Phytoplankton Ecology of the Strait of Georgia, British Columbia

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Observations of phytoplankton production, abundance, and distribution were made at 16 stations in the Strait of Georgia from 1975 to 1977. The discharge of turbid Fraser River water exerts a strong influence on phytoplankton production and distribution in surface waters by rapid light attenuation and horizontal advection. At plume boundaries and back eddies where light conditions improve, very high production occurs (>4–5 g $C \cdot m^{-2} \cdot d^{-1}$), because of rapidly replenished nutrients supplied by the Fraser River. Advection, turbulence, zooplankton grazing, and summer nitrate depletion collectively impart a heterogeneous distribution pattern to phytoplankton in the surface waters of the Strait of Georgia. Mean annual production varies from lows of 150 g $C \cdot m^{-2}$ in Fraser River plume to highs of over 500 g $C \cdot m^{-2}$ in sheltered boundary waters of inlets. Recent increases in ammonia and nitrate from land drainage and domestic sewage, mainly through the Fraser River, are related to increases in phytoplankton standing stocks in the Strait.

Key words: phytoplankton, primary production, eutrophication, coastal marine, phytoplankton distribution and succession, chlorophyll *a*, pelagic

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De 1975 à 1977, on a fait des observations sur la production, l'abondance et la distribution du phytoplancton à seize stations dans le détroit de Géorgie. Le débit d'eau turbide du fleuve Fraser influe fortement sur la production et la distribution du phytoplancton en surface par le biais d'une rapide atténuation de la lumière et de l'advection horizontale. À la limite des couches superficielles et des remous où les conditions lumineuses sont meilleures, il y a très forte production (>4–5 g $C \cdot m^{-2} \cdot d^{-1}$), par suite du renouvellement rapide des éléments nutritifs fournis par le fleuve Fraser. Le phytoplancton des eaux superficielles du détroit de Géorgie doit sa distribution hétérogène à l'advection, la turbulence, le broutage par le zooplancton et l'épuisement estival des nitrates. La production annuelle moyenne varie de creux de 150 g $C \cdot m^{-2}$ dans la couche superficielle du fleuve Fraser à des pics dépassant 500 g $C \cdot m^{-2}$ dans les couches limites abritées des bras de mer. Il existe une relation entre les récentes augmentations d'ammoniac et de nitrates provenant du ruissellement et les égouts domestiques, surtout par le fleuve Fraser, et l'accroissement de la biomasse phytoplanctonique dans le Détroit.

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The whole of the Strait of Georgia is essentially an estuary because it has free access to the open ocean and its surface waters are measurably diluted with fresh water from land drainage. The Strait of Georgia is extremely important as a nursery and rearing ground for valuable Pacific salmon and herring fisheries. It also provides a lesser fishery for cod, groundfish, shellfish, shrimps, and crabs.

There have been many studies of the Strait of Georgia that span nearly 70 yr of observation. Among the notable physical and chemical oceanographic works are those by Tully and Dodimead (1957), Waldichuk (1957), and Waldichuk et al. (1968). Plankton studies have dominated the biological literature over the decades and include the descriptive works of Hutchinson and Lucas (1931), Légaré (1957), and the more theoretical treatments by Parsons et al. (1969a, b), Parsons and LeBrasseur (1970), and Takahashi et al. (1973). The majority of these studies are limited because they deal either with specific regions, i.e. Fraser River plume, or they lack some continuity because of a paucity of observations over the entire area for several consecutive seasons.

The primary objectives of this study were (1) to describe over two growing seasons the wax and wane of phytoplankton populations, including their production, distribution, and seasonal succession; (2) to assess, where possible, the impact of natural and man-induced stress on phytoplankton; and (3) to compare our recent annual and daily primary production rates with earlier published values from the strait and with world

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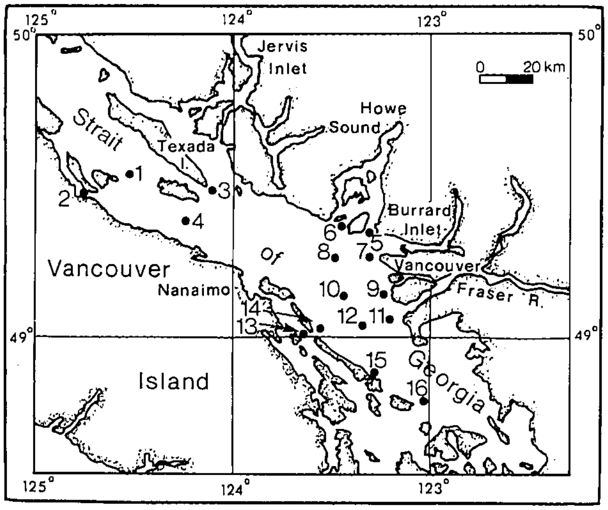


FIG. 1. Strait of Georgia showing station locations and major geographic features.

oceanic and coastal marine values, so as to place in perspective the production potential of the Strait of Georgia.

Description of Study Area

The Strait of Georgia is a complex marine waterway bounded on the west by Vancouver Island, on the east by mainland British Columbia, and on the south by Washington State (Fig. 1). Its length is 200 km, average width 33 km, and mean depth 156 m. Passages to the Pacific Ocean are generally narrow and restrict tidal flow, resulting in extreme tidal turbulence.

