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During the spring of 1980 in East Sound, Washington, the silicoflagellate Dictyocha speculum was observed in unprecedented high abundances. Maximum silicoflagellate concentration during the bloom was 3.76×10^5 cells/l, accounting numerically for 80% of total phytoplankton. Although the spring diatom bloom in East Sound did not occur until late April, the observed silicoflagellate bloom took place several weeks earlier. An examination of concurrent environmental data indicates that while the late spring diatom increase is explained by the critical depth concept, silicoflagellates can increase prior to water-column stratification and the achievement of critical depth conditions. Possible explanations include the motility of the cells and their apparent affinity for low light environments.

The Spring Bloom of the Silicoflagellate *Dictyocha speculum* in East Sound, Washington, with Respect to Certain Environmental Factors

by

Vicki L. Fagerness

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INTRODUCTION

Silicoflagellates have been observed in the sea for over a hundred years, but during this time little information has been obtained concerning these organisms. Although they constitute a numerically small portion of most phytoplankton assemblages, silicoflagellates are of interest for several reasons: First, because geological researchers have recently begun using silicoflagellate microfossil assemblages in sediments to date geological strata and estimate paleotemperatures (Ciesielski and Weaver, 1973; Poelchau, 1974; Murray, 1982), it is important that their assumptions concerning silicoflagellate temperature tolerance be biologically valid. Secondly, silicoflagellates are thought to be remnants of an ancient group of organisms possibly on their way to extinction (Frenguelli, 1935; Deflandre, 1948). Taxonomically isolated, but with features in common with both diatoms and radiolarians, silicoflagellates may be of importance in understanding phylogenetic relationships. Lastly, and of most importance in this study, the occasional high abundance and local dominance of silicoflagellates in the phytoplankton communities of some neritic areas makes them a significant component of the production and trophic ecology of those regions.

Silicoflagellates are small (<100 μm) planktonic algae with golden-brown chloroplasts, a single flagellum, and a delicate, exterior siliceous skeleton composed of tubular elements. There is

great disagreement concerning silicoflagellate taxonomy and nomenclature. In this study the genus Distephanus Stohr 1880 is regarded as a synonym of the genus Dictyocha Ehrenberg 1937. In citation of data of other workers their usage will be followed, but in this discussion and in figures and illustrations, the senior synonym will be used. The reader is referred to Van Valkenburg (1970, 1980) or Poulchau (1976) for a complete history and discussion of this taxonomic debate.

Table 1 is a summary of some of the few published data concerning living silicoflagellates, either from specific studies of this group or extracted from general phytoplankton investigations. Most major oceanographic expedition reports have sparse accounts of silicoflagellates. The first extensive and so far only detailed investigations of pelagic silicoflagellates are those of Gemeinhardt (1934) in the South Atlantic. For the Pacific there are some generalized abundance data without details on species composition (Kozlova and Mukhina, 1967).

High silicoflagellate abundance values have been reported in coastal areas, with studies in various parts of the Mediterranean and Aegean Seas and to a lesser extent near Norway, Japan, and California. As Table 1 shows, there is a large range in recorded maximum concentrations of silicoflagellates: from less than 2 cells/l in the tropical Pacific to 5×10^4 cells/l in coastal waters of Norway.

Seasonal growth cycles have been described for the silicoflagellate species Dictyocha fibula. Travers and Travers (1968) in reviewing Mediterranean studies indicate that seasonal increases of D. fibula are found in winter and spring. Similarly, Nival (1965)

Table 1. Summary of recorded observations of living silicoflagellates (in part, after Poelchau, 1974).

Reference	Location	Maximum Abundance (cells. l^{-1})	Month Observed	Temp. (°C)	Species
Open Ocean					
Gemeinhardt, 1934	S. Atlantic	---	---	20-27	D. fibula
				0-2	D. speculum
Kozlova & Mukhina, 1967	N. Pacific				
	temperate	2-35	---	7-11	total
	tropical	≤2		26-27	total
Coastal Waters					
Gran, 1912	Norway	50,400	Oct	---	D. speculum
Kokubo, 1932	Japan	724	March	---	D. speculum
Nival, 1965	Villefranche	5,500	Jan-Mar	13-15	D. fibula
Strickland et al.,1968	La Jolla, CA	50-100,ave.	May-Aug	>18	D. speculum
Travers & Travers, 1968	Marseilles	9,890	Feb-Apr	<15	D. fibula
Ignatiades, 1970	Aegean Sea	600	Feb-Mar	<15	D. fibula
O'Kane, 1970	Monterey Bay, CA	175	Mar & June	11-14	D. speculum
Leger, 1971-72	Monaco	6,500	Feb	13-15	D. fibula

described high relative abundance of D. fibula from January to March in the bay of Villefranche-sur-Mer, France. Ignatiades (1970) also observed the maximum abundance of D. fibula in the Aegean Sea in February and March. The seasonal pattern of D. speculum abundance is less clear, although Strickland et al. (1968) observed late spring and summer blooms off La Jolla, California.

Little autecological research concerning silicoflagellates has been done. This is due in part to difficulties in maintaining these species in laboratory culture. Van Valkenburg and Norris (1970) were the first to report successful isolation and culture of a silicoflagellate, Dictyocha fibula, but Van Valkenburg (pers. comm.) reported many difficulties in maintaining and transporting the cultures. D. speculum was successfully isolated by R. Waters of the University of British Columbia from Patricia Bay, Nanaimo, in 1978, but it is no longer maintained in culture. Until culturing problems are overcome, information concerning silicoflagellate ecology must come largely from field observations.

As with all phytoplankton, silicoflagellate abundance and distribution is presumed to be influenced by environmental variables, including temperature, salinity, and nutrient supply. Water temperatures favoring production of silicoflagellates range from 0° to 27° C (Table 1). Gemeinhardt (1934) distinguished warm- and cold-water genera using data from the South Atlantic, believing Dictyocha fibula to prefer comparatively warmer water than Distephanus speculum. However, the actual temperature ranges observed are often quite disparate. Gemeinhardt reported an optimum of $20-27^{\circ}$ C for D. fibula, but Nival (1965), Travers and Travers (1968), and Ignatiades

(1970) described maximum abundances at 12-15° C, and Van Valkenburg and Norris (1970) determined an optimum laboratory culture temperature of 10° C. Similarly, the range of 0-2° C given by Gemeinhardt for D. speculum contrasts with the increased abundance of this species in Monterey Bay at temperatures between 11-14° C (O'Kane, 1970) and the observation that D. speculum was not found off La Jolla, California below 18° C. (Strickland et al., 1968). Most of the discrepancies in temperature data arise in coastal rather than open ocean areas. Lipps (1970) suggested that in near-shore areas other parameters such as nutrient availability may be more important than temperature.

The nutrient requirements of silicoflagellates have not been investigated. Nival (1965) observed greatest abundances under those conditions and times of year that permit the best mixing or upwelling. Lipps (1970) suggested that the motility of silicoflagellates may enable them to compete more efficiently for the available nutrients than some other species of plankton which are commonly more abundant.

Salinity does not seem to greatly affect silicoflagellate abundance. Gemeinhardt (1934) gave an optimum range of 33.5 - 34.4‰ for D. speculum. However, the same species was observed in this study at salinities ranging from 28.0 - 30.5‰, so some degree of tolerance is evident. Van Valkenburg and Norris (1970) determined an optimum salinity of 24‰ for D. fibula in culture.

Like all phototrophic organisms, silicoflagellates must require a certain level of illumination for normal development. The depth of greatest silicoflagellate abundance varies for different areas but generally does not exceed 100 to 150 m. In high latitudes where the light intensity is low, maximal numbers of these organisms are

reported to be near the surface. Gran (1912) found the main mass of the silicoflagellate population off the coastal waters of Norway in the water layer between the surface and 1 m depth, although an appreciable number of specimens were found to a depth of 50 m. Where time series observations were available (Travers and Travers 1968; Leger, 1971-72) the cells were shown to migrate seasonally to lower depths, often below the thermocline.

Clearly, much remains to be learned about this unusual yet sometimes important group of organisms. A field study of phytoplankton species succession in East Sound, Washington in the spring of 1980 offered an opportunity to investigate further the ecology of Dictyocha speculum, the least studied of common silicoflagellate species. The occurrence of this species in high concentrations or in bloom conditions has been rarely reported and never described in detail. Kokubo (1932) in Aomori Bay, Japan, and O'Kane (1970) in Monterey Bay, California, observed D. speculum but in maximum concentrations of only 724 and 175 cells/liter, respectively. Strickland et al. (1968) reported a maximum of 2,100 cells/liter off La Jolla, California, but until the present study, the greatest recorded abundance of D. speculum was 50,400 cells/liter, briefly noted by Lohman (1908, in Gran, 1912) in Kristianaia Fjord, Norway. Silicoflagellate concentrations during the bloom in East Sound, however, reached 376,000 cells/liter and accounted numerically for up to 80% of total phytoplankton. In addition, frequent sampling of major environmental parameters allowed for examination of potentially important factors determining the abundance and distribution of this silicoflagellate species.

The objectives of this work are threefold:

1) To describe the phytoplankton spring bloom and the succession of dominant species in a temperate fjord, East Sound, Washington.

2) To investigate probable environmental factors responsible for silicoflagellate dominance at a time when nutrient and temperature conditions appeared favorable for high diatom production.

3) To consider the role and potential importance of silicoflagellates in the phytoplankton community and trophic ecology of this area.

FIELD SITE DESCRIPTION

East Sound is a long, narrow fjord-like embayment on the south shore of Orcas Island, Washington, branching off from the junction of Lopez Sound and Harney Channel (Fig.1). It extends northwestward for ca. 12 km and is ca. 2 km wide with a mean depth of 25 m along its midline. The bottom is essentially flat except for a large sill extending about two-thirds of the way across the bay mouth to within 10 m of the surface.

