

DISTRIBUTIONAL ECOLOGY OF PLANKTONIC DIATOMS IN THE STRAIT OF GEORGIA, B. C.

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ABSTRACT

In order to determine the distributional ecology, and to investigate factors influencing these features, the diatom communities in plankton at depths of one, twenty-five, fifty, and seventy five meters in the area were studied and measured over a fifteen month of period. Measurements of environmental factors including temperature and salinity and algal nutrients such as phosphate, silicate, nitrate, nitrite and ammonia were also made at the same depths and locations.

The results indicate that the size of diatom communities and the species population changes were heavily dependent upon to season and location parameters as well as nutrient concentrations and hydrographic factors. Major factors influencing population distributions varied with principal species responsible for dominant species and species succession.

Two distinct distributional patterns in total diatom crop were observed in the study area. Maximum standing crop observed during spring and/or summer were related to the concentration of nutrients available at the onset of the spring bloom on a large scale. On a small scale, however, the distributions of total diatom standing crops were significantly correlated with both season/location factors and with hydrographic parameters as well. Vertical stratification of diatoms was observed only in the presence of the thermocline in the water column. Within the study area there was some seasonal consistency in the composition of the species groups. However, some species association in these environments may vary with the change of season.

INTRODUCTION

Studies of marine diatoms in the strait of Georgia and neighbouring coastal waters had already begun in the 1860s (Lord, 1866; Peck and Harrington, 1897). Some early studies of marine diatoms of the east area of Vancouver Island were carried out by of Bailey and MacKay (1916), in the vicinity of the Fraser River by Lucas and Hutchinson (1927), Hutchinson (1928) in the strait of Georgia by Hutchinson *et al.* (1929), Legare (1957), and in the area between Juan de Fuca Strait and Puget Sound (Gran and Thompson, 1930; Phifer, 1933, 1934 a,b; Thompson and Phifer, 1936). The most notable studies of taxonomy of marine planktonic diatoms

in the area and North Pacific coast of America were made by Gran and Angst (1931) and Cupp (1943). Since then no further taxonomic studies have been done. Recently, Lewin and her co-workers (Lewin and Mackas, 1972; Lewin and Hruby, 1972; Lewin, 1973; Collas and Lewin, 1974, 1976; Lewin, *et al.*, 1975; Lewin and Rao, 1975) have carried out a series of studies on surf-zone diatoms along the coast of the Olympic Peninsula, Washinton. They have been devoted mainly to studies of the physiological adaptation of two diatoms (always dominants and extremely concentrated in the area) to the unusual habitat, but have included some environmental data as well.

In general coastal waters and near shore

environments are strongly influenced by the proximity of land. This occurs both directly through terrestrial runoff and by the inflow of inorganic and organic nutrients, growth factors, and inhibitors, and indirectly, by the upwelling of the coastal waters due to local winds and currents. Furthermore, the life cycles of many neritic diatoms include the formation of heavily silicified resting spores under unfavorable conditions (Wimpenny, 1966). These species depend upon the proximity of the sea floor to retain the spores within the depth range of winter turbulence which returns them to the euphotic zone. Thus, the physical complexities of the near shore environment, as well as the specialized life cycles of neritic species, may give the planktonic diatom community of coastal waters dynamic characteristics and distinct ecological patterns.

This study was one of the three parts which were undertaken to fill a need in the study of diatoms in British Columbia coastal waters. In this part more detailed studies of planktonic diatom populations and species distribution were carried out that include reference to environmental factors. Measurement of physical and chemical parameters that could affect the diatom populations were made concurrently to permit some interpretation of their possible relative importance in determining spatiotemporal distributions, while the limitations of this type of approach are evident, it forms a valuable counterpart to less discriminatory studies of phytoplankton ecology in the field, and more highly specific, controlled laboratory studies.

MATERIALS AND METHODS

This study was carried out in the Strait of Georgia/Juan de Fuca system which is the inside passage between Vancouver Island and British Columbia mainland (Fig. 1). This system

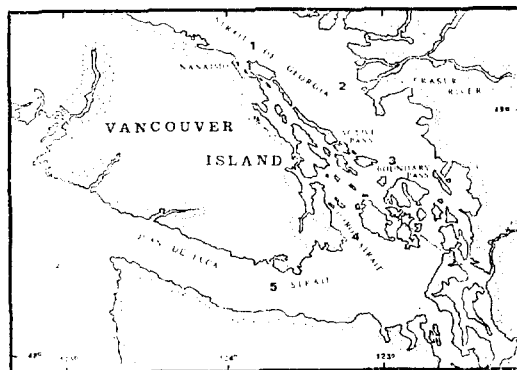


Fig. 1. Strait of Georgia and Juan de Fuca system, showing five station positions.

is approximately 480 km in length and up to 48 km wide, and has an average depth of between 90 m and 180 m. The waters within this area possess distinctive physical and chemical characteristics and are divisible into a number of domains (Tully and Dodimead, 1957; Pickard, 1961).

Waldichk (1957) divided this system into three basic water masses distinguished vertically: (1) the brackish surface water from runoff in the Strait of Georgia; (2) the deep water of oceanic origin in Juan de Fuca Strait; and (3) a mixture of both. More recently Herlinveaux and Giovando (1969) indicated that this system consists of a central domain between Nanaimo and Active Pass; a homogeneous domain between Active Pass and Haro Strait; and a coastal seaways domain in Juan de Fuca Strait.

On this basis the following stations were chosen for this study.

- Station 1 : Strait of Georgia 49°17.0'N-123°50.51'W
- Station 2 : Fraser River plume 49°01.3'N-123°18.5'W
- Station 3 : Boundary Pass 48°50.1'N-122°57.4'W
- Station 4 : Haro Strait 48°29.2'N-123°9.0'W
- Station 5 : Juan de Fuca Strait 48°15.0'N-123°42.5'W

Station 1 in the Strait of Georgia is located in the relatively homogeneous brackish water. Fraser River runoff affects the stability of the water column in this location. Station 2 in the Fraser River plume is most heavily affected by the fresh water discharge showing very low salinity. Station 3 is at the junction of Boundary Pass with the of Georgia; Station 4 is located in Haro Strait. Both Stations 3 and 4 are located in the areas of intensive tidal mixing. Station 5 in Juan de Fuca Strait is located in the coastal seaways domain.

The diatoms considered in this study were collected from 5 stations which were located in the Strait of Georgia/Juan de Fuca Strait system. The collections were made at more or less monthly intervals during 15 cruises between May 1972 and July 1973 on CSS *Vector*. Stations were taken at approximately 20 mile intervals. At each station samples were collected from depths of 1, 25, 50, and 75 meters, using plastic N.I.O. (National Institute of Oceanography) water samplers of 1200 ml capacity with reversing thermometers. For the quantitative studies of diatoms 230 ml of each sample was preserved with Lugol's solution (Utermöhl, 1958) which was modified by adding sodium acetate. In order to prevent oxidation during storage each sample was resealed with black electrician's tape and kept in the dark. The remaining water was used for the measurement of salinity, phosphate, silicate, nitrate, nitrite and ammonia.

Utermöhl's sedimentation method (Utermöhl, 1931, 1958; Lund *et al.*, 1958) was used for the enumeration of the diatom species. The sample in a bottle was shaken thoroughly by hand in order to loosen any organisms attached to the glass and to distribute them evenly throughout the water. An aliquot was poured into a cylindrical chamber of 10 ml capacity with an inside diameter of 25 mm, covered and left

undisturbed for at least 12 hrs to settle on the glass bottom plate. The plate was 0.3 mm thick and the chamber was closed by a cover plate of 32 mm thick and the chamber was closed by a cover plate of 32 mm diameter. Depending on the total abundance of the diatoms, 5 ml and 100 ml chambers were also used. In this case the total abundances were usually decided by using the net samples in the bottles. The success of this method depends on the effectiveness of the settling of the suspended materials. A full discussion concerning this problem has been made separately (Shim, 1977a).