Major factors influencing hydrography of the area are fresh water runoff, tide, wind, and insolation. The turbid Fraser River water contributes ~80% of the total land runoff and causes most of the salinity variation in surface waters. Tides are mixed semidiurnal with a maximum daily range of 5 m. Precipitation ranges from 90 $cm \cdot yr^{-1}$ in parts of the southern Strait of Georgia to over 200 $cm \cdot yr^{-1}$ near the British Columbia mainland in the north. Pritchard's (1967) definition classifies the Strait of Georgia as a positive estuary, since precipitation and runoff exceed evaporation, and net flow is seaward. Prevailing winds are SE during winter and NW in summer, mean air temperatures are 2°C in winter and 18°C in summer, and annual insolation ranges from 2163 h in the south to 1489 h in the north near the B.C. mainland (Waldichuk 1957).

The strait may be divided into three oceanographic areas:

1) The stable main body where distinct stratification occurs, and tidal currents rarely exceed 2–4 $km \cdot h^{-1}$.

2) Areas of turbulent tidal mixing where currents may exceed 9 $km \cdot h^{-1}$ and stratification is indistinct (near north and south passages to the Pacific Ocean and in the narrow Gulf Island passes).

3) The area contiguous to the Fraser Delta and overlain by the turbid Fraser River plume, whose total area is highly variable and dependent on river discharge, wind, and tide.

Materials and Methods

Total incident solar radiation was recorded on a Belfort pyrheliometer mounted on board ship, and extinction of surface light with depth was measured by a Montedoro–Whitney Underwater Illuminance meter (Model LMT-8A). The natural logarithm of light intensity was plotted against depth, and the slope of a straight line fitted to the points by linear regression provided an estimate of the mean downward extinction coefficient (k). A standard 30-cm white Secchi disc was used to measure water transparency at every station.

Temperature profiles to a depth of 50 m were obtained with a bathythermograph and surface temperatures were measured with a bucket thermometer.

Water samples were collected from 1, 3, 5, and 20 m depths, and later analyzed for carbonate alkalinity, salinity, dissolved oxygen, nitrate (NO_3^{-1}), total phosphate (TPO_4^{-3}), and silicate (SiO_4^{-4}). The method of Strickland and Parsons (1968) was used to determine carbonate alkalinity, using an Orion digital pH meter (Model 801). However, if after acid titration final pH values fell below 3.00, then the sample analysis was repeated using the APHA et al. (1971) standard titrimetric method. Salinity was analyzed with an Auto-lab salinometer (Model 601) to an accuracy of ±0.5‰. Density was computed by nomograph from temperature and salinity records. Dissolved oxygen (samples fixed within an hour of being taken) was determined by use of the Winkler titration method (Strickland and Parsons 1968). Samples for nutrient analysis were immediately frozen and later analyzed by the Environmental Protection Service analytical laboratory, Pacific Environment Institute, West Vancouver, using methods outlined in their manual (Fisheries/EPS 1974).

The standard ^{14}C method as initially proposed by Steemann-Nielsen (1952) was used, with some modifications. Water was collected from surface skim, and 0.5, 1, 2, 3, 5, 10, 20, and 30 m depths using a 6-L polyvinylchloride Van Dorn bottle. Productivity bottles (two 125 mL light and one 125 mL dark) were inoculated with 1 mL $NaH^{14}CO_3$ (37 $kBq \cdot mL^{-1}$). For each experiment, the number of disintegrations $\cdot min^{-1}$ (dpm) $\cdot mL^{-1}$ was determined by placing 1 mL in each of three scintillation vials. In most cases, samples were incubated in situ for 4–5 h, normally from 0930 to 1430. Water was filtered through 0.45 μm BDH cellulose nitrate filters and placed in 10 mL of a specially prepared toluene-based fluor (POPOP, PPO, 2-ethoxyethanol, and toluene). Samples were analyzed within 24 h for activity in a Packard Tri-Carb Liquid Scintillation Spectrometer (Model 3375). The equation of Strickland (1960) was used to convert dpms to mg $C \cdot m^{-3}$. Using incident solar radiation for the entire light day and for the incubation period, data were converted to mg $C \cdot m^{-3} \cdot d^{-1}$ and integrated by a Hewlett–Packard Calculator and Plotter (Model 9820 A, 9862 A) to give phytoplankton production on an area basis (mg $C \cdot m^{-2} \cdot d^{-1}$). This involved linear interpolation between data points to the depths where light and dark uptake were equal.

Detailed examination was made of phytoplankton samples from only 1 and 5 m depths to assess (a) species composition and (b) phytoplankton volumes during key spring and fall bloom periods. Phytoplankton samples were preserved in Lugol's acetate solution and enumerated, using the Utermöhl (1958) sedimentation method. Volumes were determined by equating phytoplankton cells to known geometric shapes. Each phytoplankton sample was examined under 175 and 700× magnification using a Wild M40 inverted plankton microscope. Results were expressed as cells and total volume · m^{-3}.

One liter of sea water was taken for chlorophyll *a* analysis from 1, 3, 5, and 20 m depths and filtered onto 5.5-cm Whatman GF/C glass fiber filters with a small amount of $MgCO_3$ added. Filters were macerated in a tissue grinder with 10 mL of 90% acetone, and the filtrate analyzed on a Cary recording spectrophotometer (Model 15). The equation of Strickland and Parsons (1968) was used to calculate chlorophyll *a*.

Vertical zooplankton hauls from 50 m were made at each station with a SCOR–UNESCO plankton net, with mouth diameter of 57 cm and screen mesh size of 350 μm. Samples were preserved in 5% formaldehyde, returned to the laboratory, and split into two equal subsamples. One portion was dried overnight at 90°C, and results expressed as zooplankton biomass in mg (dry weight) · m^{-3}. The other portion was preserved for future reference.

Results

Physics and Chemistry

Thermal stratification developed by April and broke down in October except in areas of strong tidal flow, where stratification was transitory or entirely lacking. Surface temperatures ranged from 4°C in winter to 18°C in summer (Table 1). In turbulent passages, surface temperatures varied with each tidal cycle (Tully and Dodimead 1957).