Freshwater runoff from the surrounding island is minimal. The tidal range is 2-4 m. Circulation is periodically wind-driven. Rattray (1967) studied circulation in East Sound during a ten-hour period of steady 10m/sec wind blowing up the sound, and found the average longitudinal component of current to be a three-layer circulation with inflow at the surface and bottom and outflow at intermediate depths. Wind events of sufficient strength and duration to produce this circulation, however, occur only occasionally, and comparisons of both zooplankton and phytoplankton communities within the sound and in the outer channel indicate that plankton populations retained within East Sound develop without significant influxes of new species or populations from outside the bay. When wind events do occur, there is temporary blending of populations. Without further disturbance, however, the populations rapidly restabilize and become distinct assemblages (Dexter, 1983).

Phifer (1934) conducted the earliest descriptive study of phytoplankton species in East Sound, documenting phytoplankton abundance patterns and species present with monthly samples from February to November, 1932. Correlation of plankton production in the general

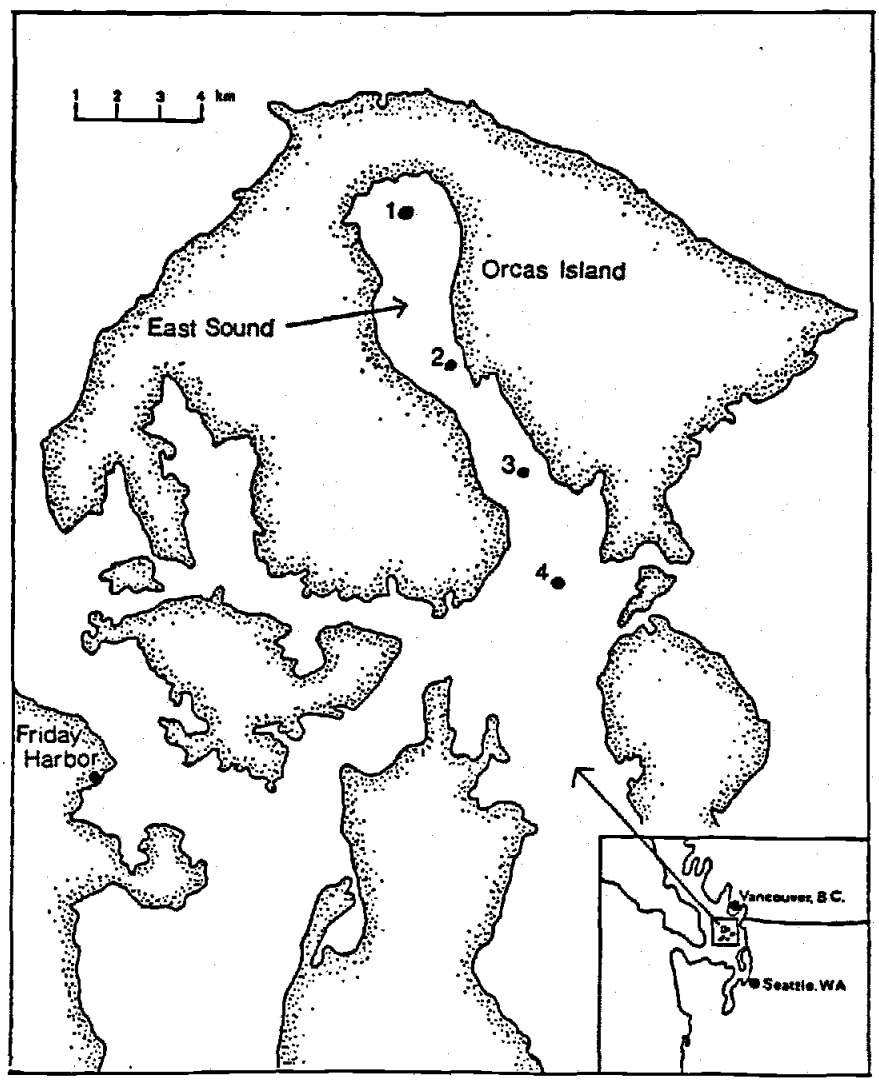

Fig. 1. Map of East Sound, Washington, showing the positions of the sampling stations.

area of the San Juan Archipelago with some chemical and physical factors was attempted by Gran and Thompson (1930); however, observations were made on only a few days. Yentsch and Scagel (1958) conducted a diurnal study of phytoplankton pigments throughout the water column in East Sound to observe the relationship of light intensity to pigment concentrations in a natural crop of phytoplankton. Again, only two days observations were obtained. This is the first reported study in East Sound measuring environmental and plankton community characteristics at frequent intervals.

METHODS

Sampling

Four stations were established at the field site: three along the midline of East Sound and one immediately outside the sound in Harney channel (Fig. 1). Measurements were taken at these stations from depths of 0, 5, 10, 15, 20, and 25 meters approximately every three to five days from March, 1980 through June, 1980, and intermittently through July. All four stations were sampled in one day, although the order in which they were sampled varied. Approximately 45 minutes to one hour was required for complete sampling of all depths at one station, and travelling time between adjacent stations averaged 30 minutes.

At all stations water samples were obtained from discrete depths using a shipboard pumping system. Temperature and salinity were measured with a YSI temperature - salinity probe. Nutrient samples were filtered and stored in a dark ice chest for analysis within 1 - 4 hours of return to the laboratory. Concentrations of nitrate plus nitrite, reactive silicate, and ammonium were determined on a Technicon Auto-Analyzer according to methods described by Atlas et al. (1971). Continuous profiles of light transmission were obtained periodically with an optical transmissometer developed by the Optical Oceanography Group at Oregon State University. In addition, a continuous daily record of surface irradiance was obtained from the Canadian Atmospheric Environment Service station at Departure Bay, Nanaimo, B.C., 86 km from East Sound, and its applicability to East Sound was confirmed with our own irradiance measurements.

In vivo fluorescence measurements were made at discrete depths

using a shipboard Turner Designs fluorometer. These provided estimates of phytoplankton biomass (Lorenzen, 1966). Water samples for chlorophyll a, phaeophytin, and particulate carbon and nitrogen analysis were syringe-filtered through Whatman GF/C filters and frozen for subsequent analysis. Chlorophyll concentrations were determined in the laboratory by the acetone extraction procedure described by Strickland and Parsons (1972). Particulate carbon and nitrogen concentrations were determined on a Perkin Elmer model 240 CHN analyzer. In situ ^{14}C incubation experiments to measure primary productivity were conducted concurrently with the three-month field sampling program (Wolniakowski, unpublished data).

Zooplankton samples for species identification and enumeration (Dexter, 1983) were obtained using a shipboard pumping system and a 64µm-mesh plankton net. The samples were preserved in formalin.

Phytoplankton Collection

One-liter water samples for phytoplankton studies were preserved immediately after collection with 20 to 30 ml of 25% glutaraldehyde. A 500 ml subsample was then filtered through a small plankton net constructed of 10µm-mesh Nitex. Repeated rinsing and backfiltering of the net with a measured amount of filtered seawater allowed for retention of nearly all cells of greater than 10µm diameter and produced a final sample that could be analyzed for species both quantitatively and qualitatively. The remaining 500 ml of filtrate were then passed through a second small net constructed of 1-µm mesh. This net was cleared in the same manner as the 10µm-net, and the sample saved for future examination. This second sample not only

allowed for examination of smaller species but also provided a check on the efficiency of the first 10µm-mesh net. Occasionally a few Nitzschia spp. or two-to-three cell chains of Skeletonema costatum passed through the 10µm-mesh, but this amount of error had a negligible effect on the final cell counts. The 500 ml subsamples remaining after the 1µm-mesh filtrations were periodically refiltered through Millipore filters, after which the filters were prepared for microscopic examination (Holmes, 1962; Moore, 1963) and scanned under the microscope to determine the efficiency of both nets used in conjunction. No diatoms, silicoflagellates, or dinoflagellates were observed. While the shortcomings of nets are well known, comparison of this rapid filtration method of concentration with standard settling methods showed no significant differences in abundance of dominant species observed.

Phytoplankton Enumeration

A Wild M40 inverted microscope was used for identification and counting, according to Utermohl's inverted microscope technique (Lund et al., 1958). Replicate aliquots were counted for each sample. Cells were counted until the number of the dominant species exceeded 200. Total cells counted in each sample ranged from 300 to 500.

Due to the time involved in obtaining accurate species identifications and counts, not all phytoplankton samples were enumerated. Samples were selected for counting in the following manner. Prior to beginning any counts, three days shown to represent different hydrographic and phytoplankton biomass conditions were chosen from throughout the four-month sampling period. For these

three days, samples from all four stations and all depths (0,5,10,15,20,25 m) were examined. Complete details of station similarity data and analyses are given in Appendix A. In summary, from calculations of an index of percentage similarity (Whittaker, 1960), the agreement between stations 1, 2, and 3 showed station 2 to be characteristic of the relative species abundances of the in-bay stations (percent similarity>80), while channel station 4 was different. Likewise, samples from 0,5,10, and 15 m were similar, but differed from those at 20 and 25 m. Therefore, for every sampling day, phytoplankton were identified and counted at depths of 5 and 20 m at both stations 2 and 4.

The counting methods imposed limitations on the phytoplankton data. First, very small species such as microflagellates were not always included in the phytoplankton counts. However, these species were a very small proportion of phytoplankton biomass (<5%) in the samples in which they were enumerated. Secondly, the absolute numerical abundance at a single depth can not be accurately extrapolated to the entire water-column. Fluorescence and chlorophyll measurements provided a more accurate comparison of total phytoplankton abundance between depths. Discrete fluorescence measurements showed that on 16 of 22 days the phytoplankton maximum was at 5 m.