Measurements of temperature and the collection of samples for salinity and nutrient analyses were made by using N.I.O. bottles equipped with reversing thermometers. Temperatures were read on board with an accuracy of $\pm 0.01^\circ\text{C}$. Water samples for salinity analysis were brought to the laboratory and salinity was estimated by using the Model 601 MK3 Auto-Lab Inductively Coupled Salinometer (Extended Range Model). Water samples for nutrient analysis were poured into different plastic bottles, and phosphate, silicate, nitrate, nitrite and ammonia were measured in the laboratory by using the methods described by Strickland and Parsons (1968).

RESULTS

The temporal fluctuations in both temperature and salinity from 1 m to 75 m at five stations are shown in Figure 2 through Figure 6. All data collected during 15 cruises have been reported in the Institute of Oceanography Data Reports (1972, 1973).

The temperature of the subsurface waters (1 m) at all five stations ranged from 5.5°C to 17.7°C with a mean of 8.72; values were lowest in winter and early spring, and highest in late summer and fall. This variation is mainly due to seasonal changes in the effect of solar radi-

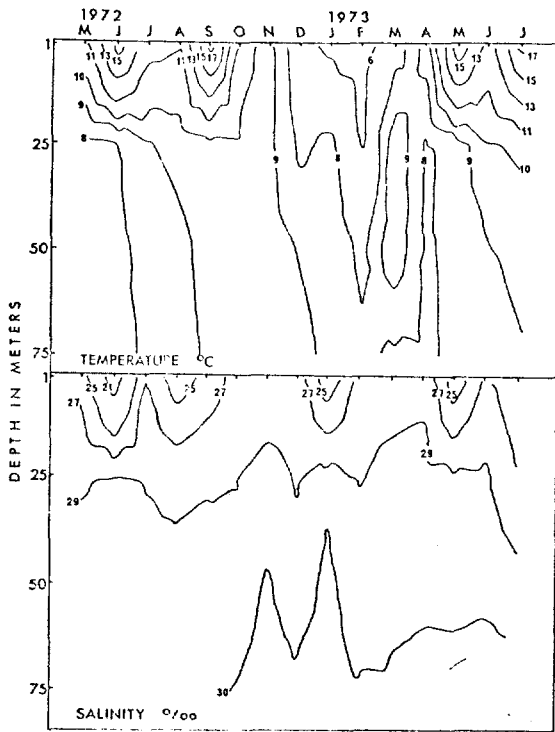


Fig. 2. Seasonal cycle of temperature and salinity at station 1.

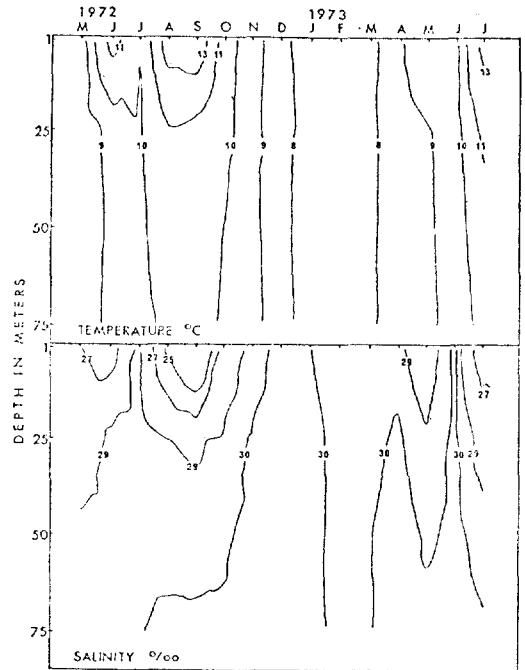


Fig. 4. Seasonal cycle of temperature and salinity at station 3.

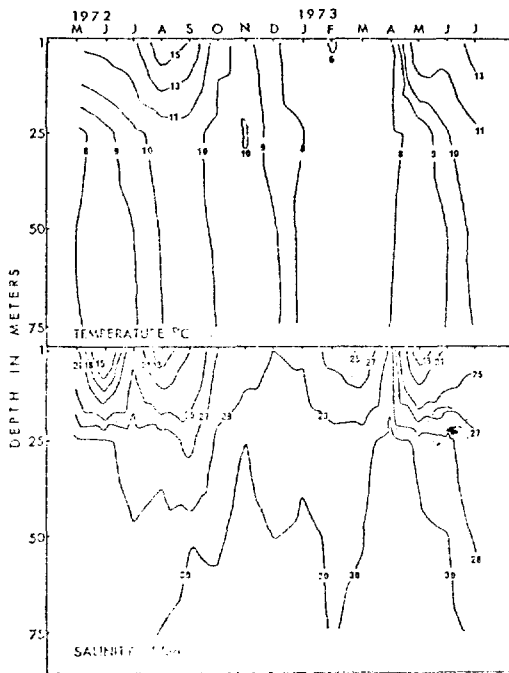


Fig. 3. Seasonal cycle of temperature and salinity at station 2.

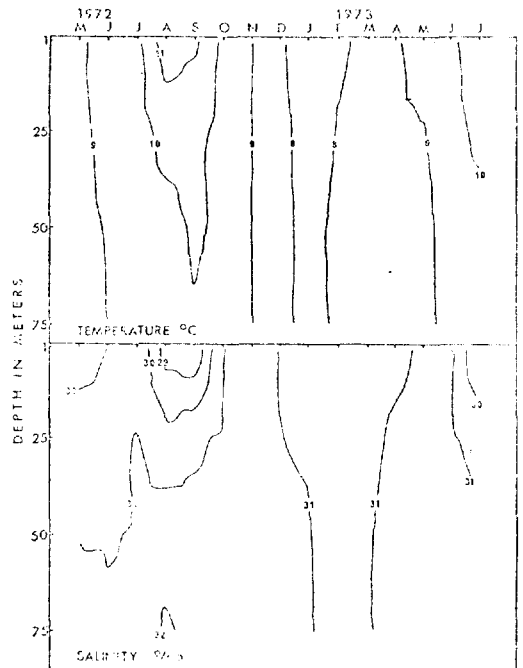


Fig. 5. Seasonal cycle of temperature and salinity at station 4.

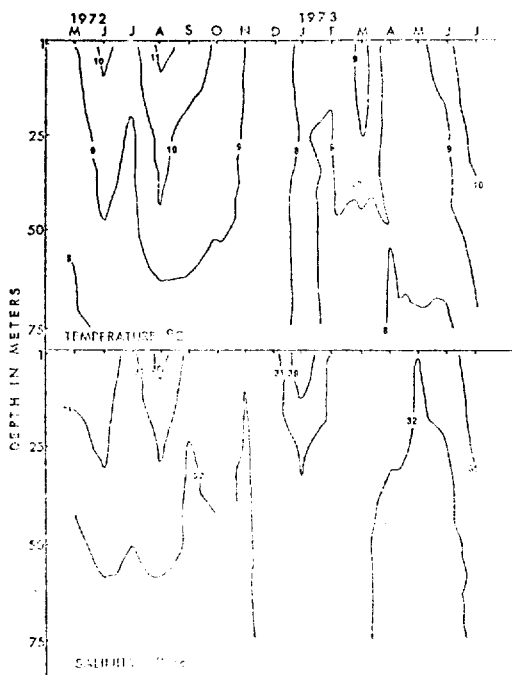


Fig. 6. Seasonal cycle of temperature and salinity at station 5.

tion heating the water. Comparing figures showing the vertical profiles in temperature for all five Stations show that Stations 1, 2 and 3 in the Strait of Georgia underwent considerable variations in the upper layers, while stations 4 and 5 in Haro Strait and Juan de Fuca Strait showed very slight seasonal variation.