Surface layer salinities ranged from 0.5‰ near the Fraser River during spring freshet to 30‰ away from fresh water influences in winter. Deep-water salinities varied little and were rarely <28‰. A distinct halocline existed in all but the winter months, except near the turbulent passes, where well-mixed water prevented its development.

The pycnocline depth ranged from 5 to 14 m in the Strait of Georgia, with surface σ_T values ranging from 5 to 24. Deep waters varied little around a mean of 22 (Table 1). The pycnocline disappeared in the turbulent passages.

Dissolved oxygen ranged seasonally from 4 to 10 mg · L^{-1} over the whole water column. Highest values occurred at or just below the surface during the vernal phytoplankton bloom.

Ranges of nitrate-N, total phosphate-P, and silicate-Si in Georgia Strait were <0.01–0.47 mg · L^{-1} (<0.7–33 μg-atoms · L^{-1}), <0.01–0.19 (<0.3–5.9), and <0.50–3.40 (<17.8–121.4), respectively. Nitrate depletion in the surface layer occurred in areas and times of stable stratification, usually during July, August, and September. Highest mean values of nitrate occurred at Stations 15 and 16 contiguous to turbulent passages (Table 1). At Station 16 in the turbulent Haro Strait the mean TPO_4 value was higher than that recorded at other stations in the strait.

Mean extinction coefficients (k) ranged from 0.11 in winter to 2.90 near the Fraser River during the spring freshet.

Plankton

By early April, sufficient light ($\bar{x}$ >502 J · cm^{-2} d^{-1}) and surface layer stability occurred to permit substantial increases in phytoplankton standing stock. The increases were noticeable first in the more sheltered and protected waters of the southern strait, but with increasing vertical stability, phytoplankton increased in northern sectors of the strait, where peaks occurred in late May or early June. This phase lag between north and south was due largely to differences in vertical stability among regions of the strait (Parsons 1965).

At all stations except those in areas of strong tidal flow, the spring phytoplankton bloom resulted in maxima of chlorophyll *a*, primary production, and phytoplankton numbers and volume. In areas of strong tidal flow, these factors showed only slight seasonal increases (Fig. 2). Fall increases of chlorophyll and primary production occurred at stratified and stable stations, but a distinct bimodal pattern was not apparent at stations in exposed or tidally mixed areas.

Definite seasonal trends in phytoplankton species succession for the Strait of Georgia were not apparent in this study, as variability among stations made generalization difficult (Fig. 3A, B). Diatoms, mainly *Chaetoceros* spp., *Thalassiosira* spp., *Skeletonema costatum*, *Coscinodiscus* spp., and *Cerataulina bergonii*, were the dominant group throughout the Strait of Georgia in spring and fall periods. At times in August the dinoflagellates *Peridinium* spp., *Gymnodinium* spp., and *Dinophysis* spp. were also common. Other common phytoplankters were unidentified flagellates, occurring over a wide size range and the silicoflagellates *Ebria tripartita* and *Distephana speculum*.

Mean annual chlorophyll *a* and mean annual production were highest in the sheltered waterways of the Gulf Islands (Station 13, Fig. 4), and lowest in areas of strong tidal flow (Station 16), and at stations near the discharge of the turbid Fraser River, where shifting plume boundaries and rapidly changing light conditions affected production (Station 11). Annual production ranged from 149 to 511 g C · m^{-2} · yr^{-1}, integral chlorophyll *a* from 1.0 mg · m^{-2} at some stations in winter to 480 during the vernal bloom, mean phytoplankton numbers from 4.00×10^6 to 1.79×10^{10} · m^{-3}, and mean phytoplankton volume from 1.00 mm^3 · m^{-3} to 3.46×10^4 mm^3 · m^{-3} (Table 1 and Fig. 5).

Mean zooplankton biomass among stations ranged from <1 to 320 mg · m^{-3}, with lowest values recorded in winter and highest in spring, with a phase lag in peak density occurring ~1 mo after the vernal phytoplankton bloom (Stockner et al. 1977). Lowest mean annual zooplankton biomass in the Strait of Georgia occurred at Station 1, while the highest was recorded at Station 3 in the northern strait off the tip of Texada Island (Table 1).

TABLE 1. Maximum–minimum values and 2-yr means of selected physical, chemical, and biological variables in the surface layer (0–5 m) of the Strait of Georgia in 1976 and 1977.