The data set emphasizes a high frequency of sampling, enabling even brief phytoplankton species changes or blooms to be observed. For the purpose of a time-series study, the advantage of counting a few representative samples from every sampling day outweighs the information gained by counting all samples from only a few days.

Phytoplankton Identification

For identification of diatoms, Gran and Angst (1930) and Cupp (1943) were the primary references. Each cell was identified to the lowest possible taxonomic rank. The species of concern here were mostly the planktonic diatoms and silicoflagellates that were overwhelmingly dominant in the spring of 1980 in East Sound; however, other groups were recorded at higher taxonomic levels; e.g., *Peridinium*.

Even among the planktonic diatoms there were problems in identifying some small delicate species of *Chaetoceros* and *Thalassiosira*. Mounted slides were sometimes examined at higher magnification, but when cells were in poor condition (e.g., missing spines) identification to species was not possible. For most samples, species of questionable identity were present in low numbers and were of minor importance in numerical calculations. However, indistinguishable species occasionally abundant in the samples included: 1) *Thalassiosira nordenskioldii* and *T. aestivalis*; and 2) *Nitzschia (Cylindrotheca) closterium* and *N. longissima*. Only one silicoflagellate species, *Dictyocha speculum*, was observed.

RESULTS

Seasonal variations in the vertical distributions of the major environmental parameters are shown in Fig.2. Only the data for station 2 are presented, as this station typifies conditions throughout the sound.

Water temperature varied from 7.5 to 15.5°C over the three-month study period (Fig.2), and from 8.1 to 12.2°C during the time *D. speculum* was observed in the phytoplankton. Measurements in April indicated the continuation of winter conditions, with uniform 9 - 10°C temperatures throughout the water column. Warming of the surface water (>11°C) began the last week of April and relatively warmer surface temperatures persisted through July at the end of the study period. Salinity (not shown) ranged from 28.0 to 30.5‰ but showed very slight vertical differences. Due to calibration irregularities, salinity values obtained on different days were not directly comparable and so are not illustrated.

Inorganic nutrient concentrations underwent marked changes that were related to hydrographic events and phytoplankton blooms (Fig. 2b and 2c). Throughout the season periods of nutrient depletion were interspersed with periods of mixing and nutrient replenishment. Highest concentrations of both (NO_3^- + NO_2^-) and $Si(OH)_4$ were observed from March to early April, with values throughout the water column of 21-26μM and >40μM, respectively. With the onset of stratification and the rapid increase of phytoplankton in late April, concentrations of both nutrients in the surface layer rapidly declined. Between April 29 and May 2, (NO_3^- + NO_2^-) concentration in surface water dropped from 6.59 to 0.47μM, and $Si(OH)_4$ from 15.04 to 1.12μM; however, by May

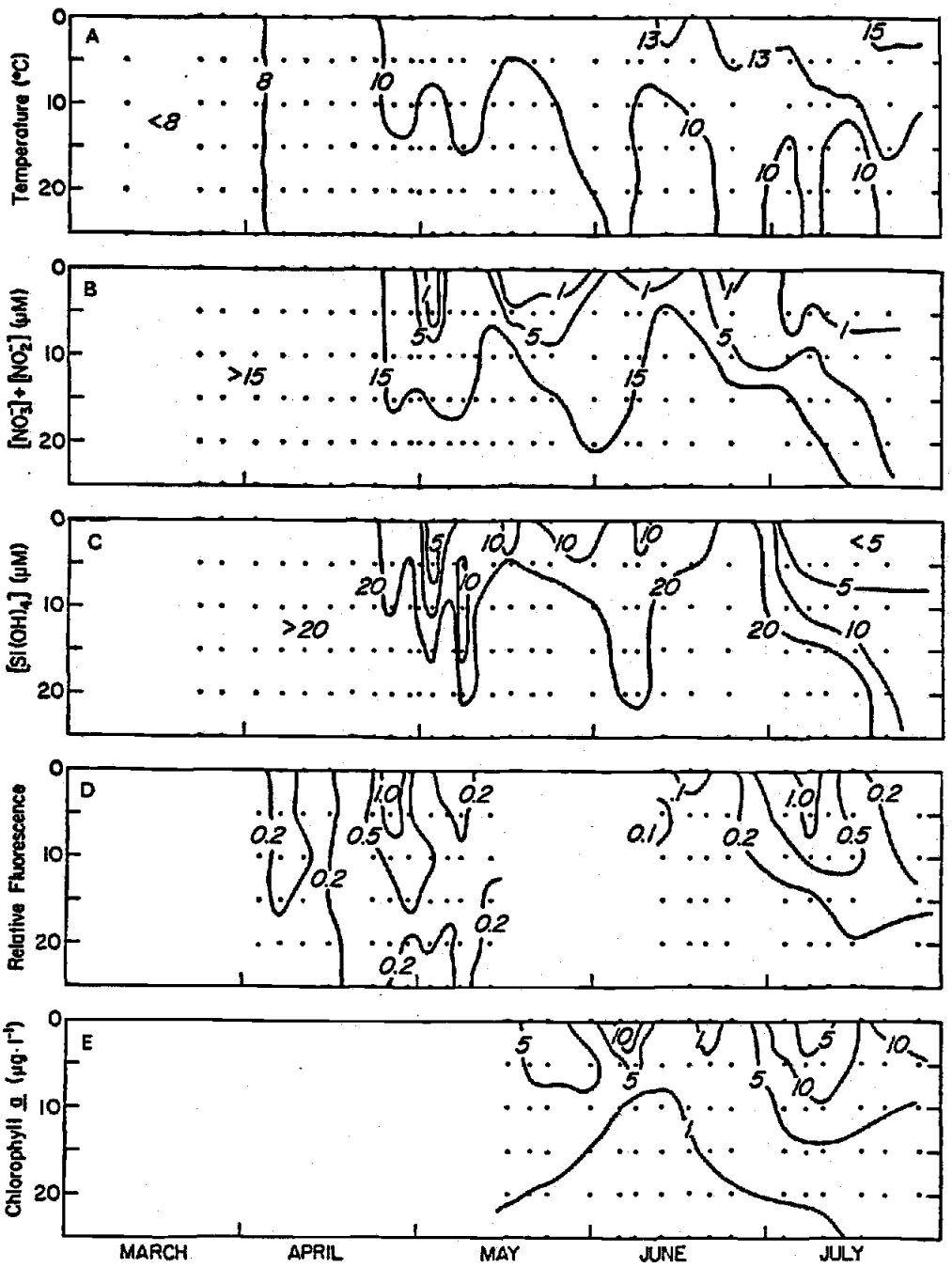

Fig. 2. Variation with depth of temperature, $[NO_3^-]$ + $[NO_2^-]$, $[Si(OH)_4]$, chlorophyll a, and relative fluorescence, at station 2, March through July, 1980.

5 concentrations of both nutrients exceeded 5μM and were greater than 15μM during most of May. A second decline in surface-water nutrient concentrations was observed the last week of May, although $[Si(OH)_4]$ remained greater than 5μM and ($[NO_3^-]$ + $[NO_2^-]$), while less than 1μM, did not become undetectable. NH_4^+ concentration was also measured. Surface layer values ranged from 0.30μM on April 29 to 5.0μM on May 5.

The general pattern of water-column stratification is shown best by the vertical contour plot of temperature in Fig.2a. The water column was mixed in early April, but by April 24 surface warming and water column stratification became evident. With isolated, storm-related periods of mixing throughout the spring, the water column remained stratified to varying degrees for the remainder of the study period. The onset of stratification is shown clearly by comparing the temperature difference between the surface and 20 m for the four-month period (Fig.3). Clearly, warming of the upper 15 m and the onset of stabilization of the surface layer occurred during the last week of April.

Phytoplankton Standing Stock

Spring phytoplankton growth in East Sound was typified by a generally increasing phytoplankton biomass, increasing slightly in late April but not reaching its maximum value until the end of May and early June.

Vertical profiles of *in vivo* fluorescence and chlorophyll *a* (Fig.2d and 2e), while incomplete and not directly comparable, give some indication of the bloom pattern. Biomass was concentrated in the upper 10 m, with the maximum at 5 m 75% of the time and at 10 m on