The overall temperature variation in the study area was relatively low. Takahashi, Fuji and Parsons (1973) investigated phytoplankton photosynthesis in the Fraser River estuary and have shown that temperature is one of the limiting factors in the area, especially below 10 m. It is general thought that plankton organisms are able to tolerate a wide temperature range (Hutchinson, 1967) and the optimum temperature for growth in the sea has been reported as being between 12°C and 20°C (Fogg, 1975). Although it has been indicated that the direct influence of temperature on phytoplankton in

the sea is insignificant (Steemann-Nielsen, 1963), coastal estuarine waters with rapid nutrient regeneration processes show significant variation in phytoplankton production with temperature (Eppley, 1972). Also, there are significant temperature optima for different species (Brarud, 1962; Bunt, *et al.*, 1966; Smayda, 1973; Soeder and Stengel, 1974). Thus, the prevailing low temperatures and their seasonal fluctuations in the study area are particularly important in determining the principal species of diatoms present and population changes.

Variations in salinity are usually associated with temperature changes. Salinity varied from 15.10 to 33.5‰ with a mean of 29.76. Low salinities occurred twice during spring and summer at Stations, 1, 2, and 3. The first low salinities in early spring were directly associated with the period of the greatest precipitation and the second low salinities in summer were due to the increased discharge of rivers, mostly from the Fraser River. Salinities at Stations 4 and 5 were relatively constant, showing marine conditions. At stations 3 and 4 the vertical regimes in salinity as well as in temperature were relatively homogeneous (except in summer) in the 75 m water column. This is mainly due to the intense tidal mixing action which reduces fresh water input in the upper layer (Herlinveaux and Giovando, 1969).

In a study of the relationship between the saline environments and marine fungal distribution in the Strait of Georgia and Juan de Fuca Strait system, Hughes (1969) has shown that the entire area can be divided into three hydrographic regions on the basis of salinity and that the distribution of some fungal groups are associated with these environments.

According to the present data the Strait of Georgia has an estuarine-type salinity structure as Tully *et al.* (1957) have shown, while the

areas of Haro Strait and Juan de Fuca Strait are more marine. These different features could be very important in forming species associations of planktonic diatom communities in the study area, because salinity has considerable physiological effect upon planktonic algae (Soeder and Stengel, 1974) and variations in total salt content of water inhibits the spatial distribution of phytoplankton organisms (Boney, 1975).

Plant Nutrients

Marked seasonal variations in nutrient concentrations were evident at Stations 1 through 5. These variations occurred between the surface and 75 m.

The concentration range of phosphorus during this study was 0.3~2.8 $\mu\text{g-at P/l}$ with a mean of 1.7 (Table 1) at station 1 in March 1973

when the phosphorus concentrations below 25 m were undetectable. The reason for these unusual values of phosphorus concentration are not known. Seasonal distribution was very similar to that previously observed in the Strait of Georgia (Parsons *et al.*, 1973; Stockner and Cliff, 1975). Low levels prevailed during summer through fall, followed by increasing concentrations in November, and high levels in winter. Spring was characterized by decreasing concentrations. Relatively small differences were observed below 25 m, although there somewhat marked variations at stations 3 and 4. Values of phosphorus at stations 4 and 5 showed in April through July and in November through December respectively. Phosphorus concentrations in the study area are much higher throughout the year than those known to limit phy-

Table 1. Phosphorus concentration ($\mu\text{g-at/l}$) during May 1972~July 1973.

Station/Depth	1972	1973													
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
1- 1m	0.9	0.8	0.7	0.0	0.2	0.8	2.0	1.9	1.1	2.1	2.0	0.8	0.3	0.3	0.5
25m	2.1	1.7	1.8	1.3	1.8	1.4	2.8	2.0	1.6	2.0	0.0	2.5	2.2	2.1	2.2
50m	2.1	1.6	1.9	1.5	2.0	1.4	2.6	1.9	1.6	2.2	0.0	2.0	2.3	2.6	2.0
75m	2.3	2.0	1.8	1.6	2.1	1.4	2.8	2.2	1.6	2.1	0.0	2.6	2.2	2.7	2.3
2- 1m	2.6	1.5	0.6	0.0	0.6	0.9	2.0	1.7	1.5	1.5	1.6	0.9	0.9	0.7	0.6
25m	2.2	1.8	1.6	1.2	1.6	1.3	2.4	1.9	1.5	1.8	2.1	2.2	2.2	1.7	1.5
50m	2.1	1.8	1.7	1.4	1.6	1.2	2.4	2.2	1.4	1.9	1.5	2.4	1.9	1.4	1.8
75m	2.5	1.9	1.7	1.4	1.7	1.2	2.4	2.0	1.4	2.2	1.9	2.5	1.9	1.4	2.0
3- 1m	1.3	0.7	1.4	0.2	0.7	1.0	2.1	1.8	1.2	2.1	2.0	1.6	1.8	1.9	0.7
25m	1.9	1.4	1.6	1.0	1.7	1.2	2.4	1.9	1.3	2.1	2.0	2.0	1.9	1.8	1.5
50m	2.2	1.8	1.6	1.2	2.0	1.2	2.2	1.9	1.3	2.2	1.8	2.3	2.0	2.3	1.8
75m	2.1	1.6	1.7	1.1	1.9	1.2	2.4	2.0	1.3	1.6	1.9	2.0	1.1	2.3	1.7
4- 1m	2.0	1.4	1.7	0.8	1.5	1.3	2.5	1.9	1.0	1.7	1.8	1.7	2.0	2.0	1.7
25m	2.1	1.2	1.7	1.2	2.1	1.2	2.5	2.1	1.1	1.6	1.8	3.0	1.9	1.9	1.9
50m	2.3	1.5	1.8	1.6	2.0	1.2	2.4	1.9	1.3	1.6	2.0	2.2	2.1	2.0	2.1
75m	2.3	1.5	1.8	1.6	2.1	1.2	2.5	2.2	1.3	1.5	1.6	2.4	2.0	2.1	2.0
5- 1m	2.0	1.4	1.7	0.9	1.7	1.3	2.4	2.0	0.7	1.4	1.6	1.9	1.9	2.2	1.5
25m	2.1	1.5	1.7	1.2	2.0	1.3	2.4	2.1	1.9	1.5	1.6	2.0	2.1	2.0	2.0
50m	2.1	1.6	1.9	1.5	1.9	1.3	2.3	2.1	1.2	1.5	1.7	2.1	1.8	2.3	2.0
75m	2.4	1.6	1.8	1.5	1.9	1.5	2.3	1.9	1.2	1.4	1.6	2.4	2.1	2.6	2.0

toplankton growth. For example a value of *ca* 0.6 $\mu\text{g-at P/l}$ has been reported as growth limiting by Kuhl(1974). Strickland and Austin (1960), and McAllister *et al.* (1961) reported that phosphorus reserves were never exhausted in the area of the Strait of Georgia.

