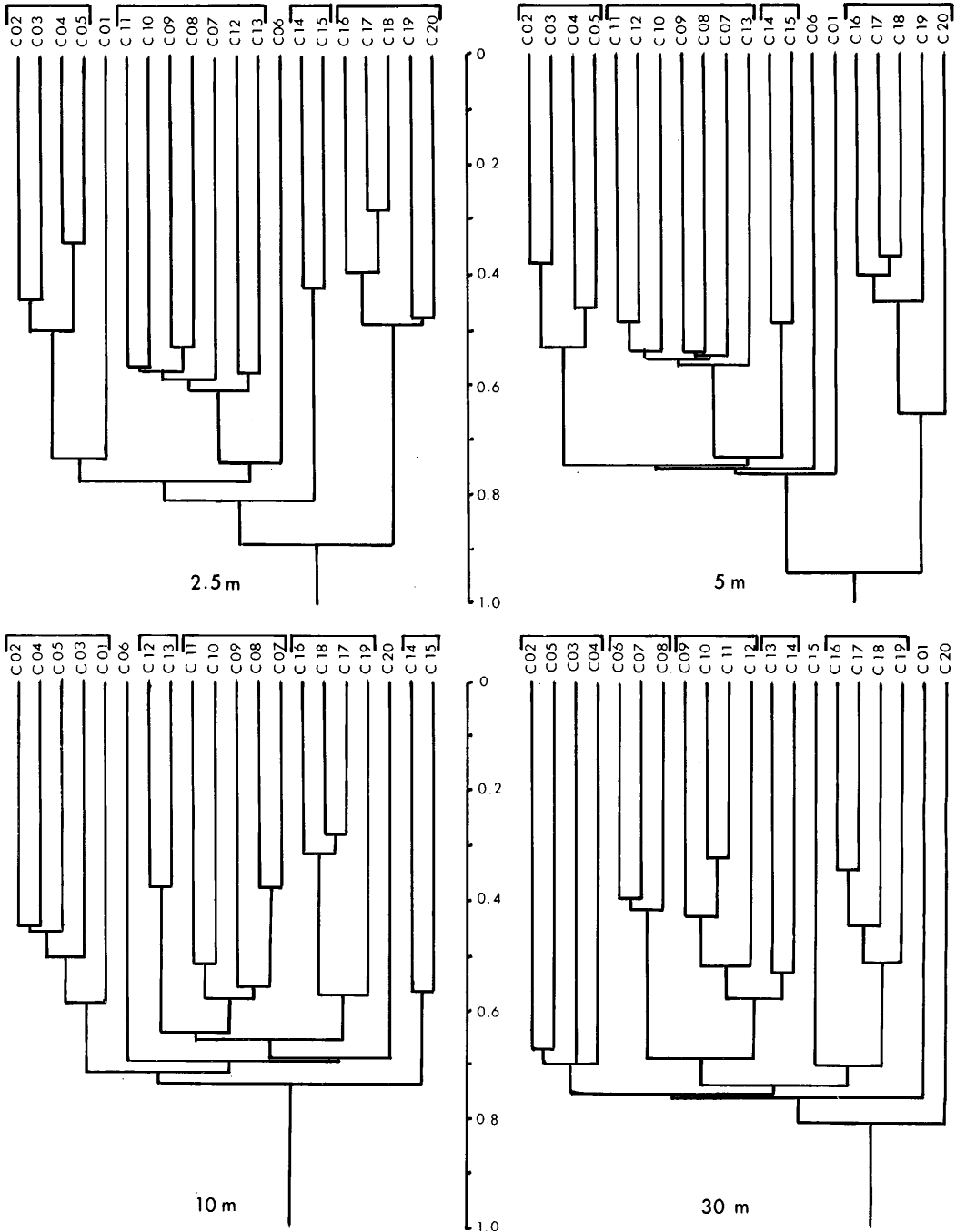


Fig. 5. Dendrograms resulting from single linkage clustering of correlation matrices (first transformed to distance matrices) between the 20 Coulter Counter channels (C01 to C20) at each sampled depth. Table 1 shows correspondence between channels and size.