Station	Temp (°C)	Salinity (‰)	Density (σ_T)	Mixed layer depth (m)	Dissolved oxygen ($mg \cdot L^{-1}$)	NO_3-N ($mg \cdot L^{-1}$)	Total PO_4-P ($mg \cdot L^{-1}$)	SiO_4 as Si ($mg \cdot L^{-1}$)	Extinction coeff. (k)	Secchi depth (m)	Chl. *a* $\int_0^{25m}$ ($mg \cdot m^{-2}$)	Primary production $g\,C \cdot m^{-2} \cdot yr^{-1}$	Algal no. no.$\times 10^6 \cdot m^{-3}$	Algal vol ($mm^3 \cdot m^{-3}$)	Zooplankton biomass ($mg \cdot m^{-3}$)
1	7.3–18.6 11.7	25.5–29.6 28.1	17.9–22.9 21.2	8.3	5.0–7.3 6.5	0.02–0.47 0.21	0.03–0.09 0.05	0.50–1.70 0.86	0.17–0.58 0.29	7.0–10.0 8.3	9.7–106.7 35.5	216	12–6013 1954	6–3047 651	4.3–16.3 8.9
2	7.5–17.4 11.4	26.6–29.4 28.2	19.0–22.7 21.4	13.5	5.0–7.0 6.3	0.01–0.40 0.20	0.02–0.08 0.05	0.50–1.65 0.83	0.17–0.35 0.28	6.5–16.0 9.0	12.2–149.2 61.0	465	69–3936 1872	62–14829 2605	1.9–18.8 10.8
3	6.2–18.9 11.7	12.9–29.4 24.6	11.7–22.7 19.1	11.8	5.8–10.0 7.4	0.01–0.38 0.13	0.02–0.12 0.05	0.50–2.25 1.07	0.11–0.37 0.24	4.3–12.0 8.0	6.6–113.4 31.4	342	31–4968 1216	26–6015 951	0.4–315.2 59.8
4	6.6–16.5 11.2	11.7–29.2 25.3	11.8–22.8 19.6	12.3	6.4–9.4 7.2	0.01–0.35 0.14	0.02–0.14 0.05	0.50–2.28 0.99	0.11–0.46 0.25	3.5–12.0 8.8	8.5–183.2 48.9	455	4–5459 1511	2–12055 2242	1.5–192.9 34.9
5	6.0–18.5 10.8	10.2–29.6 22.2	6.4–23.2 16.7	7.7	5.0–10.0 7.0	0.01–0.39 0.14	0.01–0.10 0.05	0.50–2.75 1.05	0.16–1.33 0.42	1.3–8.0 4.6	<1.0–460.4 54.7	374	8–17916 3159	1–27218 5203	0.8–157.3 19.1
6	5.5–18.8 10.9	13.9–28.9 22.6	9.2–22.6 17.4	8.2	5.2–10.0 7.1	0.01–0.37 0.13	0.01–0.14 0.04	0.41–2.80 0.94	0.15–0.94 0.39	2.3–8.5 5.7	<1.0–479.3 46.2	292	24–13315 2506	6–17538 3863	1.2–319.8 22.1
7	5.7–17.0 11.0	7.8–29.4 21.1	5.0–22.8 16.1	6.8	4.5–8.6 6.9	0.01–0.30 0.13	0.02–0.17 0.05	0.50–3.20 1.05	0.21–1.54 0.55	0.3–10.5 3.1	4.3–209.2 46.5	338	28–10878 2124	35–32512 3109	1.8–116.4 20.4
8	5.6–18.7 11.1	9.1–28.1 23.0	6.0–21.9 17.4	8.6	6.4–8.0 7.2	0.01–0.35 0.12	0.01–0.14 0.05	0.50–2.25 1.00	0.13–0.73 0.37	0.3–13.0 5.2	2.0–270.2 51.5	349	12–11035 2026	2–21414 2751	1.7–316.6 42.2
9	6.2–14.8 10.7	20.5–27.1 24.1	15.2–21.0 18.2	4.0	5.9–8.2 7.1	0.02–0.32 0.12	0.02–0.18 0.08	0.50–1.65 0.92	0.21–2.90 0.79	1.0–5.0 2.3	9.7–105.5 40.7	297	46–8634 3079	28–34637 5103	7.2–42.8 17.5
10	6.3–15.7 11.3	19.2–27.2 24.1	14.0–21.4 18.3	7.0	6.4–9.0 7.5	0.03–0.37 0.12	0.01–0.16 0.07	0.50–1.50 0.81	0.14–1.15 0.48	2.5–7.0 4.5	14.5–202.9 56.0	401	75–9210 3226	13–32494 5035	2.7–122.6 30.5
11	5.1–18.0 11.2	11.1–28.3 20.4	8.1–22.3 15.4	5.6	5.7–8.1 6.8	0.01–0.30 0.13	0.01–0.07 0.05	0.50–2.80 1.23	0.21–1.96 0.73	0.5–6.5 2.8	3.9–424.7 43.1	149	20–6855 1374	3–26892 1785	3.2–298.1 46.7
12	5.9–15.8 11.1	10.9–28.4 22.0	7.6–22.1 16.4	8.0	6.2–8.7 7.0	0.01–0.30 0.13	0.01–0.07 0.05	0.50–3.40 1.23	0.18–1.31 0.42	0.8–7.0 3.2	3.1–254.3 50.6	262	8–10279 1817	6–18522 2498	1.5–232.8 35.0
13	6.8–15.0 10.2	24.8–29.0 27.6	18.8–22.8 21.2	6.0	4.5–7.4 6.4	0.04–0.34 0.19	0.04–0.10 0.07	0.50–2.00 1.09	0.17–0.38 0.26	4.0–11.0 6.9	8.0–156.4 65.3	511	14–4121 1558	34–11444 2550	2.9–70.6 16.8
14	6.9–15.8 10.3	16.2–29.1 26.4	11.9–22.9 20.5	7.7	4.6–7.8 6.5	0.01–0.37 0.22	0.02–0.13 0.06	0.50–1.75 1.01	0.17–0.53 0.28	2.5–11.5 7.6	4.2–136.4 42.7	377	4–4950 1334	6–16812 2314	2.0–74.1 21.8
15	6.4–19.2 10.6	19.5–29.6 25.7	13.2–23.8 19.5	8.0	4.7–7.8 6.8	0.01–0.38 0.20	0.02–0.13 0.06	0.50–1.92 0.98	0.16–0.36 0.24	2.5–9.0 6.7	8.0–156.4 40.9	397	12–4205 1717	12–17595 2654	2.9–70.6 28.7
16	7.0–14.3 9.4	28.0–30.5 29.5	21.3–23.8 22.8	un- stable	4.5–7.3 5.7	0.16–0.40 0.29	0.05–0.19 0.08	0.50–2.10 1.11	0.17–0.43 0.26	3.8–9.5 7.2	4.5–93.6 28.5	289	8–4213 1385	4–4771 1605	4.0–31.0 12.8