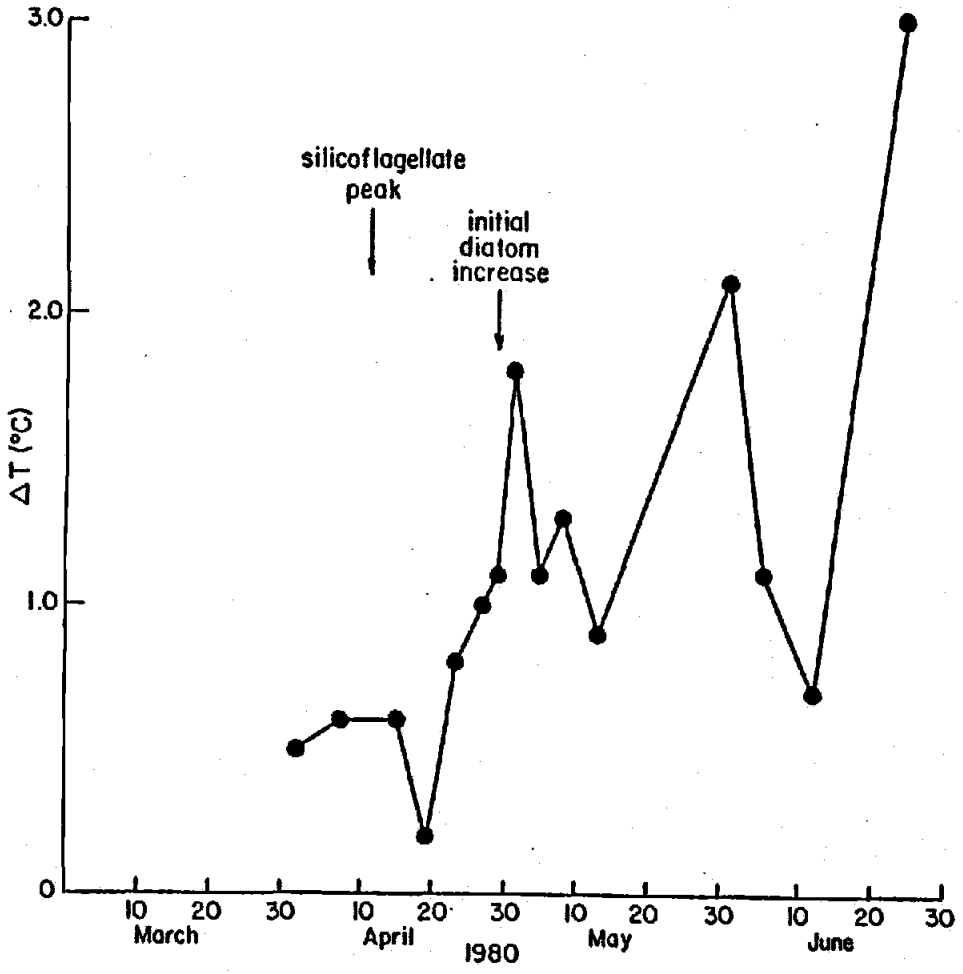

Fig. 3. Difference between temperatures at 5m and 20m, station 2.

remaining days.

There were two time scales of biomass change: 2 to 2.5 weeks for single-species blooms superimposed on a 2-to-3 month general spring bloom (Fig.4). Comparison of phytoplankton and nutrient profiles in Fig.2 show the expected inverse relationship. Phytoplankton cell concentrations remained relatively low (5×10^4 cells/l) until the last days of April and early May. However, it was the generally low-abundance period of early April that was dominated by the silicoflagellates. The early May bloom of approximately two-week duration was followed by a week of declining biomass. Another period of cell increase began the last week of May, and this bloom ultimately yielded the maximum cell concentration (4×10^6 cells/l) observed during the three-month study period. Phytoplankton biomass remained low through the second half of June, but in mid-July a fourth period of increase was observed. These cell concentrations, and chlorophyll-a values, are characteristic of productive areas, and are comparable to Phifer's (1934) observations in East Sound.

Phytoplankton Species Succession

In conjunction with the changes in biomass described above, the seasonal changes in phytoplankton species in the upper 15 meters were characterized by a series of distinct single-species blooms within the overall phytoplankton spring increase (Fig. 4). The first, small biomass increase in early April was comprised almost entirely of the silicoflagellate Dictyocha speculum (>80% numerically); after which diatoms were by far the dominant phytoplankton group. The intermediate-sized bloom during the first week of May was numerically

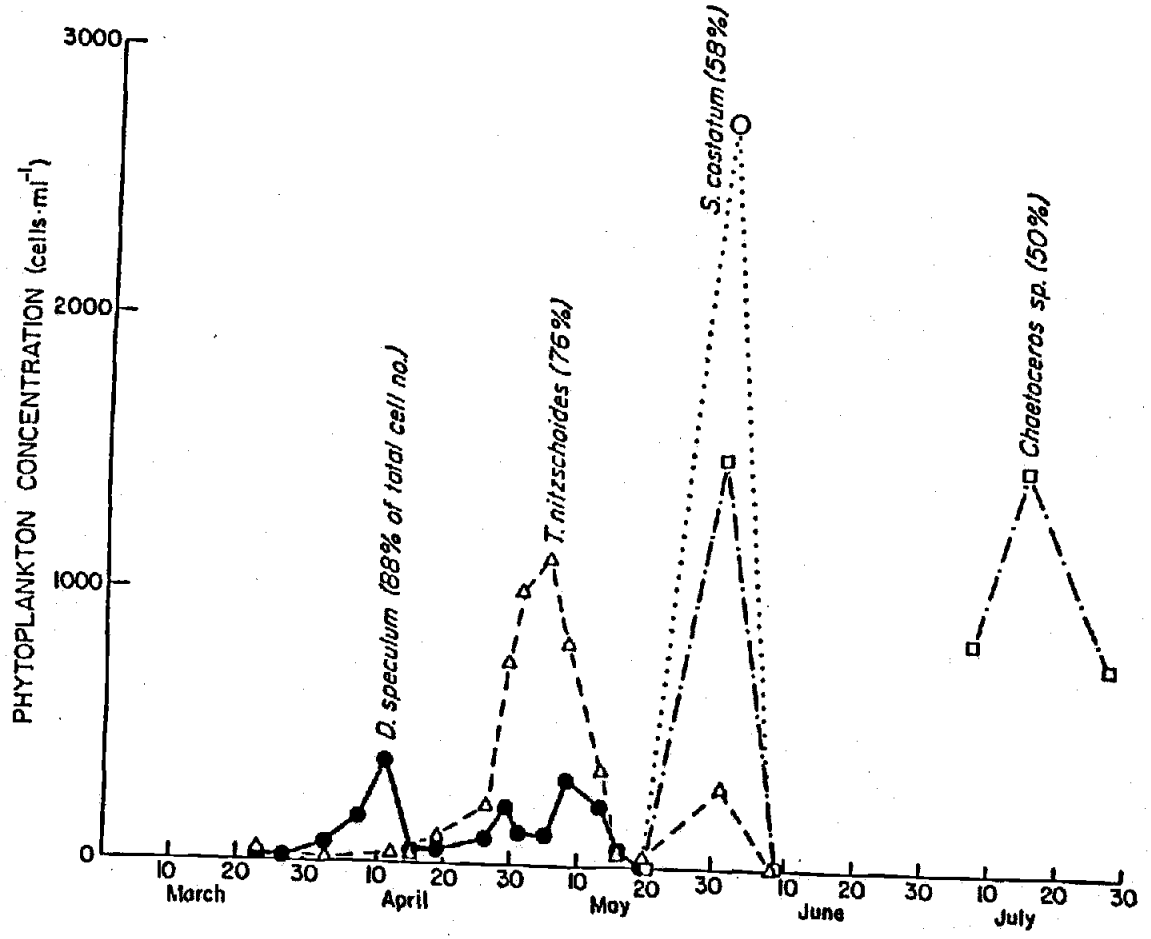

Fig. 4. Abundance of numerically important phytoplankton species in the upper water column of East Sound, March - July, 1980.

76% Thalassiothrix nitzschoides, the following bloom in late May and early June was 58% Skeletonema costatum, and the last bloom in July was over 50% Chaetoceros spp. Phifer (1934) also observed strong S. costatum dominance on May 18 and C. debilis, C. radicans, and C. vanheurckii abundance throughout late June and July. Similarly, though with some time delay, King et al. (1976) observed S. costatum dominance on June 24, and its subsequent decrease was accompanied by an increase in Chaetoceros spp. Concentrations of cells in all three studies were similar; however, the exact timing of changes in species abundance varied from year to year.

Similar species changes were observed at depth, as indicated by samples taken at 20 m; however, single species dominance was not as overwhelming as in surface waters and pennate diatoms, specifically Thalassiothrix nitzschoides, were much more abundant.

Complete species cell counts for all stations and depths enumerated are given in Appendix B.

DISCUSSION

If the relative abundance of a species is an indication of that species' ability to adapt to and survive in a particular set of environmental conditions, then the dominance of a species may be an indication of its ability to grow and reproduce better than any other species under the conditions existing at that time. The bloom of the silicoflagellate D. speculum is therefore of interest not only for the unusually high numbers observed, but also for the information on the ecology of this species that can be inferred. In the absence of laboratory cultures and experiments, the initial information and hypotheses on silicoflagellate ecology must necessarily come from field observations.

In 1980, the spring diatom bloom in East Sound did not occur until late April, but the silicoflagellate bloom took place several weeks earlier. Analysis of environmental conditions during this period indicates that the increase in diatom biomass is explainable in terms of the critical depth concept originally proposed by Gran and Braarud (1935) and quantified by Sverdrup (1953). Fig.2a shows clearly the stratification of the water column with a mixed surface layer above 15m formed the last week of April. This stratification coincided with increasing surface irradiance (Fig.5). Estimates of critical depth (D_{cr}) were calculated using the weekly mean surface irradiance values (I_c) and equations from Sverdrup (1953). The light extinction coefficients (k) were obtained from the transmittance data, and the approximate range of I_c, 0.5-3.5 ly/day(Hobson and Guest, 1983), gave maximum and minimum D_{cr} values. The depth of the mixed layer was distinguished as that depth at which the temperature gradient was