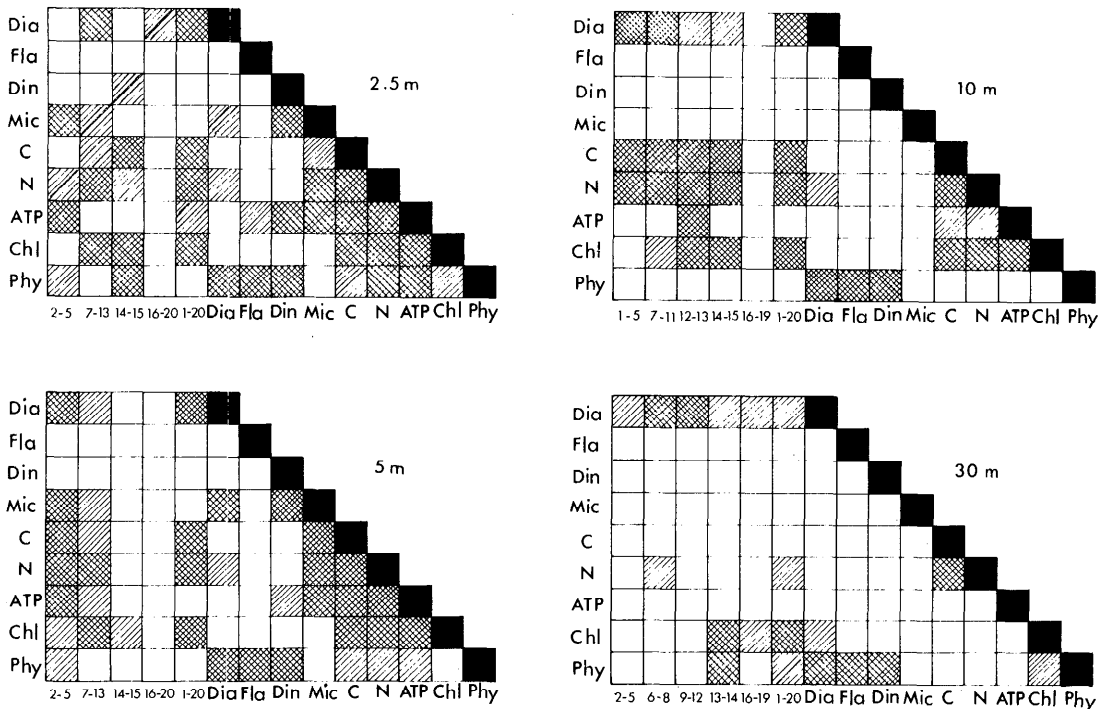


Fig. 6. Shaded correlation matrices (one for each sampled depth) showing significant correlations between groups of Coulter Counter channels, diatoms (Dia), flagellates (Fla), dinoflagellates (Din), microzooplankton (Mic), particulate organic carbon (C), particulate organic nitrogen (N), ATP, Chl *a* (Chl), and phytoplankton (Phy). Correlations between groups of channels (upper triangles) omitted. Spearman's nonparametric rank correlation coefficients significant at the 0.05 level hatched, and cross-hatched at the 0.01 level.

(Figs. 7, 8) is always positively defined by those intermediate groups of channels (8.0–25.4  $\mu\text{m}$ ) which best represent the biological activity, and it explains an increasing amount of variance with depth (from 31.1% at 2.5 m to 49.5% at 30 m). The second axis separates large and small particles and seems related to the changes in living material; it explains a decreasing amount of variance with depth (24.5% to 2.5 m and 19.6% at 30 m). The third factorial axis separates small particles from those corresponding either to channels 14–15 (40.3–50.8  $\mu\text{m}$ ) or 13–14 (32–40.3  $\mu\text{m}$ ), depending on depth, and it singles out the fall bloom and the resulting sedimenting material. The multifactorial grouping of channels (Figs. 7, 8) shows few deviations from what was obtained through cluster analysis (Fig. 5). The major differences concern the 2.5- and 10-m depths. At 2.5 m, the channels 7–13 (8.0–32  $\mu\text{m}$ ) group is subdivided into two

(8.0–12.7 and 16.0–24.5  $\mu\text{m}$ ). At 10 m, the channels 7–11 (8.0–20.2  $\mu\text{m}$ ) group is also subdivided (6.35–12.7 and 16.0–20.2  $\mu\text{m}$ ), whereas the channels 12–13 (25.4–32.0  $\mu\text{m}$ ) and 14–15 (40.3–50.8  $\mu\text{m}$ ) groups are lumped together.

The projections of the taxonomic and chemical parameters as supplementary variables give some new insights into the multidimensional correlations existing between these variates and the Coulter Counter particle groups (Figs. 7, 8). At 2.5 m, the biologically active channels relate well to the descriptive parameters (Fig. 7). Some associations are present in all three multivariate planes considered. Microzooplankton seasonal profiles are similar to those of the size group 2.5–5.0  $\mu\text{m}$ , flagellates to those of the 8.0–12.7- $\mu\text{m}$  size group, and diatoms to those of the 16.0–25.4- $\mu\text{m}$  group. Dinoflagellates do not show permanent associations, except on axis 3 where they appear