Data for nitrogen concentration is available on three forms, nitrite and ammonia. Recorded concentrations of nitrate nitrogen (Table 2) ranged from undetectable to 32.1 $\mu\text{g-at N/l}$ with a mean value of 19.59. Marked seasonal variations were evident throughout the stations in the upper 25 m level. Indicated nitrate was more or less homogeneous in vertical distribution below 25 m except during the summer months. This vertical profile of nitrate is similar to those of phosphate. The general structure of annual nitrate concentration shows that levels

were high during winter and spring, and low during the rest of the year. However, the pattern in 1972 was somewhat different from that in 1973. Takahashi, Fuji and Parsons (1973) pointed out that nitrate below 1 $\mu\text{g-at N/l}$ is a limiting factor for phytoplankton photosynthesis in the Fraser River estuary. During the present study nitrate concentration below 1 $\mu\text{g-at N/l}$ occurred only in the subsurface water during the summer months at station 1 and at 1 m in June at station 2. This indicates that nitrate is rarely limiting with depth. However, some limiting levels occurred in the surface zone at all stations.

Nitrite nitrogen was usually found in the water of the study area in amounts ranging from 0.0 to 0.5 $\mu\text{g-at N/l}$ with a mean of 0.16 (Table 3). The high values were observed

Table 2. Nitrate concentrations ($\mu\text{g-at/l}$) during May 1972~July 1973.

Station/Depth	1972						1973								
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
1— 1m	27.5	24.1	5.9	2.3	1.2	14.5	12.1	24.4	20.2	18.4	24.3	0.3	3.8	0.5	0.0
25m	14.3	30.2	26.7	27.9	26.2	26.8	20.7	23.5	25.1	21.3	26.2	26.2	18.1	9.3	11.8
50m	24.6	32.1	26.6	23.1	28.6	25.9	23.6	26.8	27.8	24.6	26.0	26.1	25.9	10.9	14.0
75m	24.5	27.6	26.5	29.3	28.6	29.4	21.0	28.3	15.5	18.7	24.5	25.5	26.4	0.9	14.5
2— 1m	11.7	5.5	4.3	2.6	4.6	15.9	18.9	25.4	15.5	16.3	20.1	2.8	9.6	7.5	1.2
25m	16.1	25.1	23.9	23.5	23.0	27.6	22.8	25.7	19.3	16.9	25.3	24.8	27.0	12.3	9.7
50m	21.1	24.4	26.6	23.1	23.6	22.2	11.7	27.5	25.0	15.8	24.4	25.1	23.1	7.2	9.7
75m	24.6	22.9	26.4	23.8	24.6	22.0	18.8	27.0	22.7	14.8	22.6	23.4	22.5	23.7	18.8
3— 1m	24.6	6.1	19.6	4.8	6.6	17.1	18.2	26.3	19.2	12.2	21.9	12.6	16.5	14.4	2.1
25m	13.2	24.8	20.9	21.0	21.5	22.3	17.0	26.3	17.6	13.3	22.5	19.4	19.3	6.3	7.3
50m	24.3	16.9	19.8	20.7	21.1	22.8	13.3	26.2	20.0	13.3	21.9	20.1	22.3	13.4	9.8
75m	24.8	19.1	18.6	22.4	22.6	23.1	16.5	26.0	19.3	15.8	22.5	20.4	22.4	16.2	10.5
4— 1m	23.8	20.0	23.9	14.3	17.1	25.4	21.6	26.4	16.9	15.2	18.9	19.0	20.7	10.5	4.9
25m	23.9	23.4	24.6	21.8	23.4	26.0	17.3	26.6	15.9	13.4	20.1	20.2	21.3	8.3	7.3
50m	16.2	—	24.8	25.3	24.4	20.2	17.9	26.4	24.9	15.8	20.4	21.2	21.8	17.2	13.0
75m	23.7	26.4	25.1	25.5	23.0	24.2	18.3	26.5	17.4	16.0	19.8	21.1	22.2	17.3	11.6
5— 1m	23.6	23.4	21.9	15.0	23.0	25.0	17.5	25.6	8.9	13.0	17.9	20.8	23.5	10.9	8.4
25m	15.9	24.7	25.8	22.7	26.9	26.6	20.2	25.9	12.5	11.3	17.8	21.7	23.9	21.6	8.0
50m	23.8	26.6	26.3	23.3	27.3	27.6	19.7	25.8	18.2	13.0	18.2	27.0	25.1	6.4	11.4
75m	23.2	23.6	27.3	29.4	28.1	31.2	19.7	25.8	11.5	12.6	16.1	22.5	22.5	20.0	12.9

Table 3. Nitrite concentrations ($\mu\text{g-at/l}$) during May 1972~July 1973.

Staction/Depth	1972								1973						
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
1— 1m	0.1	0.2	0.2	0.1	0.1	0.3	0.2	0.2	0.0	0.2	0.2	0.1	0.0	0.0	0.0
25m	0.2	0.1	0.0	0.1	0.0	0.1	0.0	0.2	0.0	0.1	0.0	0.2	0.2	0.4	0.1
50m	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.3	0.1
75m	0.2	0.1	0.1	0.1	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2— 1m	0.3	0.4	0.1	0.0	0.2	0.2	0.2	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1
25m	0.3	0.3	0.1	0.0	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.1	0.2	0.5	0.4
50m	0.1	0.2	0.1	0.3	0.3	0.2	0.1	0.0	0.1	0.1	0.0	0.2	0.2	0.4	0.4
75m	0.3	0.2	0.2	0.4	0.2	0.1	0.5	0.0	0.0	0.0	0.2	0.1	0.2	0.2	0.5
3— 1m	0.3	0.2	0.2	0.0	0.2	0.3	0.4	0.1	0.1	0.1	0.2	0.2	0.2	0.3	0.2
25m	0.4	0.3	0.2	0.0	0.2	0.3	0.3	0.1	0.0	0.1	0.2	0.2	0.2	0.2	0.2
50m	0.3	0.2	0.1	0.3	0.2	0.3	0.3	0.1	0.0	0.1	0.2	0.2	0.2	0.2	0.2
75m	0.4	0.2	0.1	0.2	0.2	0.3	0.3	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.3
4— 1m	0.4	0.3	0.1	0.2	0.3	0.3	0.2	0.1	0.0	0.1	0.2	0.2	0.1	0.3	0.2
25m	0.3	0.2	0.1	0.2	0.2	0.3	0.3	0.1	0.0	0.1	0.2	0.2	0.2	0.3	0.2
50m	0.4	0.0	0.1	0.2	0.2	0.2	0.3	0.1	0.1	0.1	0.2	0.2	0.2	0.3	0.2
75m	0.3	0.2	0.1	0.3	0.2	0.3	0.2	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.2
5— 1m	0.3	0.2	0.1	0.2	0.2	0.3	0.2	0.0	0.1	0.1	0.2	0.2	0.2	0.3	0.3
25m	0.3	0.2	0.2	0.2	0.2	0.3	0.3	0.1	0.1	0.0	0.1	0.2	0.2	0.3	0.2
50m	0.4	0.2	0.1	0.2	0.2	0.3	0.3	0.1	0.1	0.0	0.1	0.1	0.2	0.2	0.3
75m	0.2	0.2	0.1	0.2	0.1	0.1	0.3	0.1	0.1	0.0	0.1	0.1	0.3	0.2	0.2

Table 4. Ammonia concentrations ($\mu\text{g-at/l}$) during May 1972~July 1973.

