

Importance of wind and river discharge in influencing nutrient dynamics and phytoplankton production in summer in the central Strait of Georgia

Yin, K.D.; Goldblatt, R.H.; Harrison, P.J.; St. John, Michael; Clifford, P.J.; Beamish, R.J.

Published in:
Marine Ecology - Progress Series

Link to article, DOI:
[10.3354/meps161173](https://doi.org/10.3354/meps161173)

Publication date:
1997

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Yin, K. D., Goldblatt, R. H., Harrison, P. J., St. John, M., Clifford, P. J., & Beamish, R. J. (1997). Importance of wind and river discharge in influencing nutrient dynamics and phytoplankton production in summer in the central Strait of Georgia. *Marine Ecology - Progress Series*, 161, 173-183. DOI: 10.3354/meps161173

DTU Library

Technical Information Center of Denmark

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Importance of wind and river discharge in influencing nutrient dynamics and phytoplankton production in summer in the central Strait of Georgia

Kedong Yin^{1,*}, Robert H. Goldblatt¹, Paul J. Harrison¹, Michael A. St. John², Peter J. Clifford¹, Richard J. Beamish³

¹Oceanography Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

²Danish Institute for Fisheries and Marine Research, DK-2920 Charlottenlund, Denmark

³Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, British Columbia, Canada V9R 5K6

ABSTRACT: A cruise was conducted during August 6–14, 1991 to investigate the dynamics of nutrients and phytoplankton production in the central Strait of Georgia, British Columbia, Canada, during a period when strong stratification resulted in nitrogen-limited primary productivity. High resolution vertical profiles of salinity, temperature, fluorescence and nutrients (nitrate and phosphate) were taken daily along a transect. A wind event occurred on August 7 and a rapid increase in the Fraser River discharge took place from August 8 to 14. The wind event mixed the water column and nutrients increased at the same time. Phytoplankton responded to the increase in nutrients and a bloom occurred soon after the wind event. The rapid increase in river discharge caused the entrainment of nitrate in the estuarine plume and, as a result, a subsurface maximum of chl *a* was developed. Our results clearly demonstrated that summer phytoplankton productivity in the central Strait of Georgia is fueled by a supply of nutrients from the nitracline through vertical mixing induced by the interaction of winds, river discharge and tidal cycles. Of these 3 factors, winds are the most variable and therefore a summer with frequent wind events could result in higher than normal productivity. The mechanism for this is that part of the nitracline was maintained above the euphotic zone due to various physical processes in spite of the strong stratification, and therefore, nutrients were frequently available for phytoplankton uptake caused by across-pycnocline mixing due to wind, river discharge and tides.

KEY WORDS: Nutrients · Nitracline · Primary productivity · Vertical mixing · Entrainment · Wind · River discharge · Fraser River · Strait of Georgia

INTRODUCTION

After depletion of nutrients in the photic zone, the supply of nutrients across the pycnocline and the regeneration of nutrients control the dynamics of nutrients and hence primary productivity (Mann & Lazier 1991). The period of nutrient depletion in most temperate estuaries is usually in summer since river discharge

is low after its maximum in spring. The driving forces for vertical mixing in the water column of estuaries are tidal cycles, winds and river discharge. Due to the variable nature of these forces, nutrients and primary productivity in estuaries are highly variable as well (Boyn-ton et al. 1982). The effects of these driving forces are often episodic. It is a series of these episodes that supply nutrients and enhance primary productivity in the water column in summer. Tidal cycles are well known for this effect (Bowman et al. 1986). Effects of winds are commonly reported, for example, in San Francisco

*E-mail: kedong@unixg.ubc.ca

Bay estuary (Cloern 1996), Chesapeake Bay estuary (Horrigan et al. 1990), and in coastal oceans such as the one off the coast of Washington, USA (Dortch & Postel 1989) and Dogger Bank in the North Sea (Riegman et al. 1990). Blooms often occur in summer after wind events (Iverson et al. 1974, Hitchcock et al. 1987, Pitkanen et al. 1993).

The physical processes in the Strait of Georgia (British Columbia, Canada) are subject to the Fraser River discharge, winds and tidal cycles (LeBlond 1983). The Fraser River discharge starts to increase in March, reaches a maximum (up to $10\,000\text{ m}^3\text{ s}^{-1}$) in June, gradually decreases in July, August and September, and then remains near the minimum levels (as low as $700\text{ m}^3\text{ s}^{-1}$) throughout the rest of the year. The daily freshwater outflow in the Fraser River is tidally modulated, being dammed during tidal floods and released during tidal ebbs. When the Fraser River outflow is released during ebb tides, it forms the riverine plume in the Strait. The riverine plume is mixed with saltier water by winds and entrainment, and the mixture becomes the estuarine plume. The estuarine plume extends over most of the central and southern region of the Strait (Waldichuk 1957).