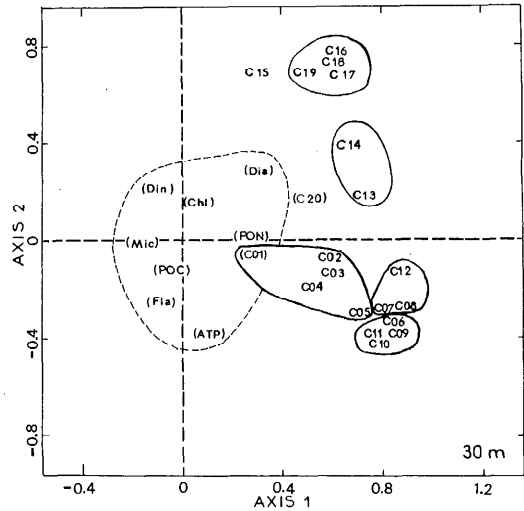
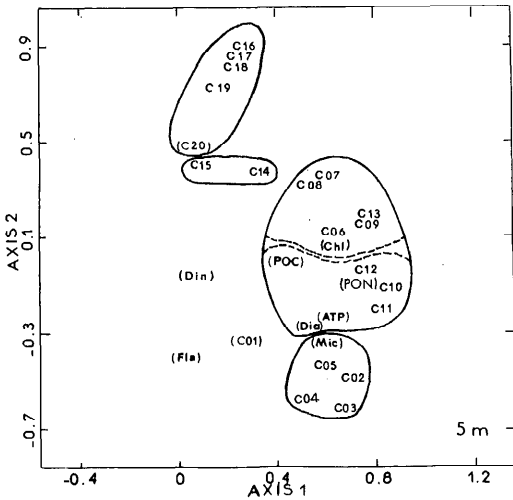
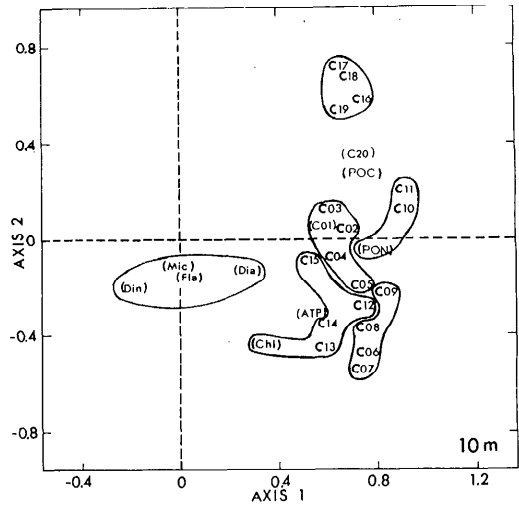
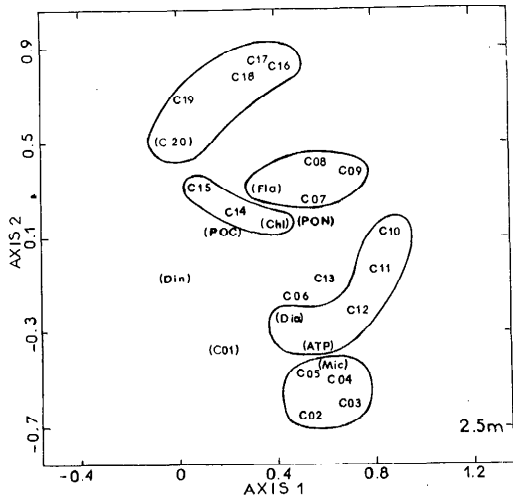


Fig. 7. Principal component analysis of the correlation matrices between channels 2 to 19 (C02 to C19), with projection of channels 1 and 20, taxonomical, and chemical parameters as “supplementary variables” for 2.5- and 5-m depths. Factor loadings on selected axes (but grouping of channels made considering the first three axes). Supplementary variables, as defined for Fig. 6, in parentheses plus POC and PON. Table 1 gives correspondence between channels and size.

Fig. 8. As Fig. 7 but for 10- and 30-m depths.

related to channels 14 and 15 and represent the fall bloom. As expected, chemical variables integrate a larger body of information and relate to more than one group of channels. In all three projections, chlorophyll is associated with channels 14–15 and ATP

with channels 10–12. It is interesting that ATP always occurs close to the small size group (channels 2–5). Carbon and nitrogen are not related to any specific group of biologically active channels (2–15) since they occur close to the set of channels ranging from 7 to 15. Similar conclusions can be reached for the 5-m depth, though flagellates seem to have lost all associations with any multivariate groupings of channels (Fig. 7). Drastic changes in the relations described above occur at 10 m. All four taxonomic counts are separated from the size

groups on the first (Fig. 8) and third multifactorial axes and they seem to describe a different aspect of the particulate matter than that of the electronic counting. Similarly ATP and carbon are not associated with any particular particle size group. Only nitrogen and chlorophyll are associated with channels 10–11 and 12–15. As noted for the linear correlations, the 30-m depth (Fig. 8) is characterized by a complete lack of similarity between the active and the supplementary variables, thus confirming the detrital nature of the material.

**Particle size spectral changes and seasons**—The seasonal succession of nanoplankton, net phytoplankton, and microzooplankton is bound to affect the particle size distributions. Correspondence analysis, being in essence a profile analysis, is particularly well suited to describe simultaneous changes with time of the particulate matter.

Regardless of depth, the analysis indicates that three multifactorial axes are needed to explain 70–80% of the total variance. The percentage of inertia accounted for by the first axis (C1) increases with depth and ranges from 32% at 2.5 m to 43% at 30 m. On the other hand, the percentage of the variance explained by the second (C2) and the third (C3) axes decreases with depth. The second varied from 27 to 20% and the third from 17 to 9%.

Projections of the active and supplementary channels for the 2.5-m depth on the first three multifactorial planes show that the first axis separates the large particles (channels 16–19) from the others (Fig. 9). It also separates winter from summer and fall. This axis can be considered as an expression of the intensity of the seasonal size spectrum heterogeneity. The second axis separates the 6.35–10.08- $\mu\text{m}$  (channels 6–8) size group from the 40.3–50.8- $\mu\text{m}$  (channels 14–15) group. It also separates the period 22–25 March from that of 6–20 November (Fig. 9). Because it identifies the spring and fall blooms, the second axis could be considered an expression of primary production. The third axis is positively defined by channel 5 and to a minor extent by channels 2–4. It is also negatively defined by channel 8. It identifies the period from 24 July to 18 September and 25 March to 3 April. Obviously this third axis describes

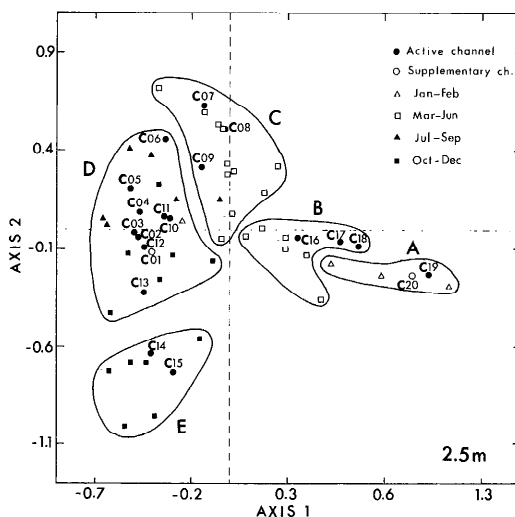


Fig. 9. Correspondence analyses of the data matrix at 2.5-m depth, plane of factors 1 and 2. The two sets of points in correspondence are the Coulter Counter in channels 1–20 (with channels 1 and 20 treated as supplementary), and the samples (identified by a symbol according to time of year). Points are grouped considering the projections on the first three axes.

the production of small particles at one peak of the spring bloom and during summer and early fall.