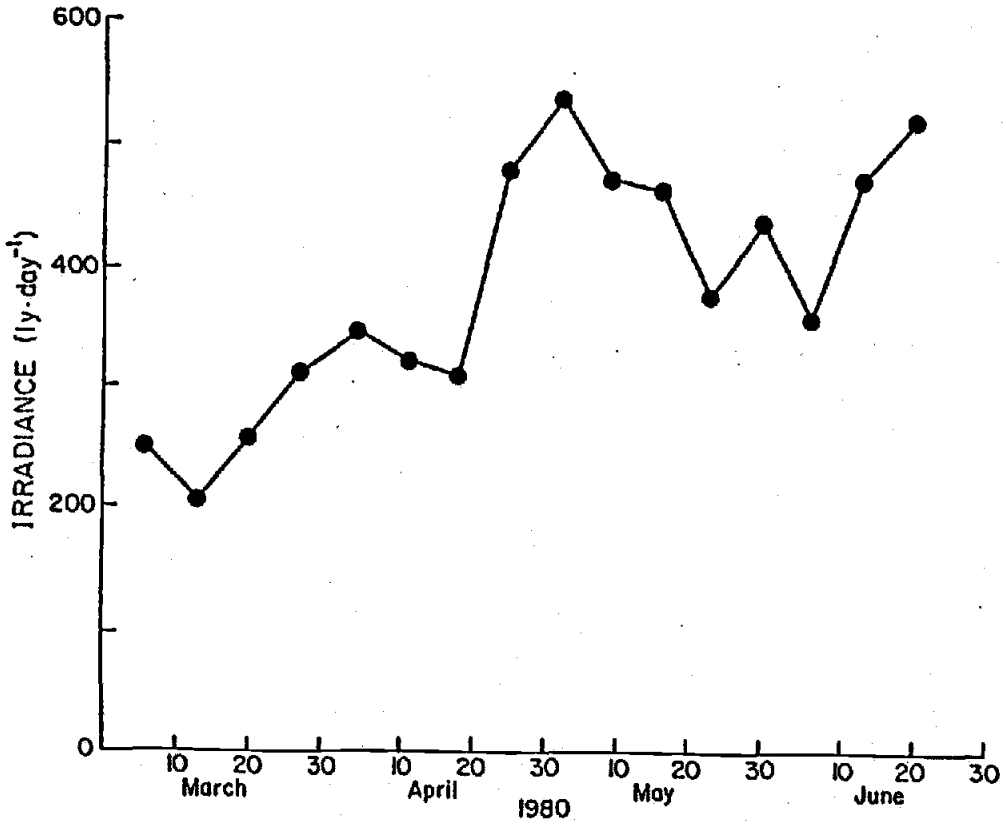

Fig. 5. Weekly mean of total surface illumination based on daily measurements at Departure Bay, Nanaimo, B.C.

greater than 1°C over 5m, and for which temperatures in the water column above varied less than 0.3°C. These mixed layer depths and calculated D_{cr} values are shown in Fig. 6. Clearly, the first occurrence of critical depth greater than the depth of the mixed surface layer occurred the last week of April, and this condition was followed shortly by the initial increase in diatom biomass.

While water-column stabilization and increasing irradiance could account for the increase in abundance and dominance of diatoms in May, the question of why silicoflagellates dominated the phytoplankton in early April, prior to stratification, remains. Nival (1965) also observed maximum silicoflagellate abundance prior to water column stabilization; however, he speculated that critical depth considerations must be met for silicoflagellate blooms to occur. This is not the case in East Sound. It is apparent that silicoflagellates are controlled very differently from diatoms, despite their apparently similar temperature ranges and presumably similar nutrient requirements.

Although it's unlikely that a single factor was responsible for the D. speculum bloom, it is possible from the data available to narrow the range of potential explanations. Multiple linear regression analysis showed very weak correlations between silicoflagellate abundance and the major environmental factors: temperature, salinity, $[NO_3^-] + [NO_2^-]$, or $[Si(OH)_4]$ ($r = -0.44$, 0.10, 0.27, and 0.12, respectively). The results of principal component analysis also indicated that D. speculum abundance was not highly correlated with any of the environmental components listed above ($r = 0.22$).

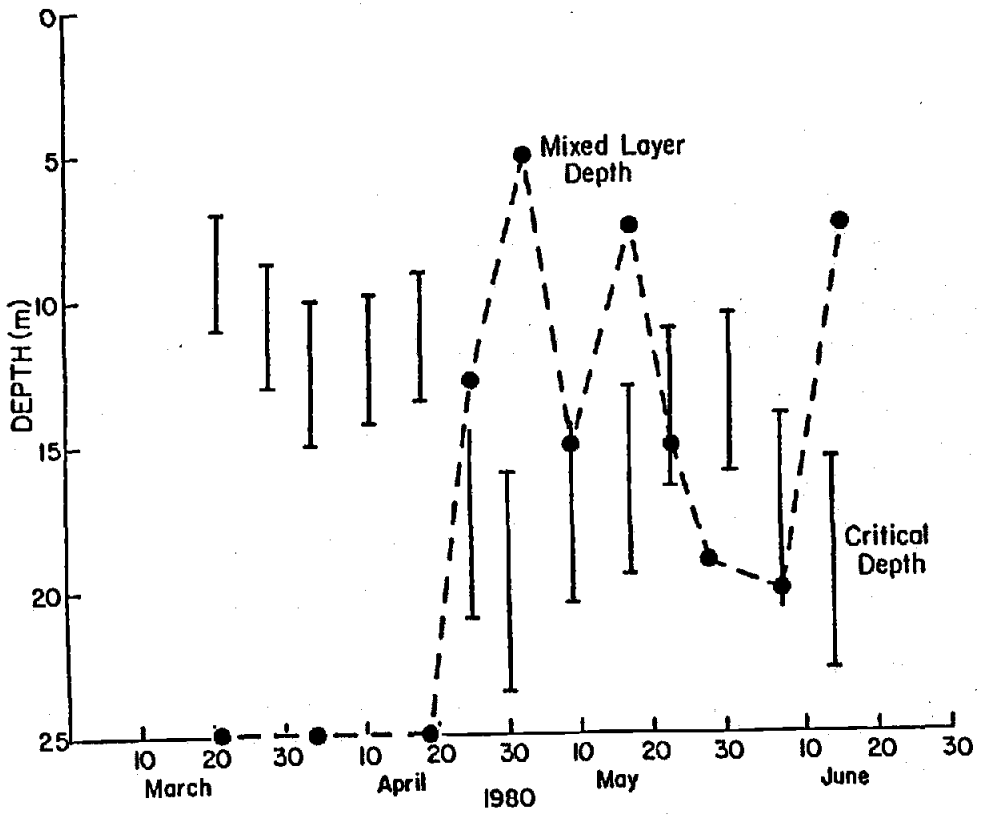

Fig. 6. Comparison of mixed layer depth and the estimated range of critical depth during the spring of 1980.

Observations of yearly cycles of the silicoflagellate D. fibula have indicated that temperature was a major factor determining abundance of this species. Both Nival (1965) and Ignatiades (1970) showed that maximum temperature tolerance of D. fibula was 15°C, and when water temperatures exceeded this limit D. fibula was not observed in the plankton. Although it is likely that limits also exist for D. speculum, the range is less clear. D. speculum was observed in this study at temperatures of 8.1 to 12.2°C; however, Strickland et al. (1968) found the same species off California at 18°C. Clearly, though, the initiation of the April silicoflagellate bloom in East Sound was not due to changes in the temperature regime. Water temperatures immediately before the initial D. speculum increase did not differ greatly from those occurring in East Sound throughout the winter.

Similarly, salinity and major nutrient concentrations did not change prior to the silicoflagellate bloom. Although Van Valkenburg and Norris (1970) showed optimum silicoflagellate growth in culture at 24‰, salinities in East Sound during the period when silicoflagellates were present varied from 28.0 to 30.5‰. More importantly, salinity showed no consistent change prior to or during the silicoflagellate bloom and therefore was not likely to be a major influence. Concentrations of all major nutrients in East Sound were high throughout the winter, and no nutrient was limiting during the period silicoflagellates were present in the phytoplankton; therefore, this factor can also be eliminated. This is not to say that these variables are unimportant to silicoflagellate ecology, and in fact they may explain the low abundances observed at other times of the

year. However, it is unlikely that any of the above factors were important in actually initiating the silicoflagellate bloom.

The spring increase in solar radiation was one environmental variable that was clearly changing prior to the silicoflagellate bloom. Although the mixed layer remained deep throughout early April and restricted diatom production, D. speculum appeared not to be affected by a critical depth limitation. There are two characteristics that may enable silicoflagellates to benefit from increasing light levels and yet not be restricted by the depth of mixing. First, silicoflagellates are motile. While silicoflagellate locomotion has not been critically analyzed, the cells seem capable of maintaining themselves in the euphotic zone of the water column (Lipps, 1970). In East Sound, when cell concentrations of silicoflagellates and diatoms at both 5 and 20 m were compared during the period in which the water column was completely mixed, there were clear differences in silicoflagellate abundance with depth that were not seen in diatom numbers (Fig.7). If the greater abundance of cells at 5 m was attributable only to a higher growth rate at increased light intensity relative to downward mixing or sinking, it seems unlikely that only the silicoflagellates, and not the diatoms, would exhibit this characteristic.

Due to the difficulties in measuring vertical velocities of water in the mixed layer, it is difficult to assess the swimming capabilities necessary for a cell to maintain itself in the upper water column. However, migration rates of up to 24 m/day have been observed for dinoflagellates, clearly enough to compensate for sinking of less than 2 m/day in a stable water column, (Eppley et al., 1968;

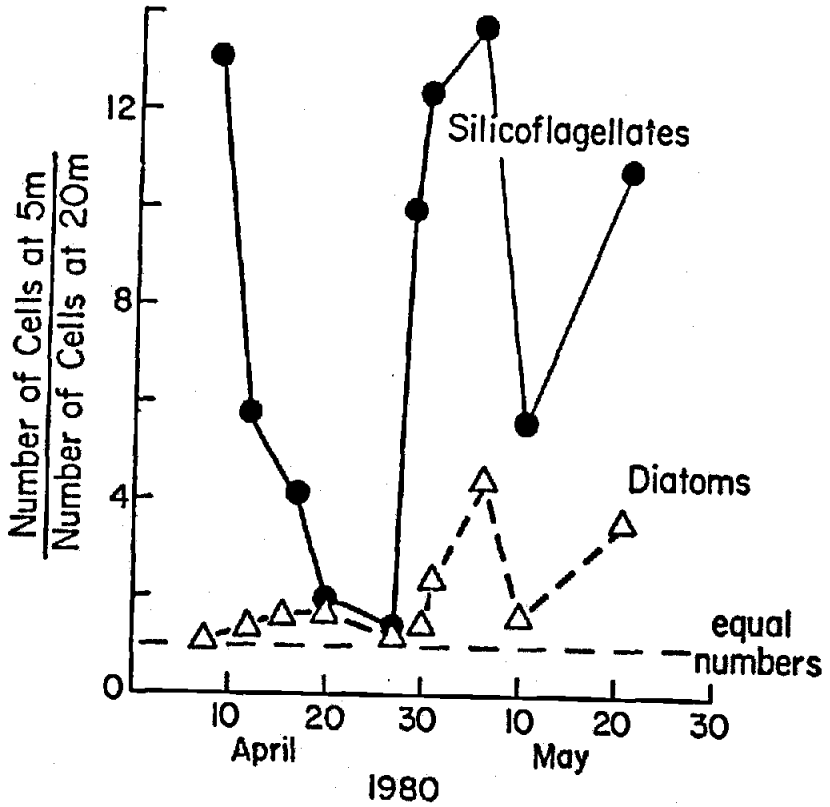

Fig. 7. Difference between phytoplankton concentration at 5m and 20m, April and May, 1980.