Station/Depth	1972								1973						
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
1— 1m	1.5	2.1	0.2	1.2	1.2	1.2	1.9	1.4	1.7	1.3	0.5	0.5	0.2	1.5	1.3
25m	2.1	0.7	0.6	1.1	1.1	1.3	2.0	1.3	1.4	1.3	0.6	0.6	1.4	2.2	0.3
50m	2.1	1.1	0.6	1.0	—	1.3	2.0	1.2	1.4	0.5	0.6	0.6	0.1	1.3	0.3
75m	1.6	0.8	0.6	1.1	1.1	1.0	1.8	1.3	1.6	1.1	0.5	0.6	0.4	1.0	0.8
2— 1m	1.5	4.0	0.0	1.9	1.5	1.7	1.9	1.5	1.6	1.3	0.7	0.5	1.5	2.5	1.9
25m	0.9	1.2	0.0	1.1	1.0	1.2	2.0	1.2	1.4	1.2	0.5	0.4	0.3	1.9	1.6
50m	1.4	1.7	0.7	1.0	1.1	1.4	2.0	1.2	1.3	1.3	0.6	0.4	0.6	1.3	1.9
75m	1.4	1.9	0.7	1.5	1.2	1.5	1.7	1.3	1.3	1.4	0.6	0.4	0.5	1.2	1.5
3— 1m	1.5	1.4	0.9	1.5	1.4	1.6	2.3	1.3	1.3	0.9	0.5	0.5	0.5	1.6	1.1
25m	2.0	1.5	0.9	1.6	1.2	1.5	2.5	1.4	1.4	1.4	0.5	0.5	0.7	1.9	1.4
50m	1.9	1.5	1.0	2.0	1.3	1.6	2.2	1.2	1.4	0.2	0.5	0.6	0.9	2.0	1.3
75m	2.2	1.5	1.0	1.8	1.3	1.6	1.9	1.5	1.4	0.2	0.5	0.6	0.9	1.8	1.4
4— 1m	1.3	1.5	1.0	1.2	1.4	1.6	2.3	2.1	1.4	1.4	0.5	0.6	0.0	1.8	1.1
25m	1.3	1.4	1.0	1.7	1.3	1.5	2.1	2.2	1.4	1.4	0.5	0.7	0.4	1.7	1.8
50m	1.4	1.3	1.1	1.6	1.3	1.6	2.5	2.1	1.4	1.1	0.4	0.9	0.7	1.8	1.6
75m	1.5	1.4	1.0	1.5	1.3	1.4	2.0	2.2	1.5	1.2	0.5	0.6	0.5	1.8	1.2
5— 1m	2.8	1.1	0.8	1.4	1.3	1.4	2.3	1.3	1.5	1.4	0.4	0.6	0.7	1.7	1.0
25m	1.7	1.0	0.8	1.6	1.2	1.5	2.0	1.2	1.4	1.2	0.7	0.5	0.6	1.5	1.4
50m	1.5	1.5	0.8	1.3	1.5	1.7	2.1	1.3	1.4	1.2	0.5	0.6	0.4	0.0	1.2
75m	1.5	0.8	0.6	1.2	1.1	—	1.9	1.3	1.3	1.3	0.5	0.6	0.1	0.0	1.2

during spring months at Stations 1 and 2, and during the spring and summer months at Stations 3, 4 and 5, showing the highest values below were observed in the winter months at all Stations. The seasonal distribution of nitrite was similar to the results given by Stephens *et al.* (1967).

Ammonin nitrogen concentration varied from 0.0 to 2.8 $\mu\text{g-at N/l}$ with a mean value of 1.23 (Table 4). No consist depth differences were noted. Seasonal variations in ammonia concentrations were evident in July 1972 and during spring months in 1973. The concentrations of ammonia increased in late summer and were high until late winter. High concentrations of ammonia usually coincident with diatom blooms.

In general the seasonal distribution of nitrogen were similar to those observed for the Strait of

Georgia by Fulton *et al.* (1967, 1968) and described previously for the Strait of Georgia/Juan de Fuca system by Tully and Dodimead (1957). Data suggest that the entrainment of fresh water input from the Fraser River provided nitrogen for the study area, while ocean waters, including Juan de Fuca Strait and the passages, were mainly responsible for the phosphorus concentration of the area.

The seasonal variations of reactive silicate were more evident in the study area and ranged from 4.7 to 68.5 $\mu\text{g-at Si/l}$ with a mean of 31.5 (Table 5). During the fall the concentration of silicate increased, reaching a high concentration in winter and decreasing during spring and summer. The first low concentrations in April and in July 1973. This pattern of annual variation in silicate concentration is similar to that

Table 5. Silicate concentrations ($\mu\text{g-at/l}$) during May 1972~July 1973.

Station/Depth	1972												1973				
	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.		
1— 1m	37.3	17.1	33.3	36.2	14.7	8.4	21.2	52.3	—	57.6	57.1	4.8	21.6	8.3	25.9		
25m	21.0	17.0	6.9	42.8	46.8	24.3	33.8	42.2	32.5	48.0	58.8	18.8	47.9	40.9	41.1		
50m	35.2	18.2	5.8	45.0	47.6	7.5	42.5	49.6	40.7	46.7	54.8	20.1	51.0	50.2	46.4		
75m	35.1	17.0	6.6	45.2	45.8	5.3	14.9	47.7	27.8	68.5	—	21.6	50.3	53.0	34.6		
2— 1m	9.2	17.0	—	35.8	31.1	26.8	17.3	47.8	23.8	55.2	55.9	4.7	31.2	37.5	26.5		
25m	22.2	17.0	28.4	43.4	27.7	19.6	12.6	48.8	35.4	49.6	55.1	25.0	46.5	38.4	37.1		
50m	25.7	17.3	11.3	44.5	43.8	18.9	18.7	53.9	30.2	51.0	50.8	25.6	46.2	44.3	38.1		
75m	33.6	15.5	11.3	45.2	38.2	16.1	7.9	50.6	36.7	53.6	36.4	20.9	42.9	45.8	37.9		
3— 1m	10.3	17.0	7.6	20.0	34.7	6.2	34.8	52.3	29.5	65.6	48.1	11.4	39.3	39.6	25.3		
25m	33.5	17.0	6.7	39.7	38.7	7.7	28.2	50.0	27.5	41.5	50.0	14.1	29.0	34.1	35.3		
50m	35.2	16.9	6.9	40.0	41.5	25.1	18.4	49.5	35.8	46.1	47.8	20.4	40.0	33.5	39.6		
75m	35.2	16.9	6.2	31.9	24.6	17.4	18.3	49.9	29.5	55.4	47.9	24.4	43.7	—	30.3		
4— 1m	9.9	11.1	8.0	41.1	24.8	30.8	33.3	50.6	21.0	48.7	38.9	20.7	40.2	39.5	23.3		
25m	35.2	16.8	13.8	43.4	31.7	19.8	21.4	50.0	21.3	34.3	43.2	27.1	40.0	37.8	27.1		
50m	5.8	16.9	15.6	46.2	31.4	30.1	10.4	50.9	25.4	23.1	41.2	21.3	40.8	40.0	32.5		
75m	35.2	20.0	9.8	33.3	22.5	33.6	31.8	49.5	22.6	41.0	42.0	18.4	42.9	43.6	40.7		
5— 1m	35.2	8.9	9.6	42.0	40.4	32.0	32.5	45.8	16.6	37.5	32.6	14.8	45.7	44.5	24.1		
25m	15.4	17.0	12.4	43.0	45.1	27.9	18.4	47.1	19.2	27.1	33.2	11.4	45.0	46.3	24.1		
50m	35.1	17.0	6.0	44.7	34.9	12.9	21.2	43.7	25.0	25.3	34.7	17.2	45.7	47.5	36.5		
75m	22.4	16.9	6.4	38.9	41.1	6.9	31.5	49.4	26.5	29.5	35.6	29.2	41.6	52.0	45.5		

observed by Parsons *et al.* (1970), and is directly associated with the periods in advance of diatom blooming in the area. The concentrations in the upper regions of the Strait of Georgia-Juan de Fuca System were high, while those in the lower regions especially at station 4 were low. This indicates that the principle source of silicate in the study area is the Fraser River (Tully and Dodimead, 1957).