Projections of the variables for the other three depths lead to similar interpretations for the first three factorial axes. The first one always discriminates between large and small or medium size particles and illustrates the heterogeneity of the size spectra. This heterogeneity increases with depth, essentially because of the progressive absence of small size peaks. At 30 m almost flat spectra occurred; these were never recorded in the first 10 m. The second axis at 5 m is related to phytoplankton production. It illustrates the fall bloom of dinoflagellates and the pulses of small particles during spring and fall. At 10 m, this axis singles out the spring bloom (18–28 March, channels 7–8) and the fall blooms of 1973 (November–December) and 1974 (October–November) associated with channels 13–15. However, as light penetration at that depth is minimal and phytoplankton production negligible (Taguchi unpubl. data), it seems more likely that this second axis represents sedimentation from the surface or vertical mixing of spring and fall production. Similar con-

Table 2. Time and size characteristics of the multivariate groupings for the 2.5-m depth (see Fig. 9).

| Group | Time period   | Characteristics channels            |
|-------|---|-------------------------------------|
| A     | Jan 74  | 19, 20                              |
| B     | 1, 4, 8, 14 Mar and<br>17 Apr–8 May 74                                  | 16, 17, 18                          |
| C     | 6, 11, 18–28 Mar, 3<br>Apr, 30 May,<br>Jun, and 10 Jul<br>74            | 7, 8, 9                             |
| D     | 13 Feb, 24 Jul, Aug,<br>Sep, 2 Oct, and<br>Dec 74; Oct and<br>14 Nov 73 | 1, 2, 3, 4, 5, 6,<br>10, 11, 12, 13 |
| E     | Oct and Nov 74; 27<br>Nov and 13 Dec<br>73                              | 14, 15                              |

Table 3. Time and size characteristics of multivariate groupings for the 5-m depth.

| Group | Time period   | Characteristics channels        |
|-------|---|---------------------------------|
| A     | Jan, 4, 8, 11 Mar,<br>May, Jun, 10, 19<br>Jul, and 4 Dec<br>74; 30 Oct 73 | 16, 17, 18, 19, 20              |
| B     | Feb. 1, 6, 14–28<br>Mar, and Apr 74                                       | 7, 8, 9                         |
| C     | 24 Jul, Aug, Sep,<br>and 18 Dec 74;<br>16 Oct 73                          | 1, 2, 3, 4, 5, 6,<br>10, 11, 12 |
| D     | 17, 20 Oct 74; 14<br>Nov 73   | 13                              |
| E     | 30 Oct and Nov 74;<br>27 Nov and 13<br>Dec 73                             | 14, 15                          |

clusions can be reached at 30 m, where axis 2 is defined by the 1973 fall bloom and channel 15. Related to a different aspect of the biological production, the third axis shows some biological meaning only at 5- and 10-m depths where it illustrates the summer pulses of small particles.

Five multivariate groups describe the annual cycle of the Bedford Basin particulate matter at 2.5 and 5 m. Only remnants of the surface successions are still noticeable at 10 m, while no seasonal events can be observed at 30 m. At 2.5 m, group A and B represent large detrital material that occurs both during winter and during the post-spring bloom period (Table 2). Group C includes part of the spring and early summer production of small particles. Group D corresponds to the summer and fall blooms of very small and middle size particulate material, whereas group E includes the fall bloom of dinoflagellates. At 5 m, all five groups differ noticeably from those described as they do not illustrate a true cycle (Table 3): group A includes all periods of occurrence of large detrital particles from winter, fall, pre- and post-spring bloom times; group B corresponds to the spring production of small particulate matter; group C includes most of the summer and part of the fall production of nanoplankton and middle size particles, whereas groups D and E include the fall bloom of both years considered.

### Discussion

Coastal waters have higher biomass and a larger diversity of particles than oceanic systems. Much of this diversity is related to pulses of different sizes of phytoplankton and microzooplankton (Malone 1971*a,b*; Poulet 1976; Malone and Chervin 1979; Mayzaud and Taguchi 1979). To appreciate this diversity from the point of view of the consumer, we must relate size, biomass, and chemical composition. Normally this is done through correlation analysis which describes the dominant seasonal associations between parameters. However, direct comparison of the volume indicated by each individual Coulter Counter channel and any biochemical measurement will be of little use, since the amount of information contained in a single channel is too small to be meaningful.