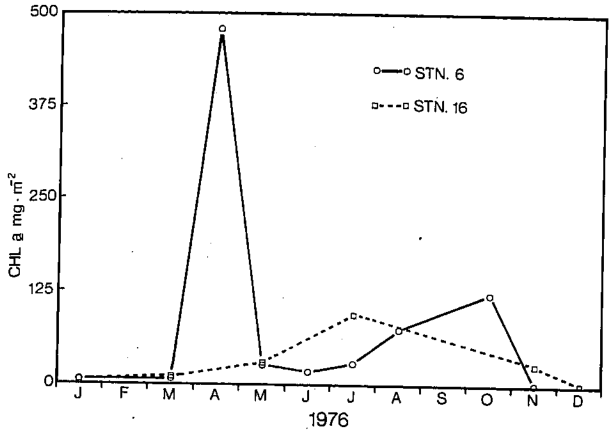


FIG. 2. Seasonal variation in chlorophyll *a* in the surface layer (0–20 m) at Station 6 in boundary waters of Howe Sound and Station 16 in the turbulent Haro Strait.

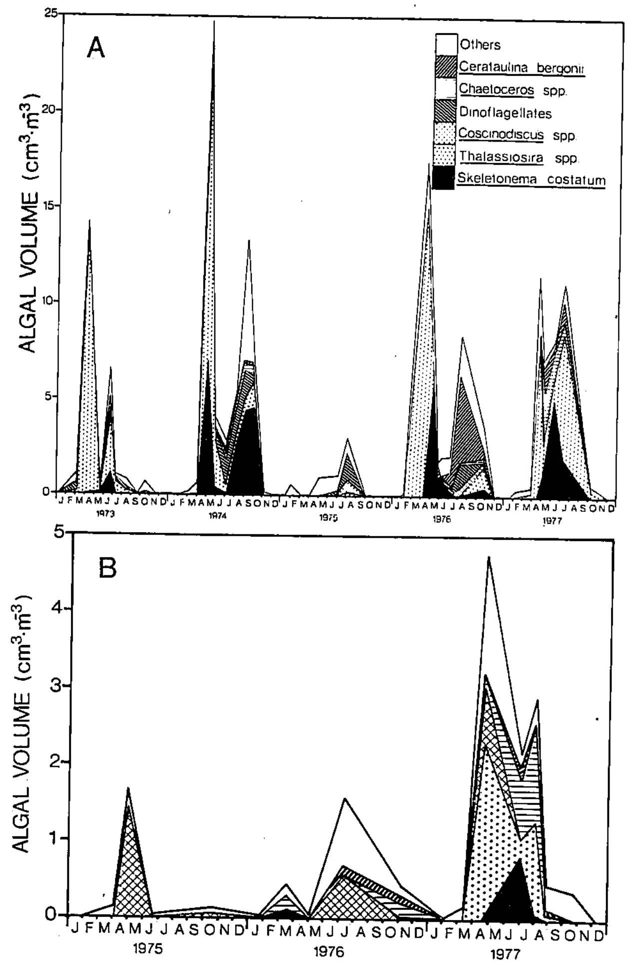


FIG. 3. A, Five-year seasonal succession of phytoplankton in the strait at Station 6 in the boundary waters of Howe Sound; B, Three-year seasonal succession of phytoplankton at Station 16 in the turbulent Haro Strait. Species shown at both stations are those contributing to >5% of the total phytoplankton volume.

Discussion

The oceanography of the Strait of Georgia is to a large extent dominated by the inflow of the Fraser River, which imparts turbidity to the surface layer and markedly affects surface layer stability and salinity. Past physical studies have demonstrated the general northward movement of the water mass from off the Fraser delta, which influences the surface layer of the north mainland coast and sets up a counterclockwise gyre in the western portion of the southern strait (Waldichuk 1957). This generalized physical transport system strongly influences the distribution and production of phytoplankton.

The impact of the Fraser River discharge on phytoplankton growth in the southern strait is illustrated in Fig. 6, where mean 1976 values of light, chlorophyll *a*, production, and P:B (photosynthesis/chlorophyll) ratios at stations along a transect from the south Fraser mouth to inside Porlier Pass are plotted. Light attenuation is one of the major factors influencing primary production from June to September in surface waters of the strait affected by the Fraser River discharge, as can be seen by the linear decline of the extinction coefficient (k), from the turbid delta front to the arbitrary limits of the plume, and its inverse relation to phytoplankton production and biomass (Fig. 6). At Station 10, which was usually sampled at the boundary of the Fraser Plume, using stepwise multiple linear regression it was clear that throughout the growing season NO_3, light (k), and zooplankton grazing were the factors, listed in descending order of importance, limiting the production of organic carbon ($R = .90$ df 4 and 13, $F = 29.73, P < 0.05$).

The primary factors limiting production in areas of the Strait of Georgia not markedly affected by the Fraser River (Station 3) are in descending order of importance: grazing, NO_3, and light ($R = .88$, df 4 and 8, $F = 15.36$, $P \leq 0.05$). Earlier work by Strickland (1958), Antia et al. (1963), and Parsons et al. (1969a) has demonstrated nitrogen limitation in June and early July in the strait, and concluded that because of its relatively slow regeneration rate, it is the limiting nutrient in most situations. Silicate levels are low in June and July following the vernal diatom increases, but never as low as values reported by Paasche (1973) to be limiting to marine diatoms.