The Diatoms

The temporal variability in the total standing crop of the diatom community in the study area is shown in Figures 7 through 11. Of particular interest to this study are the sizes and timing of any fluctuations which reoccur in an annual cycle. The general pattern of the annual cycle of the diatom community was a rapid increase in the standing crop in April followed by a sharp decrease in May, and then a second peak in the standing crop which occurred during the early summer months with diatoms remaining relatively abundant. The peak of the fall diatom population at Stations 1 and 3 were lower than that of spring. The standing crop during the winter months reached a minimum.

The seasonal variation of the standing crop of diatoms (between the surface and 75 m) at all stations apparently showed similar patterns except at Station 2; the size of the standing crop both at 50 m and 75 m was usually much lower than in the upper layer. The annual cycle in the Standing crop at Station 2 (Figure 8) was characterized by a large increase during spring months (except at 25 m). No indication of a fall peak in diatom fluctuation was observed. Vertical variations in the standing crop at Stations 3 and 4 were much less than in the other three Stations (Figure 9 and 10), indicating the probable effect of tidal mixing (Herlinveaux and Giovando, 1969) on the standing crop of diatoms.

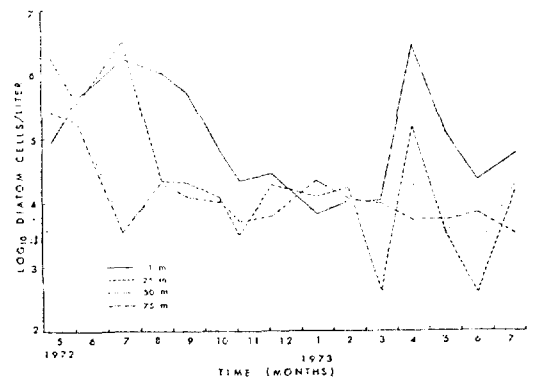


Fig. 8. Seasonal fluctuations in total diatom standing crop at station 2.

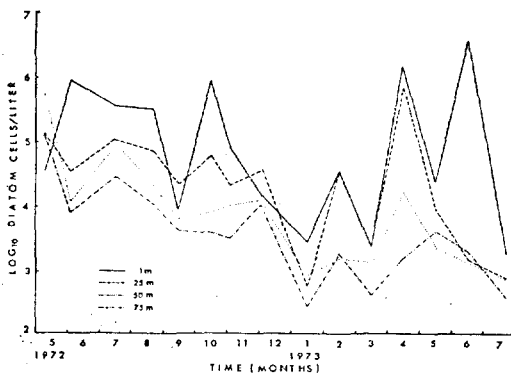


Fig. 7. Seasonal fluctuations in total diatom standing crop at station 1.

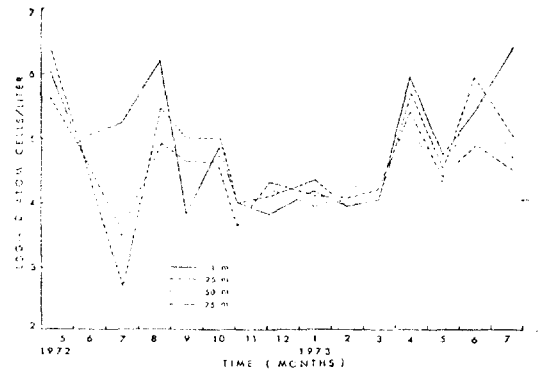


Fig. 9. Seasonal fluctuations in total diatom standing crop at station 3.

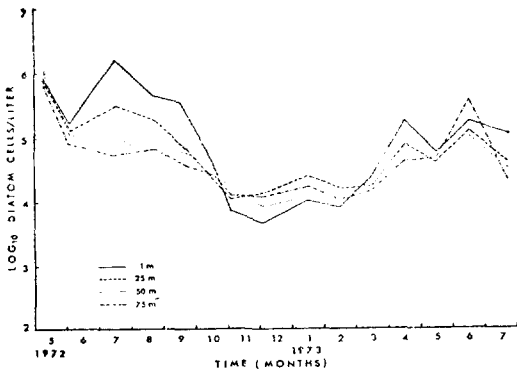


Fig. 10. Seasonal fluctuations in total diatom standing crop at station 4.

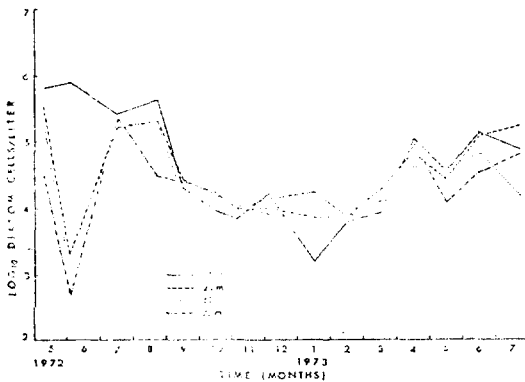


Fig. 11. Seasonal fluctuations in total diatom standing crop at station 5.

Vertical distribution of diatome population was also remarkable at all stations during spring (April-May) and in August. The dominant species was *Skeletonema costatum*: in July 1972, *Schroederella delicatula* was dominant in the subsurface water at Station 1. In October, *Corethron criophilum* was dominant at Stations 1~4 and during spring and winter (December-March) *Paralia sulcata* was dominant at Stations 1 and 2 in November.

The highest standing crops of diatoms, more than 1,000,000 cells per liter, were observed during late spring and summer at all stations. The few previous phytoplankton observations in the study area are in agreement and also show that a rich standing crop of phytoplankton is a characteristic feature of the spring/summer

months (Legare, 1957). During fall, the diatom maximum was observed at Stations 1 and 3. The maximum fall standing crop, however, was usually less than the maximum spring or summer standing crop. At the other 3 stations very high concentrations were observed during late spring and summer. Small seasonal fluctuations have also been observed. Thus, two patterns of seasonal distribution in the diatom standing crop are distinguished in the study area.

A total of 219 species of diatom species were encountered during this study. These taxa consisted of 171 marine species, 8 brackish water species, 11 marine/brackish water species and 29 fresh water species which were introduced from the Fraser River and other rivers. The seasonal distribution of individual species was extremely variable. Some species demonstrated a considerable increase in standing crop for one or two months while many others were very common but never abundant. Many species were characterized by small populations or absence over most of the year.

DISCUSSION

The General Seasonal Distribution of Standing Crop

Some studies from coastal environments have indicated that the seasonal cycle of phytoplankton abundance in a region may be interpreted in terms of the fluctuations of a relatively few ecological factors, and that these factors are similar in a wide variety of environments (Gran & Braarud, 1935; Corelett, 1953; Conover, 1956; Holmes, 1956; Bursa, 1961; Thayer, 1971). With the aid of the results of such studies, the present data can be interpreted in terms of a probable seasonal cycle.