Cluster analysis of the correlations matrix between channels led us to recognize groups of adjacent channels with similar seasonal behavior. These can be more easily compared to chemical measurements. The characteristics of Bedford Basin particulate matter as defined by such an analysis are typical of most neritic environments. Living carbon (ATP) is associated with the surface nanoplankton, and chlorophyll is associated with small and medium size particles of the spring and fall blooms (Yentsch and Ryther 1959; Durbin et al. 1975; Poulet 1976; Malone and Chervin 1979; Mayzaud and Taguchi 1979). Detritus seemed to occur in all

size classes but was dominant at larger sizes (Poulet 1976; Valkenberg et al. 1978). The nanoplankton is associated with a large population of microzooplankton. The increasing detrital content with increasing depth is illustrated by the decreasing number of significant associations between small and intermediate size groups and chemical parameters and by the shift of chlorophyll-containing particles to larger size classes. The progressive disappearance of nanoplankton at 10 and 30 m supports the suggestion by Malone and Chervin (1979) that the relative proportions of different size phytoplankton were related to the time lags between input (growth) and removal (grazing and sinking) which are greater for net plankton than for nanoplankton populations.

Grouping by principal component analysis illustrates a different aspect of these relationships, as it singles out those size classes responsible for the seasonal changes in biological activity. Indeed, regardless of depth, the spectral diversity (first factorial axis: Fig. 7) can be attributed to particles ranging from 8 to 25.4  $\mu\text{m}$ . These correspond to those responsible for all of the spring and part of the summer and fall surface production. The increasing amount of variance explained by this axis with depth illustrates the decreasing level of endogenous biological particle production at greater depths. Thus at 30 m, although the standing stock of particulate material consists mainly of large particles (Taguchi and Hargrave 1978; Hargrave and Taguchi 1978), variability through the seasons is caused by the input of smaller particles. At 30 m the factorial plane defined by the second and third axes could be considered to represent the input of different size particles at different periods (Fig. 10). There were inputs of small size particles on 20 March 1974 and 30 October 1973; of medium-small size particles on 3 and 17 April and 4 and 18 December 1974; of medium-large size particles on 27 November and 13 December 1973 and 28 March 1974; and of large size on 14 March, 8 and 30 May and 5 June 1974. The 16 January and 4 September 1974 data could not be fitted into the above groups because sedimenta-

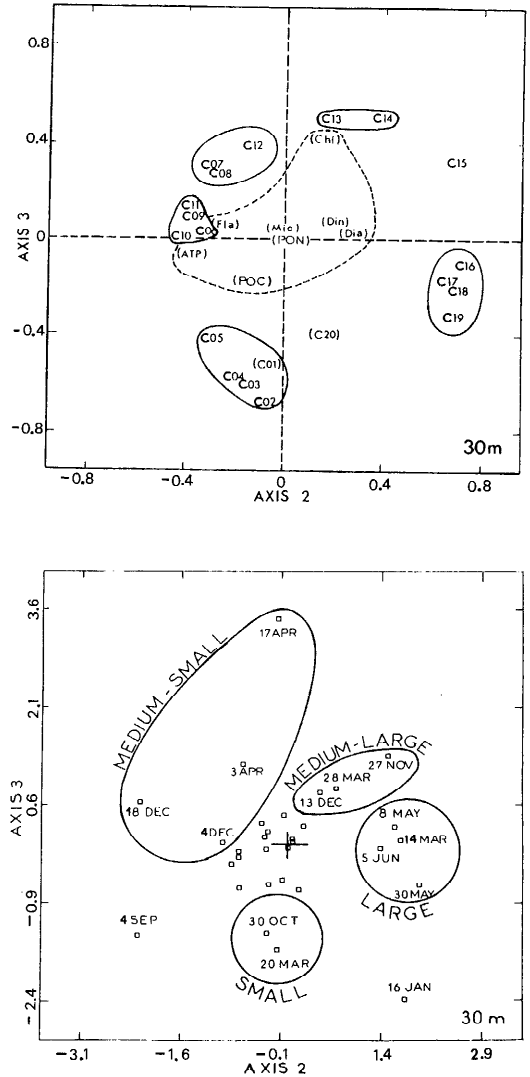


Fig. 10. As Fig. 8 (30 m), but plane 2-3. Above: factor loadings. Below: factor scores; each square symbol represents a sampling date; some periods of time (circled) are typically associated with dominant size classes of particles.

tion of several size classes occurred at the same time.

By comparing the results of principal component analysis and correspondence analysis one can illustrate the seasonal changes of the size spectra in terms of both biological production and taxonomic succession. The surface material (2.5 m) is