Though zooplankters were not studied in any detail, seasonal trends in biomass were apparent at most stations, showing a phase lag with phytoplankton peaks of about a month, and our statistical evaluation of the factors influencing primary production consistently underscored the significance of grazing on the accumulation of organic matter (chlorophyll *a*) in the strait. Gardner's (1977) recent studies have shown a

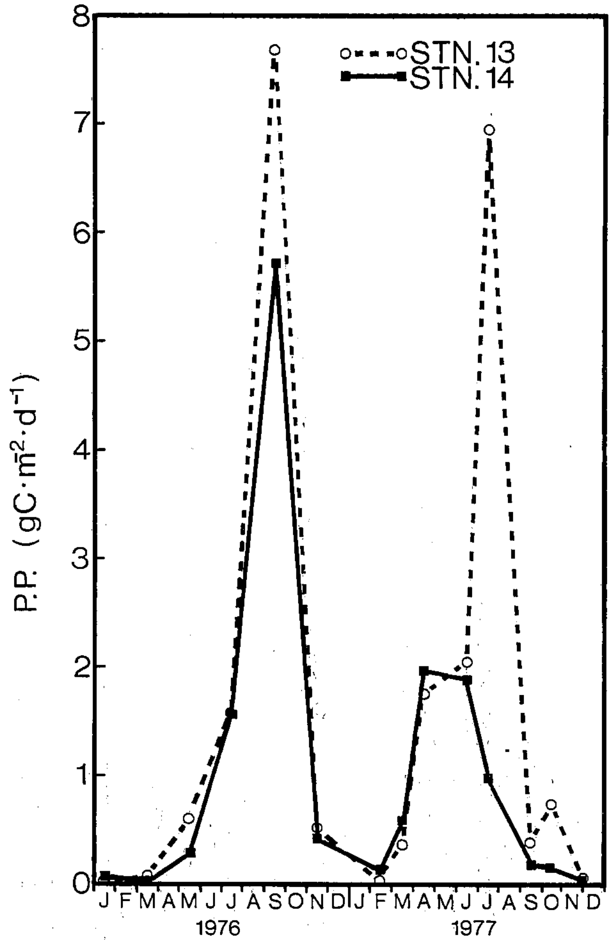


FIG. 4. Seasonal changes in primary production at Station 13 located in the sheltered waters of Trincomali Channel inside Porlier Pass and at Station 14 in the open strait outside Porlier Pass in 1976 and 1977.

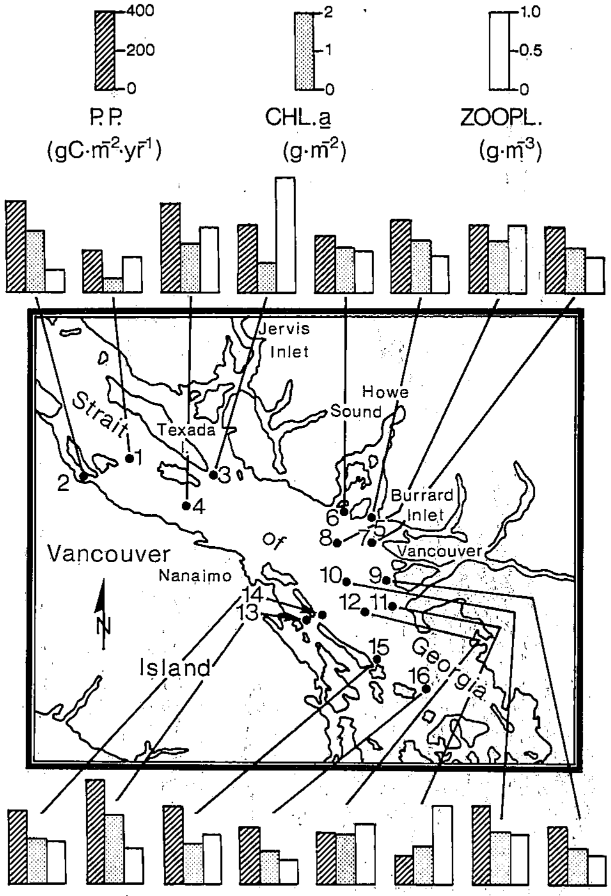


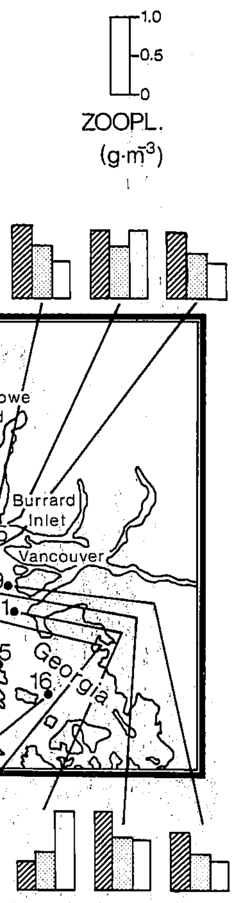
FIG. 5. Mean annual integrals of phytoplankton production, chlorophyll *a*, and zooplankton biomass by station in the Strait of Georgia.

significant relation between late summer hydrographic conditions (temperature and mixed-layer stability) and overwintering zooplankton populations. Conditions in the Strait of Georgia in the fall and winter of 1974 led to a large overwintering population that prevented any significant development of the vernal phytoplankton bloom in 1975 in some regions of the strait as typified by observations from Station 6 (Fig. 7).

The predominant northward movement of the Fraser River plume has increased production in boundary waters of Howe Sound, a region of the strait whose waters are not strongly influenced by Fraser River turbidity, yet receive by advection phytoplankton from the productive boundary waters and benefit from nutrient "recharge" supplied by periodic episodes of deep mixing in summer months (Stockner et al. 1977) (Fig. 8). In regions less affected by the Fraser River discharge, notably the mid- and north-western regions of the strait, annual production is lower, ranging from 200 to 300 g C·m^{-2}. The incoming colder and more saline oceanic water, which creates vertical instability at turbulent passages, reduces phytoplankton production in many regions of the American San Juan Islands and lower Gulf Islands (Phifer 1933; Phifer and Thompson 1937), and to the north in Johnstone Strait (Stockner and Cliff 1976a) (Fig. 8).