There is an annual cycle of phytoplankton production and standing crop which has been

observed in a wide range of habitats. This cycle is characterized by a rapid increase during the spring and often a smaller increase in the fall, and by minimum standing crops of diatoms in late summer (Gran, 1932; Strickland, 1960; Anderson and Banse, 1961). Of primary importance to this cycle are nutrient concentrations and light intensity, the availability and effect of both is directly or indirectly dependent upon the stratification of the water column. In most areas, the commencement of the spring bloom coincides with the stabilization of the water column. At this time, nutrient concentrations in the surface layers have been increased by upward mixing of deep nutrient-rich water during the winter, and conditions are favourable for maximum production of diatoms. The subsequent rapid decline in the standing crop is often attributed to grazing by zooplankton, which bloom in response to the increased food supply. The annual cycle of standing crop is accompanied by a succession of species, predictable within limits. Characteristically, diatoms predominate during the spring and fall blooms, and dinoflagellates and microflagellates during the summer minimum.

This annual cycle of variation in environmental parameters and phytoplankton standing crops has been observed in near shore waters. Parsons (1965) has summarized the productivity and standing crop data collected at two cold water coastal areas in the Eastern Pacific, the Strait of Georgia, and Queen Charlotte Sound as well as at weather Station *P* in the open North Eastern Pacific. Estimates of standing crop were obtained from surface concentrations of chlorophyll *a*. In the Strait of Georgia, a large vernal increase in the standing crop occurred in March, at the commencement of stratification. This was followed by additional increases in April and May, apparently as a result of short

periods of increased mixing which replenished the nutrient concentrations in the euphotic zone. A significant fall increase occurred in some years. The cycle observed in Queen Charlotte Sound was similar. However, a markedly different cycle pattern in the standing crop was evident at Station *P* which showed no significant seasonal fluctuations. Observations from the north western edge of the Central Pacific have revealed the typical bimodal cycle of diatom abundances with maximum in March and October (Motoda and Marumo, 1963).

Within the the Strait of Georgia/Juan de Fuca system the annual cycle in the diatom standing crop corresponds with Parsons' general productivity picture. At Station 1 in the the Strait of Georgia and at Station 3 in the Boundary Pass, the spring peaks in the diatom standing crop probably followed soon after the stabilization of the water column, in April or May (Figures 2 and 7). Stratification of the water column in coastal waters usually begins earlier, possibly because of dilution of surface waters by terrestrial run off (Tully and Dodimead, 1957; Waldichuk, 1957). The second peak of the diatom standing crop was caused by the infusion of replenished nutrients from the upwelled deeper water, because in deeper water the nutrients are always abundant (Pacific Oceanographic Group, 1953) and infused into the surface water by entrainment (Helinveaux and Giovando, 1969). Breakdown of summer stratification begins in July or August and an increase in production in the fall follows as long as there is sufficient light. The decrease of diatom standing crop in the winter months proceeds until maximum vertical mixing is fully developed. In the study area this occurs in late winter-earring (Tully and Dodimead, 1957).

The maintenance of an increase in the stand-

ing crop of diatoms may depend upon the concentrations of zooplankters, particularly at the onset of the bloom. Smayda (1973) showed that grazing was a major factor causing the decline of planktonic diatoms during the spring bloom in Narragansett Bay. A similar effect of herbivores upon the fluctuations of the standing crop of phytoplankton in the open Pacific has been reported (Parsons, 1965). The annual cycles of the standing crop of diatoms observed at Station 2 off the Fraser River, Station 4 in Haro Strait and Station 5 in Juan de Fuca Strait are different from those of Stations 1 and 3. No typical spring/fall peak pattern was found at these Stations. The second spring bloom usually occurred in early summer and high diatom concentration was maintained until the decrease began in the fall.

The annual cycle of the diatom standing crop at Station 2 was largely controlled by the effect of the Fraser River discharge. The summer bloom of diatoms in the upper layer (1~25) began soon after the formation of a high stratification both of temperature and of salinity in the water column and was maintained until the stability of the water broke down in the fall. The sharp decrease (from the previous month) in the standing crop below the 50 m level during (Figure 8) Spring, which was also observed at Station 3, was possibly caused by light limitation and not by nutrient concentration, because no limiting level of nutrients was found at this time; also a sharp reduction of total daily radiation was exactly coincident with the decline (Figure 13). Evidence suggests that the annual discharge from the Fraser River usually carries huge amounts of silt, especially in early summer (Giovando and Tabta, 1970) and that the effect of silt limits the phytoplankton photosynthesis due to reduced radiation (Takahashi, Fjui and Parsons, 1973).

In marked contrast to this cycle of the standing crop at stations 4 and 5 shows neither considerable seasonal fluctuations in fall and winter nor considerable differences in vertical variations, except at Station 5 in June 1972. The pronounced maximum of standing crop occurs in early summer, and this coincides with the stabilization of the water column. That this period of sharp decrease in the standing crop below 25 m at Station 5 was not the result of limiting physico-chemical factors may be due to the presence of large population of zooplankton at the onset of the bloom (Himmelman, pers. comm.). The modified annual diatom cycles at Stations 4 and 5 may be explained by the presence of upwelled subsurface Pacific Ocean water in Juan de Fuca Strait. The phenomenon of upwelling off the British Columbia coast is evident from April to August (Pickard, 1963). This oceanic water is gradually mixed with the overlying warmer less-saline waters in the Strait. This mixing continues through the fall and winter and results in relatively low temperatures in the area. The cold oceanic water reached Station 4 about two months later than Station 5 which coincides with the variation in the diatom standing crop between the two Stations. That the annual cycle of diatom standing crop at Stations 4 and 5 is related to temperature is suggested by the results of multiple regression analyses at each Station which show that there was a significant positive correlation between total standing crop and temperature at both Stations (Shim, 1977b).

Vertical Distribution

The available information on the vertical distribution of marine phytoplankton, much of which is based on the analysis of vertical profiles suggests that phytoplankton abundances within the euphotic zone are characteristically non-

random along vertical axes, and often have pronounced subsurface maxima. Such distributions have been reported from the Arctic (Bursa, 1961), Norwegian fjords (Hasle, 1954), Indian Ocean (Yentsch, 1965), the Kuroshio Current (Motoda and Marumo, 1963), the California Current (Lorenzen, 1966), the California coastal waters (Strickland, 1968), and in the Gulf of Mexico and the Atlantic Ocean (Hobsen and Lorenzen, 1972). In contrast, Hulbert (1966) found no significant variation in abundance of the phytoplankton of the Sargasso Sea in the upper 100 meters. He encountered vertical stratification only in the diatom populations over the adjacent continental shelf and slope, where the water was more highly stratified. A detailed study in a fresh water lake (Lund, Kipling, and LeCren, 1958) clearly demonstrated that the vertical stratification of the diatom *Asterionella* sp. depended upon stabilization of the water column. In the presence of vertical mixing, only motile algae maintained vertical stratification against the randomizing effects of turbulence.

During the present study, both the magnitude and pattern of the fluctuations in the diatom standing crop along the vertical axis were related to the presence of a temperature gradient in the water column. Within the homogeneously mixed layer during winter only a small fluctuation in the vertical distribution of diatoms was observed (Figures 7~11). Comparing the vertical distribution of total diatom standing crop with vertical temperature variation during winter, it was found that the homogeneously mixed layer extended to a depth of more than 75 m throughout the entire study area. At all Stations, the major diatom population lay within the mixed layer and its distribution seemed to be random. During spring and summer, however, a seasonal thermocline was present at about 25 meters

throughout most Stations, and only within 25 m of the shallow layer was there a significant portion of the diatom density (except Station 4 in spring). Species in this layer had maxima of abundance and this maximum layer is conspicuous in the vertical profiles of the total standing crop. This stratum was not merely a reflection of the stratification of the dominant species. Below the thermocline the abundances of all species at a Station were approximately the same.