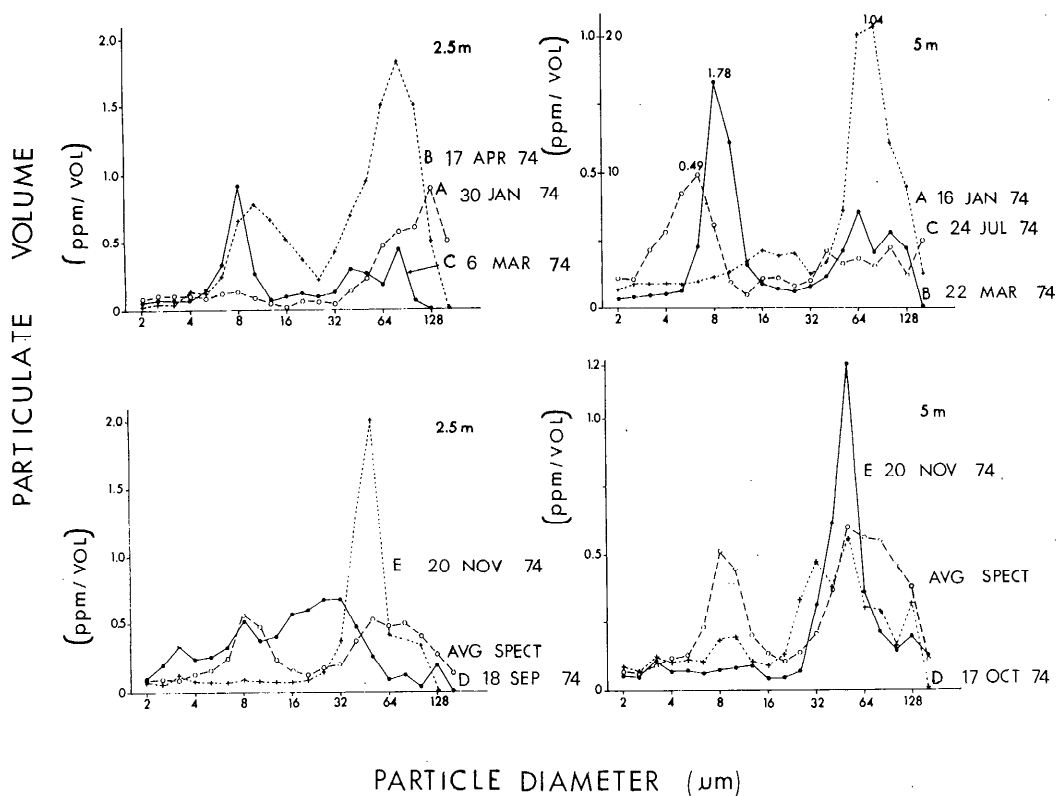


Fig. 11. Some characteristic particle spectra for 2.5- and 5-m depths. Average spectrum also shown.

the only one characterized by a clear seasonal cycle. During winter, large particles ( $>64.0 \mu\text{m}$ ) generally dominated. In contrast, flagellates and small diatoms ( $8.0\text{--}12.7 \mu\text{m}$ ), associated to some degree with PON, usually dominated for part of the spring bloom and during early summer. Summer production of very small flagellates ( $<5 \mu\text{m}$ ) and medium size diatoms ( $16.0\text{--}25.4 \mu\text{m}$ ) was responsible for the high level of ATP along with microzooplankton, while the fall bloom of dinoflagellates ( $40.3\text{--}50.8 \mu\text{m}$ ) was associated with the seasonal maxima of chlorophyll. In terms of particle spectra, the pre- and post-spring bloom periods are characterized by large particles associated with small and medium size diatoms and dinoflagellates (*Chaetoceros*, *Fragilaria*, *Thalassionema*, *Gymnodinium*) and represent times of transition between the winter and the spring and summer periods of pro-

duction. The size specificity of each time group defined by correspondence analysis and the difference from the computed mean spectrum are shown in Fig. 11. At 5 m, the seasonality is partially affected by the influence of a pool of detrital material of large size ( $>64.0 \mu\text{m}$ ). This is most apparent during winter, spring, and fall. The spring production remains associated with chlorophyll and a succession of small diatoms, dinoflagellates, and flagellates in the  $8.0\text{--}12.7\text{-}\mu\text{m}$  range (Fig. 11, spectra B). The summer and early fall periods are characterized by nanoplankton ( $<5.0 \mu\text{m}$ ) associated with microzooplankton and by larger particles (mostly diatoms) associated with nitrogen and ATP (Fig. 11, spectra C).

An association between nanoplankton and microzooplankton at 2.5 and 5 m was observed regardless of the statistical treatment used. The size of microzooplankton in Bed-



ford Basin was in the range 16–60  $\mu\text{m}$  (Mayzaud and Taguchi 1979; Poulet 1976; Paranjape 1980), yet the close association with particles  $<5.0 \mu\text{m}$  suggests a trophic relationship similar to the one observed by Taguchi (1976) in Akkeshi Bay. He found an almost linear relation between the abundance of microzooplankton and nanoplankton. Small cells ( $<8.0 \mu\text{m}$ ) are known to account for most of the primary production during summer when the water column is well stratified (Roman 1978; Malone and Chervin 1979). Rassoulzadegan and Etienne (1981) have shown that ciliates are more effective in controlling nanoplankton blooms than are microcrustaceans and concluded that competition exists between microzooplankters and those microcrustaceans that can efficiently ingest particles  $<20 \mu\text{m}$ . These results support the idea of Conover (1981) that microzooplankters are important consumers and that coastal ecosystem models should include a microzooplankton term to control the fast growth of nanoplankton cells.

The occurrence of pulses of small particles during spring and summer is certainly one of the key features of the environment of Bedford Basin. The development of small cells during water stratification seems fairly general and appears to alternate with blooms of diatoms and dinoflagellates during spring, summer, and fall. The variability is evident if one considers the lack of correlation between particulate chlorophyll and ATP, probably related to the presence during summer of a large population of microzooplankton and nanoplankton rich in ATP. The preferential concentration observed at 5 m is associated with the thermocline at which the different size particles accumulate. Grazing pressure by tintinnids and other nonchlorophyllous ciliates at that level is certainly a major factor contributing to the loss of nanoplankton chlorophyll without similar changes in ATP. Because the generation time of ciliates is of the same order of magnitude as that of nanoplankton (Rassoulzadegan 1982), growth of heterotrophic ciliates is also likely to cause an increase in ATP. Such grazing pressure is important enough to limit the small particles to the surface layers (Malone and Chervin 1979).