Heaney and Eppley, 1981), and probably enough to override many stronger water movements. These vertical migrations compare favorably with maximum vertical velocities of 18m/day measured in an upwelling region, for example (Smith et al., 1983). It therefore does not seem unreasonable to suggest that the motility of silicoflagellates enables them to maintain themselves in the upper region of a mixed water-column.

In addition to motility, a second characteristic possibly enabling silicoflagellates to benefit from the early spring increase in irradiance is their apparent affinity for low light environments. Although silicoflagellates have been observed in plankton collections throughout the year, their periods of maximum abundance were generally in winter and spring. In addition, the seasonal vertical migration of D. fibula observed by Travers and Travers (1968) and Leger (1971-72) indicated that silicoflagellates favor low light environments.

All the above evidence clearly indicates that the ability of silicoflagellates to exploit increasing light levels and to be unaffected by critical depth limitations resulted in their rapid increase and high relative abundance in early spring. The decline of this species in late April, however, is more difficult to explain.

The initial silicoflagellate bloom declined in late April. This decrease coincided with strong, storm-induced mixing of the sound. Followng this wind event, silicoflagellates were well-mixed throughout the water column, as shown in their equal concentrations at 5 and 20m (Fig. 7). It seems probable that in the face of strong mixing and water exchange the silicoflagellates were unable to maintain their advantageous position in the upper water-column and therefore

abundance declined.

When conditions in the sound normalized the following week, silicoflagellate concentrations once again increased. This was the period of water column stratification, however, and diatoms were also increasing and rapidly became the dominant species. Fig. 8 shows the major shift in dominant species (silicoflagellates to diatoms) that accompanied stratification. It is important to note, however, that silicoflagellates remained in the phytoplankton community in significant numbers until mid-May.

On the basis of data from this study alone, it is not possible to determine the cause of the final silicoflagellate decline, nor is it possible to examine all the variables of potential importance. However, by using the information available and pursuing a process-of-elimination approach, it is possible to speculate on the range of factors contributing to the decline.

As stated previously, both Ignatiades (1970) and Nival (1965) concluded that temperature was the major factor determining yearly cycles of abundance of the silicoflagellate D. fibula. However, the temperature range for D. speculum, 8.1 to 18.0°C (Table 1), encompasses the spring and summer surface water temperatures in East Sound. At the time D. speculum ceased to be abundant in the East Sound phytoplankton community, surface water temperatures did not exceed 12.2°C. In addition, at 20 m, where temperatures were less than 10°C, no silicoflagellates were observed. Therefore, it seems unlikely that temperature per se was of major importance in causing the silicoflagellate decline. Additionally, salinity showed no consistent change prior to or during the silicoflagellate decline, and therefore

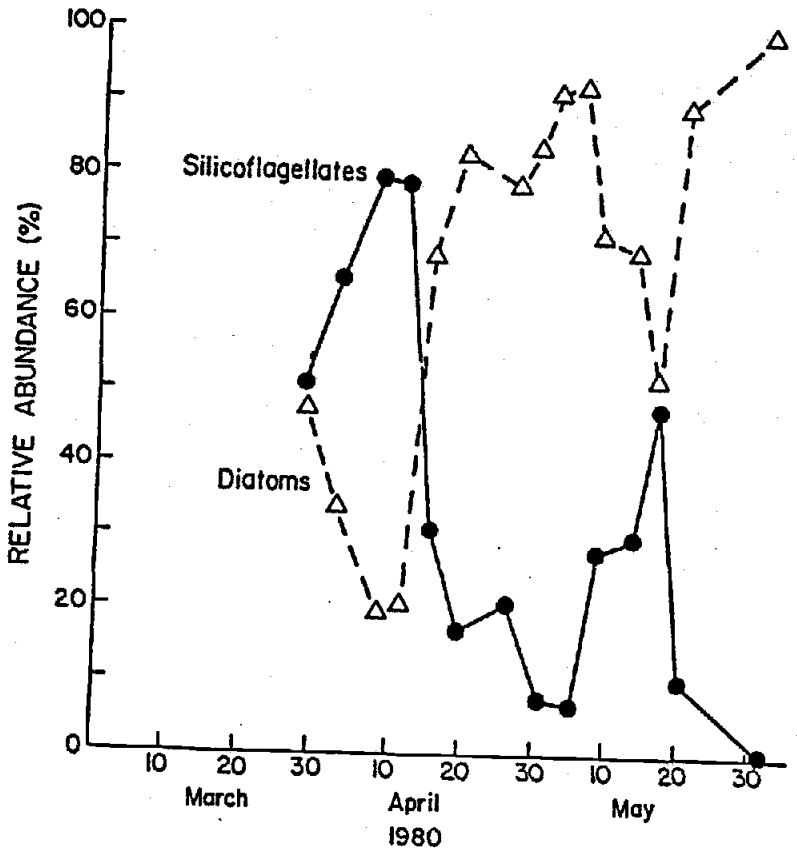

Fig. 8. Relative numerical abundance of major phytoplankton groups as percentage of total phytoplankton during the spring of 1980.

can also be eliminated as an causative factor.

Differential grazing by zooplankton can potentially cause phytoplankton species changes (Deason,1975; McCauley and Briand,1979). Although zooplankton were present in significant numbers throughout the study period, there was no evidence for selective grazing of silicoflagellates relative to diatoms. Microscopic examination of fecal pellets from copepods fed natural particle assemblages from East Sound revealed both fragmented diatom frustules and silicoflagellate skeletons. Schrader (1971) noted large numbers of silicoflagellate skeletons in copepod fecal pellets collected in sediment traps off Portugal. If, as shown, silicoflagellates are ingested by zooplankton, the degree of removal by grazing becomes important. Dexter (1983) reported a small increase in numbers of adult copepods during the East Sound silicoflagellate bloom in mid-April. However, her estimates of potential grazing removal rates, based on concentrations of juvenile and adult copepods observed on three dates (April 11, May 8, and May 16) and feeding rates derived from laboratory grazing experiments using Isochrysis and Thalassioira as food, showed a mean daily grazing removal of 33.4×10^7 cells/m^3/day, only 3.8% of phytoplankton standing stock. Although primary production estimates are the more appropriate comparison when evaluating grazing impact on phytoplankton populations, the comparison with standing stock does give some indication of the relatively small impact of grazers during this period.

Given the evidence that silicoflagellates remained in the phytoplankton community (though in comparatively low numbers) during the first diatom bloom, the possibility exists that in the absence of

a physical or chemical change in the environment acting directly on the population, it was the competitive ability of diatoms relative to silicoflagellates that was responsible for the gradual silicoflagellate decline. The growth rate of silicoflagellates may be intrinsically low. One indication of this was the notably slow growth of D. fibula in culture, 0.49 doublings/day (Van Valkenburg and Norris, 1970). Therefore, any removal process acting indiscriminantly on diatoms and silicoflagellates would inherently favor survival of the species with the higher growth rate, in this case, diatoms.

In addition, silicoflagellates may be unable to compete with diatoms for common resources, specifically nutrients. There is no direct knowledge of silicoflagellate nutrient kinetics, although observations of their occurrence (coastal regions in winter and spring, deeper water in summer) suggest that they may have high nutrient requirements. In East Sound, nutrient concentrations began to decline with the first diatom bloom. Although these were the lowest concentrations observed during the season([NO_3^- + NO_2^-] = 0.85 µM,[$Si(OH)_4$] = 0.97 µM), they may not have been limiting for some diatom species. For example, Eppley et al. (1969) gave a range of half-saturation constants for nitrate of 0.4 to 4.21 µM for neritic diatoms. The values for oceanic species are an order of magnitude less. Whether the levels of dissolved nitrogen and silicon observed in East Sound were sufficient for silicoflagellates, or more importantly, how well silicoflagellates can compete with diatoms for nutrients at these concentrations, is of potential importance in explaining the silicoflagellate decline.

Clearly there are many other variables of potential importance to

silicoflagellate ecology that were not examined here (e.g., trace metal or vitamin requirements, other species interactions). In addition, the interaction between the different environmental parameters, and the rate of change of these factors and the ability of the species to adapt, must be considered. However, this initial investigation of silicoflagellate ecology has shown that silicoflagellates are controlled very differently from diatoms. This is demonstrated most clearly in the ability of silicoflagellates to be unaffected by a critical depth limitation. In addition, the occasional high abundance and dominance of silcoflagellates in the phytoplankton community may make them of local importance in some coastal regions.

On the basis of previous observations and this work in East Sound it is possible to form several hypotheses concerning silicoflagellate physiology and ecology. The proposed hypotheses are:

1) D. speculum may have physiological capabilities that allow growth in environments unfavorable to faster growing species such as diatoms.