It is doubtless that light is one of the most influential factors for the life of phytoplankton. The light intensity at the surface varies with several factors such as latitude, season, weather and the time of day. The relation between the light intensity at depths in the water and the turbidity of the water indicates that the extremes of turbidity common to estuarine areas, can have a greater effect on light as a limiting factor than seasonal changes in intensity at the surface (Ferguson, 1972). Although the light was not measured in the present study, the data of total daily radiation from the Department of Environment Records (Figures 12 and 13) indicates that it is evident in the study area as well. Seasonal fluctuations of total daily and

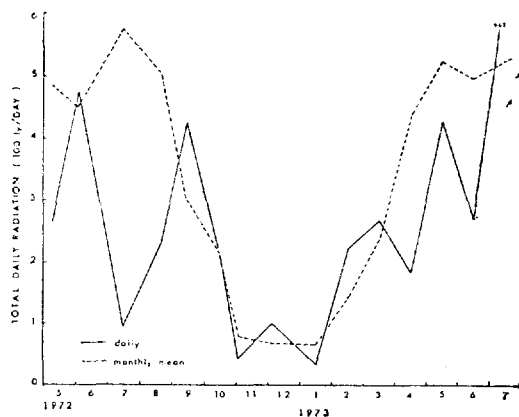


Fig. 12. Total daily and monthly mean radiation received on a horizontal surface at Nanaimo (from Department of Environment Records, 1972, 1973)

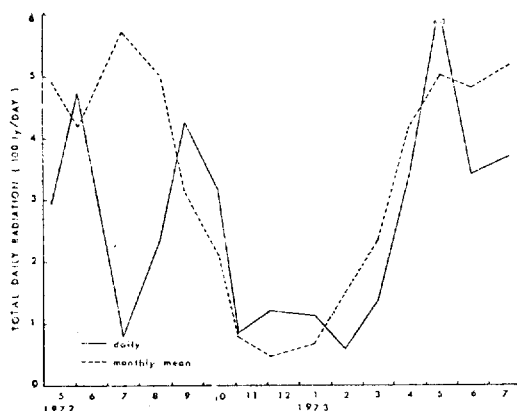


Fig. 13. Total daily and monthly mean radiation received on a horizontal surface at The University of British Columbia (from Department of Environment Records, 1972, 1973)

monthly radiation both at station 1 and at Station 2 were similar to each other (except in May and June, 1972), and this pattern of annual cycle is coincident with those of the observed diatom standing crop. In July 1972 (at Station 1), the total daily radiation below 50 m was reduced nearly to its winter levels as diatom standing crop did (figures 8 and 12), while the diatom standing crop in upper layers (1 m and 50 m) reached their maxima. In this cases, as previously pointed out, the light in the water column below 50 m was apparently limiting.

The depth of the phytoplankton maximum layer has a significance primarily in its relationship to the depth of the euphotic zone. The lower limit of the euphotic zone may be defined by the compensation depth, the depth at which photosynthesis and respiration are equal over a twenty-four hour period. This is generally assumed to be the depth at which the intensity of radiation is 1% that at the surface (Holmes, 1957; Parsons and Takahashi, 1973). Since huge amount of silt, especially in summer months, are usually included in the fresh water discharge, this compensation depth in the study area varies markedly with season.

The continuity of the maximum layer along the transect is especially remarkable considering that it passes vertically through the seasonal thermocline, and horizontally from one environment into another, undergoing a complete change in species composition as it progresses.

Large differences in the concentration of diatom populations at specific depths have been encountered in the present study and this could be due to species competition for different nutrient concentrations as well as light, because the individual diatom species have different requirement for nutrients and so succeed each other as the increasing population reduces the available nutrient supply (Hutchinson, 1967). For example, the concentration of nitrogen in natural waters can have an effect upon cell division rate. It is most frequently limiting nutrient in estuaries (Williams, 1973). The concentration of nitrate-nitrogen, which reduces uptake of this nutrient by factor of 1/2, (K_s), has been measured for a number of phytoplankton species (e.g. Carpenter and Guillard, 1970; Eppley and Coastaworth, 1968; and Eppley *et al.*, 1969). Values of K_s are related to levels of nitrate concentrations and characteristic of a species' habitat. Even clones of the same species isolated from different waters may show different K_s values (Carpenter and Guillard, 1970). Peterson (1975) developed a model with which he explained the so-called the "Paradox of Plankton". He believes that an assemblage of coexisting phytoplankton may be limited by several nutrients and each species principally limited by the availability of a different nutrient. Thus, species succession can occur by the possibility of abundant species monopolizing the nutrient and forcing a less abundant species to extinction, especially in shallow waters.

For *Skeletonema costatum* different distribution patterns were present. The extreme predomina-

nce of *S. costatum* during a greater part of the year may be due to its tolerance to the special environmental conditions: *S. costatum* has a wide and exceptional tolerance to both temperature and salinity (Smayda, 1973) and also has low light demand (Braarud, 1974). It was suggested that special floating properties might give this species an advantage compared with other members of the diatom community (Smayda and Boleyn, 1966).

Diatoms may remain viable in an inactive condition, even in darkness, for long periods of time (Miquel, 1892, cited in Lewin, 1953). Recently, Umebayashi (1972) reported that five cultured diatoms can survive for 9~25 mo at 5°C in the dark, but only very few remained alive. Smayda and Mitchell-Innes (1974) found that seven of nine marine planktonic diatom species used were viable for 90 d at 15°C in the dark and that *Skeletonema costatum* survived for 44 d in the dark and its dark survival was inversely related to temperature. They suggested that the dark survival potential of planktonic diatoms, when displaced from the euphotic zone by mixing or sinking, will vary with species, may be dependent on temperature, and may be prolonged by periodic illumination. The mechanisms by which diatoms regulate their depth, if at all, are not fully understood, but the physiological condition of the cells is obviously important. Senescent cells have a higher sinking rate than rapidly reproducing cells (Eppley, *et al.*, 1967; Smayda, 1970). Steele and Yentsch (1960) showed how the sinking rate of a population could influence the depth of its layer of maximum abundance. They demonstrated that a sinking rate which decreased with depth was necessary to account for a maximum layer, and hypothesized that phytoplankton populations within the euphotic zone, in the presence of vertical stratification, may deplete their nutrient

supply, and, as a consequence, become denser. As they sink into nutrient-rich water below the euphotic zone they assimilate nutrients, reducing their sinking rate or regaining neutral density.

For most species morphological expressions of physiological senescence have not been observed. Although laboratory experiments indicated that nutrient deficiency may have cytological manifestations which can be recognized under the microscope (Homles, 1966), the inability to recognize senescent or nutrient-deficient cells of natural population seriously impedes the recognition of senescent populations. During fall, however, *Skeletonema costatum* was restricted to depths below 50 m, dominating the population at 75 m, and, thus resembling postulated deep-living, senescent phases.

The concentration of senescent populations in a deep layer may be a phase in the annual cycle of oceanic diatoms analogous to the formation of resting spores in the neritic populations of centric diatoms. In both cases, the cells show physiological adaptations to periods of unfavorable environmental conditions. In the shallow neritic environment where the winter mixed layer extends to the bottom, the cells can sink to the bottom, accompanying the formation of heavily silicified cell walls. Such resting spores are a regular component of many planktonic diatoms considered in the present study.

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