The significance of suspended organic material in the sea can be considered in terms of the relative importance of the various particulate components to the seston consumers. The primary position of the phytoplankton in the food cycle has often been recognized, although recent studies in coastal waters indicate that, over different periods of time, nonliving particulate matter is generally the dominant fraction (Balch 1971; Sutcliffe 1972; Poulet 1976). It has been suggested that detritus can supply the major part of a neritic copepod's energy needs (Heinle *et al.* 1977), but the fact remains that given the choice a copepod will preferentially assimilate phytoplankton (Chervin *et al.* 1981). The summer maximum of zooplankton in Bedford Basin (Mayzaud and Conover 1976) would certainly support the view that growth and reproduction rely essentially on assimilation of living particles (Chervin *et al.* 1981; Heinle *et al.* 1977). That changes in size and chemical composition are key factors in the nutritional adaptability of the "herbivorous" zooplankters is now widely accepted; nevertheless Poulet and Marsot (1978) and Mayzaud and Poulet (1978) have shown that the chemical quality of the food should also be considered. In any event, variations of the seston composition is indicative of the seasonal modifications of quality and quantity of the food resources available to the seston-feeding zooplankters. Their capacity to adapt to such changes and ability to modify their feeding strategy successfully are certainly the keys to explaining their seasonal abundance and species succession.

### References

- BALCH, N. 1971. The role of living and non-living organic particles in copepod feeding. Ph.D. thesis, Dalhousie Univ. 138 p.
- BEERS, J. R., F. M. REID, AND G. L. STEWART. 1975. Microplankton of the North Pacific central gyre. Population structure and abundance, June 1973. *Int. Rev. Gesamten Hydrobiol.* **60**: 607–638.
- BENZECRI, J. P. 1969. Statistical analysis as a tool to make patterns emerge from data, p. 35–60. *In* S. Watanabe [ed.], *Methodologies of pattern recognition*. Academic.
- . 1973. L'analyse des données. 2. L'analyse des correspondances. Dunod.
- BINET, D., M. GABORIT, AND M. ROUX. 1972. Copepodes pélagiques du Plateau Ivoirien. Utilisation de l'analyse des correspondances dans l'étude

- des variations saisonnières. *Doc. Sci. C. R. Oceanogr. Abidjan* **3**: 47–79.
- CHANUT, J. P., AND S. A. POULET. 1979. Distribution des spectres de taille des particules en suspension dans le fjord du Saguenay. *Can. J. Earth Sci.* **16**: 240–249.
- , D. COSSA, AND J. C. MARTY. 1977. Factor analysis of the suspended matter distribution in the St. Lawrence estuarine system, p. 1–23. *In Mathematics at the service of man. Proc. 1st World Conf. Barcelona.*
- CHERVIN, M. B., T. C. MALONE, AND P. J. NEALE. 1981. Interactions between suspended organic matter and copepod grazing in the plume of the Hudson River. *Estuarine Coastal Shelf Sci.* **13**: 169–184.
- CONOVER, R. J. 1981. Nutritional strategies for feeding on small suspended particles, p. 363–395. *In A. R. Longhurst [ed.], Analysis of marine ecosystems.* Academic.
- , AND M. HUNTLEY. 1980. General rules of grazing in pelagic ecosystems. *Brookhaven Symp. Biol.* **31**: 461–485. Plenum.
- DURBIN, E. G., R. W. KRAWIEC, AND T. J. SMAYDA. 1975. Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA). *Mar. Biol.* **32**: 271–287.
- EPPLEY, R. W., W. G. HARRISON, S. W. CHISHOLM, AND E. STEWART. 1977. Particulate organic matter in surface waters off southern California and its relationship to phytoplankton. *J. Mar. Res.* **35**: 671–696.
- GOWER, J. C., AND G. J. ROSS. 1969. Minimum spanning trees and single linkage cluster analysis. *Appl. Stat.* **18**: 54–64.
- HARGRAVE, B. J., AND S. TAGUCHI. 1978. Origin of deposited material sedimented in a marine bay. *J. Fish. Res. Bd. Can.* **35**: 1604–1613.
- HEINLE, D. R., R. P. HARRIS, J. F. USTACH, AND D. A. FLEMER. 1977. Detritus as food for estuarine copepods. *Mar. Biol.* **40**: 341–353.
- HILL, M. O. 1973. Reciprocal averaging: An eigenvector method of ordination. *J. Ecol.* **61**: 237–249.
- . 1974. Correspondence analysis: A neglected multivariate method. *Appl. Stat.* **23**: 340–354.
- HOBSON, L. A. 1971. Relationship between particulate organic carbon and microorganisms in upwelling areas off southwest Africa. *Invest. Pesq.* **35**: 195–208.
- KITCHEN, J. C., D. MENZIES, H. PAK, AND J. R. ZANEVELD. 1975. Particle size distribution in a region of coastal upwelling analyzed by characteristic vectors. *Limnol. Oceanogr.* **20**: 775–783.
- LEBART, L., A. MORINEAU, AND N. TABARD. 1977. *Techniques de la description statistique.* Dunod.
- LEGENDRE, L., AND P. LEGENDRE. 1979. *Numerical ecology.* 2. Masson.
- MALONE, T. C. 1971a. The relative importance of nanoplankton and net plankton as primary producers in tropical, oceanic, and neritic phytoplankton communities. *Limnol. Oceanogr.* **16**: 633–639.
- . 1971b. The relative importance of nanoplankton and net plankton as primary producers in the California Current system. *Fish. Bull.* **69**: 799–820.
- , AND M. B. CHERVIN. 1979. The production and fate of phytoplankton size fractions in the plume of the Hudson River, New York Bight. *Limnol. Oceanogr.* **24**: 683–696.
- , AND D. C. BOARDMAN. 1979. Effects of 22- $\mu$ m screens on size-frequency distributions of suspended particles and biomass estimates of phytoplankton size fractions. *Limnol. Oceanogr.* **24**: 956–960.
- MAYZAUD, P., AND R. J. CONOVER. 1976. Influence of potential food supply on the activity of digestive enzymes of neritic zooplankton, p. 415–427. *In Proc. 10th Eur. Symp. Mar. Biol. Ostend, v. 2.* Universa.
- , AND S. A. POULET. 1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. *Limnol. Oceanogr.* **26**: 1144–1154.
- , AND S. TAGUCHI. 1979. Size spectral and biochemical characteristics of the particulate matter in the Bedford Basin. *J. Fish. Res. Bd. Can.* **36**: 211–218.
- NISCHIZAWA, S. 1969. Suspended matter in the sea. 2. Reevaluation of the hypothesis. *Bull. Plankton Soc. Jap.* **16**: 1–42. [FRB Transl. 3490.]
- ORLOCI, L. 1978. *Multivariate analysis in vegetation research.* Junk.
- PARANJAPE, M. A. 1980. Occurrence and significance of resting cysts in a hyaline tintinnid, *Helicostomella subulata* (Ehre) Jörgensen. *J. Exp. Mar. Biol. Ecol.* **48**: 23–33.
- PARSONS, T. R. 1969. The use of particle size spectra in determining the structure of a plankton community. *J. Oceanogr. Soc. Jap.* **25**: 172–181.
- , R. J. LEBRASSEUR, AND J. P. FULTON. 1967. Some observations on the dependence of zooplankton on cell size and concentration of phytoplankton blooms. *J. Oceanogr. Soc. Jap.* **23**: 10–17.
- POULET, S. A. 1973. Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. *Limnol. Oceanogr.* **18**: 564–573.
- . 1974. Seasonal grazing of *Pseudocalanus minutus* on particles. *Mar. Biol.* **25**: 109–123.
- . 1976. Feeding of *Pseudocalanus minutus* on living and non-living particles. *Mar. Biol.* **34**: 117–125.
- , AND P. MARSOT. 1978. Chemosensory grazing by marine calanoid copepods. *Science* **200**: 1403–1405.
- RASSOULZADEGAN, F. 1982. Le rôle fonctionnel du microzooplancton dans un écosystème méditerranéen. D.S. thesis, Univ. Paris 6. 138 p.
- , AND M. ETIENNE. 1981. Grazing rate of the tintinnid *Stenosomella ventricosa* (Clap. & Lachm.) Jörg. on the spectrum of the naturally occurring particulate matter from a Mediterranean neritic area. *Limnol. Oceanogr.* **26**: 258–270.
- RICHMAN, S., D. R. HEINLE, AND R. HUFF. 1977. Grazing by adult estuarine copepods of the Chesapeake Bay. *Mar. Biol.* **42**: 69–84.
- RILEY, G. A. 1970. Particulate organic matter in sea water. *Adv. Mar. Biol.* **8**: 1–118.