2) The growth rate of D. speculum is intrinsically low.

3) D. speculum is a low-light species. Its growth rate at low light intensities is high relative to that of other phytoplankton species. There are a number of physiological adaptations, as well as behavioral mechanisms (phototaxis) that could allow D. speculum to exploit low light environments.

4) The dissolved nitrogen and silicon requirements of D. speculum are high relative to those of diatoms. Nutrient uptake experiments would show high K_s values. The ability to maintain silicoflagellates

in culture would provide the opportunity for further testing of these hypotheses.

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APPENDICES

APPENDIX A

The major use of the phytoplankton count data from this study was for comparison of species composition over an extended time period. To reduce the amount of time-consuming sample counting required, three days were selected from throughout the sampling period and all phytoplankton samples from these days counted and compared. The three days were chosen so that each had distinctly different physical and biological characteristics. April 11 was during the early part of the study period when the entire water-column was well-mixed, nutrient concentrations high, and phytoplankton biomass low. May 8 was after stratification, just before the decline on the initial diatom bloom. Nutrient levels at this time were lower than in April but not limiting, and temperature in the surface layer was above 12°C. May 31 was at the peak of a phytoplankton bloom period, the water-column was clearly stratified with a deeper mixed layer than on May 8, and in the upper water-column nutrients were depleted and the temperature exceeded 13°C. From these three days representing different environmental conditions in East Sound, the phytoplankton samples from all stations and depths were counted and their similarity in species composition and representation compared.

The Percentage Similarity (PS) index (Whittaker, 1960) has proved to be a useful approach in determining how alike samples are with respect to species composition. The PS index compares two samples in terms of percentage composition

$$PS = 100 - 50 \sum |a - b| = \sum \min(a,b),$$

in which a and b are the percents which a particular species includes

of the total samples A and B. Miller (1970) found that with sample sizes of 2000 and 1000 individuals, a PS as low as 80% and 75%, respectively, could be obtained when comparing two samples from the same populations. Because most of my samples contained fewer than 1000 individuals and because not all phytoplankton classifications were of equal taxonomic weight, this acceptance level was even more rigorous. The following criteria were adopted:

if $PS \geq 80$, the samples showed excellent agreement and were considered to have the same species distribution

if $75 \leq PS < 80$, agreement was fair and it was likely that distributions were similar

if $PS < 75$, agreement was poor and the samples probably contained a different phytoplankton community.

The PS matrices shown in Table 2 allow station-by-station inter-comparisons for all samples at 5m and at 20m. These values, comparing stations 1 through 4 on a single day, are indicators of the uniformity of phytoplankton composition in the sound and channel. The results show that in the sound (stations 1, 2, and 3) phytoplankton species composition was homogenous at both 5m and 20m on all dates. While phytoplankton distribution in the channel (station 4) was also similar to these stations on May 8, it was clearly different from the sound on April 11. On May 31, station 4 species distribution resembled the other stations at 5m, but not at 20m. These results indicate that species counts of samples taken at station 2 could be interpreted as representative of species composition in the sound; however, separate station 4 counts were necessary to determine species composition in the channel.

To determine if sample counts at all depths were necessary, a similar comparison was done on samples from stations 2 and 4 on the

Table 2. Phytoplankton species composition percentage similarity (PS) matrix of 5m and 20m samples from stations 1, 2, 3, and 4, on three representative dates.

		April 11				May 8				May 31			
		1	2	3	4	1	2	3	4	1	2	3	4
5m	1		0.93	0.89	0.75		0.90	0.83	0.81		0.96	0.93	0.95
	2			0.87	0.81			0.85	0.85			0.91	0.95
	3				0.84				0.96				0.95
	4												
20m	1		0.86	0.89	0.85		0.95	0.94	0.91		0.85	0.87	0.55
	2			0.86	0.44			0.97	0.96			0.97	0.65
	3				0.78				0.96				0.64
	4												

same representative dates. The PS matrices of depth inter-comparisons are shown in Table 3. Species composition at the surface, 5m, 10m, and 15m, were shown to be always similar; therefore, data from 5m samples were interpreted to be representative of species composition in the upper water-column. The species distribution in the sound at 20m was clearly different from that above 15m on May 31, so 20m samples were counted separately. Samples from 25m, while most similar to 20m, remained distinct. I believe this was due to the large amount of bottom disturbance that frequently occurred in taking these samples, and was not indicative of species present in the water-column.

In summary, station 2 samples were determined to be characteristic of species composition in the sound, and station 4 samples were used for a channel comparison. Similarly, 5m samples were representative of the upper water-column, but differed from those at 20m and 25m. Therefore, for every sampling day, phytoplankton were identified and counted in samples from depths of 5m and 20m at both stations 2 and 4.

Table 3. Phytoplankton species composition percentage similarity (PS) matrix of station 2 and 4 samples from 0, 5, 10, 15, 20, and 25 m on three representative dates.

		April 11						May 8						May 31					
		0	5	10	15	20	25	0	5	10	15	20	25	0	5	10	15	20	25
st.2	0		0.88	0.92	0.87	0.93	0.66		0.95	0.87	0.80	0.73	0.73		0.77	0.89	0.91	0.72	0.34
	5			0.94	0.93	0.88	0.55			0.90	0.80	0.75	0.76			0.85	0.79	0.67	0.21
	10				0.93	0.90	0.61				0.90	0.86	0.86				0.94	0.80	0.36
	15					0.89	0.44					0.95	0.94					0.82	0.42
	20						0.75						0.98						0.54
	25																		
st.4	0		0.84	0.82	0.89	0.85	0.60		0.90	0.86	0.80	0.81	0.83		0.89	0.93	0.79	0.65	0.55
	5			0.95	0.78	0.81	0.57			0.94	0.80	0.89	0.92			0.83	0.76	0.66	0.67
	10				0.75	0.81	0.55				0.79	0.92	0.93				0.83	0.71	0.57
	15					0.90	0.71					0.78	0.85					0.74	0.46
	20						0.73						0.93						0.61
	25																		

Table 4. Phytoplankton cell count data from all samples at station 2, 5m. Concentrations in cells/ml.

DATE	MARCH, 1980				APRIL, 1980							MAY, 1980							JUNE, 1980				JULY, 1980	
	10	23	27	31	2	7	11	15	19	23	26	29	1	5	8	13	16	20	21	8	12	17	3	7	15	1
DIATOMS																										
Asterionella japonica																										
Biddulphia arctica																									114.7	82
Biddulphia laevis									observed in May 5 accpl. samples																	
Biddulphia longicruris																										
Chaetoceros compressus	1.1																								23.4	
Chaetoceros danicus	0.4							1.9			1.4	13.2	2.7	2.1												
Chaetoceros debilis																									101.5	6
Chaetoceros decipiens									1.4																	69
Chaetoceros didymus																										
Chaetoceros laciniosus	1.3																		68.5							
Chaetoceros similis	0.8							9.6																		
Chaetoceros socialis														8.3					139.7				203.1		19
Chaetoceros vanheurckii																										
Chaetoceros spp.	1.7				8.3				1.4																	171
Corethron hystrix																			1270.0				647.5	1384.9	495
Coscinodiscus centralis									•																	
Coscinodiscus curvatulus																										
Coscinodiscus excentricus	9.8							1.3							0.8			0.1								
Coscinodiscus spp.		0.5							0.9		0.8					1.6	1.6									
Dictyum brightwellii	1.9																									
Fragilaria striatula																										
Lauderia spp.																										
Leptocylindrus spp.																										69
Limnophora spp.																										
Melosira monliformis	17.8	7.6			4.8	6.4		7.7	17.16				observed in May 5 accpl. samples													
Navicula directa																4.3	0.5									
Navicula distans																										
Navicula spp.	0.8		1.3		0.5				0.4																	
Nitzschia closterium	1.3													2.1												
Nitzschia paradoxa	0.4				2.5	0.8		0.3	0.9				2.7			1.6	0.3			3.6					12.7	6
Pleurosigma spp.																										
Rhizosolenia delicatula									0.6		0.8	5.1							15.6							
Rhizosolenia fragillissima	1.7																		30.1	11.4						
Skeletonema costatum	0.8																									
Stephanopyxis palmeriana																			2755.9				76.2			25
Thalassionema nitzschioides	26.9	5.6			8.2	7.2	26.8	38.7	102.5		313.2	364.2	1001.	1130	816	349	54.2	21.1	291.1	4.6		4.6	10.2		63.5	
Thalassiosira antivalis- *f. nordenskioldii*																				1.5			630.9	346.9	787.4	69
Thalassiosira condensata														6.9					38.1							
Thalassiosira decipiens- *f. pacifica*	16.4	9.1			6.1	3.8		21.4	61.1		56.8	71.1	256.0	95.2	15.5	22.2	1.1			9.1						
Thalassiosira spp.	27.2	1.0	7.6		7.0	4.7	35.7	22.9	23.3		56.6	134.6	51.0	127.0		93.7	1.7	1.4	63.5	0.5		1.0	5.1			
SILICOFLAGELLATES																										
Dictyocha speculum	0.4	22.9	17.0		60.3	169.1	376.1	46.4	68.8		89.1	198.1	112.5	110.1	320.9	232.7	58.1	9.7		2.8	1.0				12.7	
PERIDINIANS	19.9	12.7	6.9		3.9	8.4	29.3	18.7	45.6		1.9	5.1	9.4	12.7	1.5	11.11	1.9	0.4			1.0	1.8	1.8			
DINOFLAGELLATES		3.0	1.3		4.1		3.8	0.3	0.4		6.6									1.0	3.4	0.5				
TOTAL	113	56	35	No Sample	103	192	673	150	305	No Sample	614	1173	1336	1468	3159	696	121	37	4721	37	6	8	846	1270	2502	501

Table 5. Phytoplankton cell count data from all samples at station 2, 20m. Concentrations in cells/ml.