Our mean annual estimates of production for the Strait of Georgia are very similar to recent estimates by Winter et al. (1975) of 465 g C·m^{-2}·yr^{-1} for the central basin of Puget Sound in Washington State, and to estimates by Malone (1976) and Mandelli et al. (1970) of 370 and 420 g C·m^{-2} for the apex of the New York Bight, and by Riley (1956) (380 g C·m^{-2}) for Long Island Sound, but substantially higher than open ocean estimates (Ryther and Yentsch 1958; Taniguchi 1972), ranging from 80 to 160 g C·m^{-2}.

Parsons et al. (1970), from values obtained from shipboard incubation of five depths (0, 5, 10, 20,



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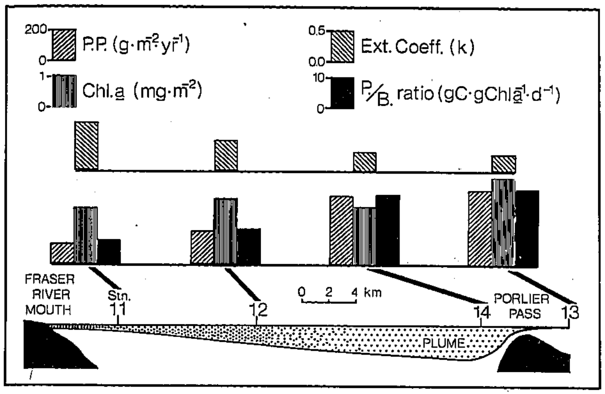

FIG. 6. Schematic illustration of the impact of the Fraser discharge on light attenuation and primary production in the Straight of Georgia. Histograms are mean 1976 values from stations on an east–west transect from river mouth to inside Porlier Pass.

and 30 m) at eight stations, estimated annual production for the Strait of Georgia to average 120 g C·m⁻² in 1965 and 1966, which is much lower than our average of 345 g C·m⁻² obtained in situ at nine depths from 16 stations. By recalculating our monthly integral production values using the five depths reported by Parsons et al. (1970), we could account for an average loss of from 5 to 30% depending on the month of observation (small error in winter, high in summer). Therefore methodological differences alone cannot account for the observed differences in annual production between 1966 and 1976–77. Using chlorophyll *a* values obtained by Stephens (1968) from his station 7, which corresponds to our Station 10, we integrated values from 1, 3, and 5 m depths for the years 1965 and 1977 and found mean amounts of chlorophyll in 1977 to be 1.6× those reported from 1965, 2.2 and 3.5 mg·m⁻³, respectively. This comparison, despite the uncertainties attributable to yearly variation, supports the hypothesis

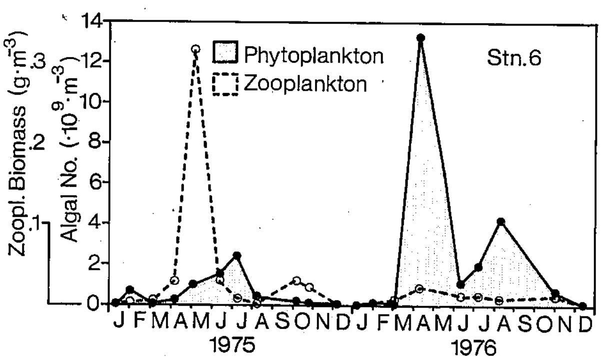

FIG. 7. Seasonal changes in the abundance of phytoplankton and zooplankton at Station 6 in the boundary waters of Howe Sound in 1975 and 1976.

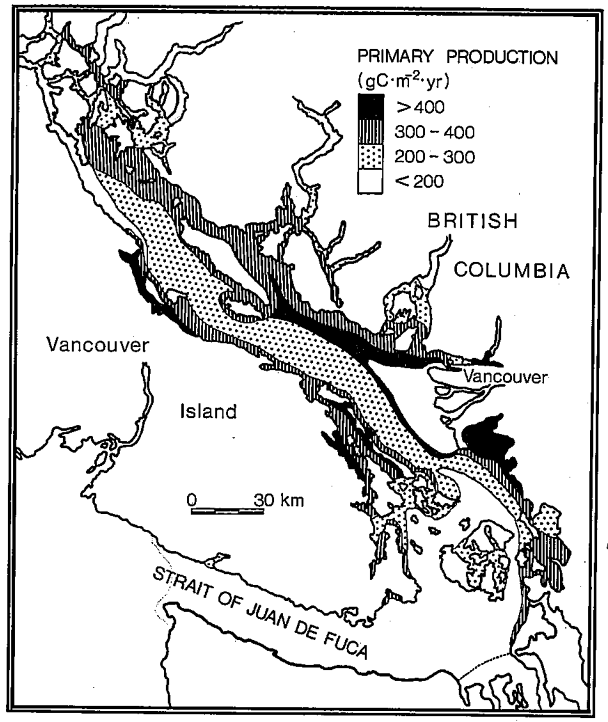

FIG. 8. Generalized spatial pattern of annual phytoplankton production in the Strait of Georgia. Data used in preparation of figure represent 5 yr of plankton studies by J. G. S. (Stockner and Cliff 1975, 1976a, 1976b; Stockner et al. 1977) and data presented by Waldichuk (1957), Waldichuk et al. (1968), Stephens (1968), Barraclough and Fulton (1967), Stephens et al. (1969), and Parsons et al. (1970).

that primary production in the strait has increased over the past 10 yr. We feel that these increases are due in part to eutrophication.