- ROMAN, M. R. 1978. Tidal resuspension in Buzzards Bay Mass. 2. Seasonal changes in the size distribution of chlorophyll, particle concentration, carbon and nitrogen in resuspended particulate matter. *Estuarine Coastal Mar. Sci.* **6**: 47-53.
- SHELDON, R. W. 1973. Direct measurement of particle concentrations in natural waters with a model T Coulter Counter. *Fish. Res. Bd. Can. Tech. Rep.* **379**. 25 p.
- , A. PRAKASH, AND W. H. SUTCLIFFE. 1972. The size distribution of particles in the ocean. *Limnol. Oceanogr.* **17**: 327-340.
- SUTCLIFFE, W. H. 1972. Some relations of land drainage, nutrients, particulate material and fish catch in two eastern Canadian bays. *J. Fish. Res. Bd. Can.* **29**: 357-362.
- TAGUCHI, S. 1976. Microzooplankton and seston in Akkeshi Bay, Japan. *Hydrobiologia* **50**: 195-204.
- . 1981. Seasonal studies of the dinoflagellate *Ceratium longipes* in the Bedford Basin, Canada. *J. Exp. Mar. Biol. Ecol.* **55**: 115-131.
- , AND B. T. HARGRAVE. 1978. Loss rate of suspended material sedimented in a marine bay. *J. Fish. Res. Bd. Can.* **35**: 1614-1620.
- , AND T. PLATT. 1978. Phytoplankton biomass in Bedford Basin: Volume, surface area, carbon content and size distributions. *Can. Fish. Mar. Serv. Data Rep.* **55**. 404 p.
- TATE, N. W., AND R. C. CLELLAND. 1957. Non-parametric and shortcut statistics. *Interstate*.
- TEIL, H. 1975. Correspondence factor analysis: An outline of its method. *J. Int. Assoc. Math. Geol.* **7**: 3-12.
- VALKENBERG, S. D. VAN, J. K. JONES, AND D. R. HEINLE. 1978. A comparison by size class and volume of detritus versus phytoplankton in Chesapeake Bay. *Estuarine Coastal Mar. Sci.* **6**: 569-582.
- YENTSCH, C. S., AND J. H. RYTHER. 1959. Relative significance of net phytoplankton and nanoplankton in the water of Vineyard Sound. *J. Cons. Cons. Int. Explor. Mer* **24**: 231-238.

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