DATE	MARCH, 1980				APRIL, 1980							MAY, 1980						JUNE, 1980				JULY, 1980	
	10	23	27	31	2	7	11	15	19	23	26	29	1	5	8	13	16	20	31	6	12	17	3	7	15	17
DIATOMS																										
Asterionella japonica																										
Biddulphia aurita																										
Biddulphia laevis																										
Biddulphia longicruris																										
Chaetoceros compressus														8.6												
Chaetoceros danicus											0.6	4.9														
Chaetoceros debilis		1.1			1.7																			64.0		
Chaetoceros decipiens																										
Chaetoceros didymus																										
Chaetoceros laciniosus																										
Chaetoceros similis						0.3																				
Chaetoceros socialis																										
Chaetoceros vanheurckii																								10.2		
Chaetoceros spp.								1.1	2.9	4.4									50.3					360.7		
Corethron hystrix																		0.8	0.5							
Coscinodiscus centralis																										
Coscinodiscus curvatulus																										
Coscinodiscus excentricus						0.2					1.9															
Coscinodiscus spp.		0.3							2.3	3.2	6.0			1.3			1.1	0.1	0.3	1.1						
Ditylum brightwelli																										
Fragilaria striatula																										
Lauderia spp.																										
Leptocylindrus spp.																										
Licmophora spp.																										
Melosira moniliformis		4.0		1.1	3.4	9.2	6.7	4.1	5.7		9.6	1.2					3.0	0.1								
Navicula directa																										
Navicula distans																										
Navicula spp.		0.1		0.1		0.3																				
Nitzschia closterium		2.3		0.6		1.9	0.6	1.9	1.3	0.8		1.9					0.4		0.3							
Nitzschia paradoxa																										
Pleurosigma spp.				0.1							0.8							0.1	7.1	2.0						
Rhizosolenia delicatula							0.6											0.1	1.3	2.0						
Rhizosolenia fragilissima																										
Skeletonema costatum		0.3												1.3					104.6	67.3						
Stephanopyxis palmeriana											0.8						0.4							10.1		
Thalassionema nitzschioides		4.4		5.6	30.3	16.2	66.4	90.2	211.0	425.8	347.1	236.8	448.3				91.8	7.9	96.3	38.8				10.1		
Thalassiosira antiqua- *f. nordenskioeldii*							13.3													6.1				171.7		
Thalassiosira condensata																	1.7			6.1						
Thalassiosira decipiens- *f. pacifica*		4.1		3.3	23.9	6.0	21.9	30.8	37.4	130.9	124.9	37.3	31.8				8.0			18.2						
Thalassiosira spp.		3.1		4.3	16.2	6.7		60.9		42.3	44.9	17.3					2.1	1.1	16.7							
SILICOFLAGELLATES																										
Dictyocha speculum		3.0		13.1	230.6	26.7	23.4	12.1	1.3	15.9	213.1	116.4	13.1				10.2	0.3	1.0							
EBRIDIANS		2.1		1.1	10.3	1.6	23.1	3.7	6.6	10.1	1.5		1.7				1.7	0.1	0.5	3.1						
DINOFLAGELLATES		0.3				1.9	1.9	1.3		6.4	1.2	1.3					0.6	0.1		1.0						
TOTAL	No. Species	27	No. Species	31	330	72	144	738	388	651	745	457	502	No. Species	121	18	284	133	No. Samples	630						

Table 6. Phytoplankton cell count data from all samples at station 4, 5m. Concentrations in cells/ml.

DATE	MARCH, 1980				APRIL, 1980						MAY, 1980							JUNE, 1980					JULY, 1980	
	18	23	27	31	3	7	11	15	18	22	26	29	3	5	8	12	16	20	31	8	12	17	5	7	23	27
DIATOMS																										
Asterionella japonica																									1.0	
Biddulphia aurita																										
Biddulphia Laevis							0.9																			
Biddulphia longicruris																									0.9	
Chaetoceros compressus																										
Chaetoceros danicus								7.8		0.6				0.5	1.1											
Chaetoceros debilis																										
Chaetoceros decipiens				0.2																50.6						
Chaetoceros didymus																		0.4	25.4							
Chaetoceros Lauderianus																										
Chaetoceros similis														2.5												
Chaetoceros socialis																										
Chaetoceros vanheurckii																			12.7						4.6	
Chaetoceros spp.												3.6	3.7	3.1			1.4	0.3	1014.0	662.0		0.2			0.8	
Corethron hystrix								0.2		0.3									6.3							
Coscinodiscus concinnus																										
Coscinodiscus curvatulus																										
Coscinodiscus excentricus		2.0								2.6		1.9	0.5	1.9												
Coscinodiscus spp.								1.0			10.9			1.3			1.3	0.3	6.3			1.0				
Ditylum brightwellii																										
Fragilaria striatula															1.9		0.6									
Lauderia spp.																										
Leptocylindrus spp.																										
Licmophora spp.													0.6		0.6											
Nitzschia multiseries		11.1		2.2		2.6		4.6		1.8	30.1	1.9	2.5	3.8			2.2	0.6								
Navicula directa		0.5																								
Navicula distans																										
Navicula spp.								0.2		0.1		0.6														
Nitzschia closterium		2.0		0.2		0.4		1.0		0.4		0.6					0.7	0.4	25.4	33.9					1.3	
Nitzschia paradoxa																										
Pleurosigma spp.																		0.1	57.1							
Rhizosolenia delicatula											2.2						1.0		44.4	8.3		3.1				
Rhizosolenia fragilissima																										
Skeletonema costatum																	0.1	2.0	1343.0	1110.7		2.1			0.5	
Stephanopyxis palmeriana																									1.3	
Thalassionema nitzschioides		8.2		0.8		13.3		4.4		17.4	234.1	100.9	61.2	136.6			33.3	36.1	209.3	110.1		39.3			3.1	
Thalassiosira antiqua-*T. nordenskioeldii*								18.2												25.4					27.3	
Thalassiosira condensata												2.3	1.0	2.3			2.4			16.9						
Thalassiosira decipiens-*T. pacifica*		2.4		1.1		8.2		17.3		9.8	29.8	35.6	8.3	21.2			3.2					1.3				
Thalassiosira spp.		1.3		1.6		14.2		8.3		1.8	50.8	13.3	9.6	5.3			3.3	3.4				9.2				
SILICOFLAGELLATES																										
Dictyocha speculum		6.1		23.3		133.4		1.3		3.8	40.3	33.8	3.3	28.9			22.9	35.4								
CRUSTACEANS		4.1		1.2		15.8		8.6			6.3						2.3	0.8				3.1				
DINOFLAGELLATES		0.3		0.1		2.3		0.2			1.8						0.3					3.6				
TOTAL	No. Samples	32	No. Samples	33	No. Samples	143	No. Samples	51	No. Samples	42	408	194	97	229	No. Samples	93	108	2944	2149	No. Samples	82	No. Samples	42	No. Samples		

Table 7. Phytoplankton cell count data from all samples at station 4, 20m. Concentrations in cells/ml.

DATE	MARCH, 1980						APRIL, 1980						MAY, 1980							JUNE, 1980			JULY, 1980	
	10	25	27	31	2	7	11	15	19	23	26	29	1	5	8	13	16	20	23	6	12	17	3	15	27
DIATOMS																									
Asterionella japonica																									
Bidduiphia arctica																									
Bidduiphia Lavis																									
Biddulphia longicruris																			0.8						
Chaetoceros compressus																									
Chaetoceros danicus							2.1					4.2			2.0										
Chaetoceros debile																									
Chaetoceros decipiens																									
Chaetoceros didymus																	3.0								
Chaetoceros Lastinosus																	3.0	8.6							
Chaetoceros similis																									
Chaetoceros socialis																									
Chaetoceros vanheurckii																									
Chaetoceros spp.																		1.6	46.9						
Corethron hystrix																									
Coscinodiscus centralis															2.0										
Coscinodiscus curvatulus																	0.3								
Coscinodiscus excentricus												0.8					0.4	0.3							
Coscinodiscus spp.							0.2					2.3		0.6			0.4		2.0						
Ditylum brightwelli																									
Fragilaria striatula																									
Landeria spp.																	0.8								
Leptocylindrus spp.																									
Licmophora spp.																									
Melosira moniliformis							4.0					9.7		31.0	3.0		3.2	3.1	7.9						
Navicula directa							0.2																		
Navicula distans							0.2																		
Navicula spp.												0.8						0.3	0.3						
Nitzschia closterium							3.2								3.0		3.0	0.9	0.3						
Nitzschia paradoxa																									
Pleurosigma spp.							0.2										0.4	0.4	2.2						
Rhizosolenia delicatula																	2.9		7.1						
Rhizosolenia fragilissima																									
Skeletonema costatum							3.9							2.5			8.2	0.8	99.8						
Stephanopyxis palmeriana																									
Thalassionema nitzschioides							7.2					38.4		234.0	291.8		33.3	68.6	103.3						
Thalassiosira antinalis-T. nordenskioeldii															2.0		0.4								
Thalassiosira condensata														0.8	3.0		0.0	1.3	2.9						
Thalassiosira decipiens-T. pacifica												35.6		49.1	33.3		0.8	0.3							
Thalassiosira spp.							34.2					16.2		36.9	15.2		1.6		10.9						
DICTYOCHOPHYCEAE																									
Distyocha speculum							56.0					9.3		30.2	12.6		31.7	8.9	3.0						
EUGLENIANS							0.2					1.7		2.3	4.7		0.8	0.4	0.4						
DINOFLAGELLATES							0.6					0.4		0.8	7.8		0.4	0.3							
TOTAL	No Samples						102	No Samples				170	No Samples		377	363	No Samples	77	96	294	No Samples				