Based on per capita contributions, a minimal estimate of the nitrogen (N) and phosphorus (P) loading to the Strait of Georgia in 1976 from the metropolitan area of Vancouver and the Fraser River drainage basin was ~15 000 t of N and 3500 of P (Table 2). The loading has increased markedly over the past two decades, owing to the rapid population growth in the lower mainland of British Columbia. Perhaps even more significant is the fact that the nutrient discharge points to the strait have changed markedly since 1974. In the 1950s and 1960s most nutrients derived from sewage from metropolitan Vancouver were discharged to the Burrard Inlet system (Vancouver Harbor and English Bay), but by 1974 almost all had been diverted to the Fraser River (S. Vernon, Greater Vancouver Regional District, personal communication). This has likely improved conditions in Vancouver Harbor (Stockner and Cliff 1979), and increased production in back eddies and plume boundaries of the Fraser River

TABLE 2. Nitrogen and phosphorus loadings to the Strait of Georgia by decade from 1951 to 1977.[a]

Year	Population[d]	Industrial[e] N*	Industrial[e] P	Storm sewer[e] N	Storm sewer[e] P	Domestic[e] N	Domestic[e] P	Total[b] N	Total[b] P	Loading[c] $g \cdot m^{-2} \cdot yr^{-1}$ N	Loading[c] $g \cdot m^{-2} \cdot yr^{-1}$ P
1951	649 200	753	280	202	64	4 300	876	6 832	1 586	0.99	0.23
1961	907 600	1 052	392	283	89	6 012	1 226	9 036	2 099	1.33	0.30
1971	1 156 505	1 340	500	361	114	7 658	1 562	12 167	2 829	1.76	0.41
1977	1 515 000	1 680	627	453	143	9 603	1 960	15 257	3 549	2.21	0.51

[a]All values in metric tons per year unless otherwise indicated.
[b]Estimates of N and P loading to entire strait increased 23% to account for loadings from other major river systems discharging to the strait (Waldichuk 1957).
[c]Surface area: 6900 km² (Waldichuk 1957).
[d]Statistics Canada census figures.
[e]Values from Dr K. Hall, Westwater Research Center, U.B.C., Vancouver, B.C.

(Fig. 8). Evidence to suggest that this has in fact occurred is provided by a comparison of the 1967 annual production value published by Takahashi et al. (1973) from their plume station with our 1977 value from Station 9 located at approximately the same position in the plume. Weather records indicate that 1967 and 1977 were similar years, yet mean primary production has increased by about a factor of 4, from 72 to 280 g $C \cdot m^{-2} \cdot yr^{-1}$, while conservative estimates of nitrate loadings have increased by ~30–40% since 1967 (Table 2).

Tully and Dodimead (1957) and Parsons et al. (1970), from studies in the 1950s and 1960s, suggested that nutrients in the surface layer of the Fraser River plume come largely from entrainment of nutrient-rich sea water, while our data suggest that nutrients necessary to support the magnitude of phytoplankton growth *now* seen in back eddies and plume boundaries may largely be derived from nitrate and ammonia from the Fraser River and adjoining tidal lands, and secondarily from sea water by physical processes. Nitrate is the limiting nutrient in the strait (Antia et al. 1963), and is rapidly incorporated into phytoplankton biomass and thus is not reflected in a concentration increase. Mean values of $NO_3(N)$ and $NH_3(N)$ in Fraser River water at Tilbury Island, several kilometres above the delta front, in 1976 were 154 and 43 $\mu g \cdot L^{-1}$ (11 and 3 μg-atoms$\cdot L^{-1}$), respectively (K. J. Hall unpublished data). Earlier values from the 1960s are sparse, but the average nitrate concentration was considerably less, ~72 $\mu g \cdot L^{-1}$ (ammonia was not measured) (Benedict et al. 1973). Clearly, the concentration of nutrients in the Fraser River has increased, and accordingly the rate of primary production in areas influenced by it. It is important to note that these comparisons pertain *only* to dissolved inorganic nitrogen and recent evidence points to the importance of dissolved organic nitrogen (DON) in regulating phytoplankton productivity and succession in the sea (Butler et al. 1979).

Takahashi et al. (1973) reported nitrate limitation of phytoplankton growth during summer 1967 at their plume station; values from 1975 to 1977 from Stations 7, 9, and 11 in the plume in summer also reached undetectable levels, but our production estimates in back eddies off the delta front in August often were in excess of 4 $g\,C \cdot m^{-2} \cdot d^{-1}$, and this production occurred over the depth integral 0–4 m. The highest daily value recorded by Parsons et al. (1969b) from 0 to 30-m profile was 2.3 $g\,C \cdot m^{-2}$ in April 1967 at their Fraser River plume station.

The impact of the Fraser River water on phytoplankton production in the Strait of Georgia is very similar both in process and impact to that described for the New York Harbor (Mandelli et al. 1970; Ryther and Dunstan 1971) and apex of the Bight (Segar and Berberian 1976; Malone 1976), where ammonia and nitrate from land drainage and domestic sources in the low salinity surface outflow were directly related to the eutrophication of this large coastal marine environment.

The present levels of production in the Strait of Georgia can only be viewed as a positive benefit to the fisheries, where there are large resident populations of coho and chinook salmon and herring, and where millions of transitory juvenile salmonids feed on their way to the northwest Pacific Ocean (Argue 1976). Future enhancement of salmonid stocks by hatcheries and other enhancement techniques in British Columbia's lower mainland could conceivably tax the carrying capacity of the Strait of Georgia unless future consideration is given to studies of factors limiting production of pelagic communities in the coastal marine environment of the northwest Pacific ocean.

Acknowledgments

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99	1.33	0.30
29	1.76	0.41
49	2.21	0.51

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