The euphotic zone in the central Strait of Georgia has been long thought to be low in nutrients, biomass and productivity in late spring and summer (Parsons et al. 1970, Stockner et al. 1979, Harrison et al. 1983). In contrast to many other temperate estuaries, during this period the Fraser River carries low concentrations of inorganic nitrogen, which is the most limiting nutrient

in the Strait of Georgia for primary production. A recent study revealed that tidal mixing increased nutrients and primary productivity (Harrison et al. 1991). During the period of the maximum river discharge, an increase in river discharge was also found to increase nitrate in the estuarine plume and to enhance primary productivity (Yin et al. 1997). The previous study was focused on the direct entrainment of nutrients by the riverine plume at the river mouth (Yin et al. 1995a, b, c) and indicated that entrainment is another major mechanism for the increase in primary productivity. Model simulations for the central Strait of Georgia also showed the importance of wind and river discharge in supplying nitrate into the euphotic zone (St. John et al. 1993), but there are almost no data to verify the model, especially for the summer months.

The Strait of Georgia has high biological production comparable to other temperate nutrient-rich estuaries where freshwater input adds high concentrations (inorganic nitrogen up to $100\text{ }\mu\text{M}$) of nutrients. This has raised the question of how such high production occurs in the Strait of Georgia since the freshwater input from the Fraser River is low in nutrients ($<5\text{ }\mu\text{M}$ nitrate in summer). In order to answer this question, we focused on spatial and temporal variations in nutrients and primary productivity caused by summer winds and changes in river discharge in the Strait over short time scales in this study. By examining day-to-day variations in salinity, temperature, fluorescence and nutrients in the water column with high-resolution continuous vertical profiles of these variables, we were able to

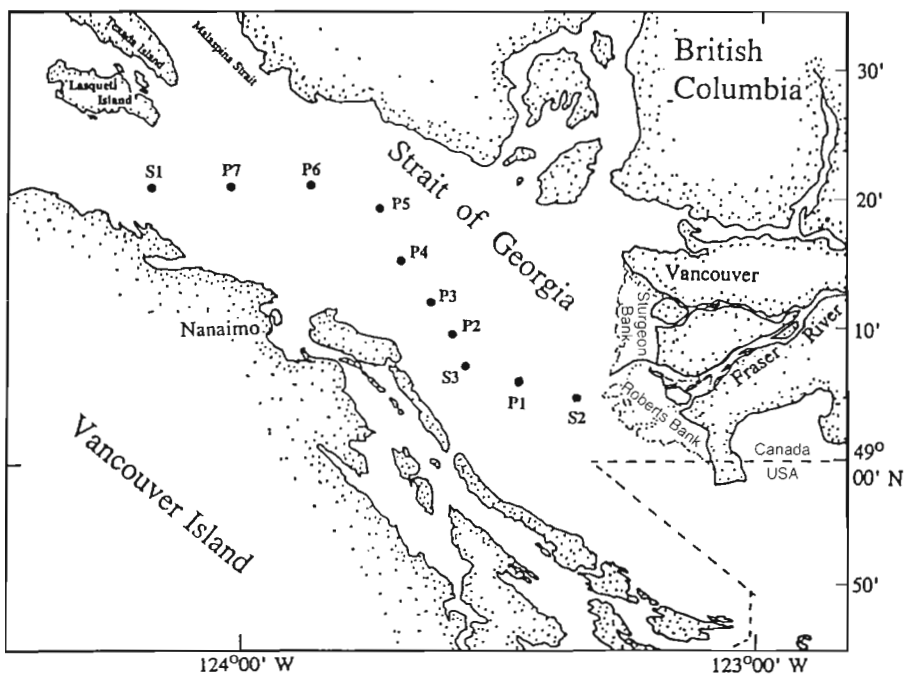


Fig. 1 Study area and stations in the central Strait of Georgia. The transect started at Stn S2 near the river mouth (8 km away) and ended at Stn S1 (108 km away), extending in a northwestward direction and covering most of the central Strait

demonstrate how these biological variables were coupled with physical variables. Finally, we show how the distribution of nutrients and phytoplankton biomass and productivity in the estuarine plume in the central Strait responded to a wind event, and to a fluctuation in river discharge in August; the latter factor has received little attention at this time of the year since river discharge in most temperate estuaries generally decreases in summer

MATERIALS AND METHODS

Station locations. The transect started at Stn S2 near the river mouth (8 km away) and continued to Stn S1 (108 km), extending in a northwest direction, and covered most of the central Strait (Fig. 1). These stations are mostly deeper than 150 m, except for Stns P4 and P5, which are shallower. Strictly speaking, there is no upper or lower estuary since the outflow of the Fraser River depends so much on winds (LeBlond 1983). In general, however, since the outflow moves northward due to the Coriolis effect, the direction from Stn S2 through Stns P1, S3, P2–P7 to Stn S1 is similar to the seaward direction in an estuary. Therefore, this northwestward outflow direction is referred to as seaward since there is also a southwestward outflow direction in the Strait when winds are from the north. The station numbers are consistent with the previous studies (Yin et al. 1995a, b, c, 1996). The sampling strategy was to investigate the distribution of nutrients associated with the movement of the estuarine plume.

Sampling and data processing. The cruise started on August 6 and ended on August 14, 1991. Either a station was occupied for 24 h, or a transect of a few stations was made within 10 h. At each station, a vertical profile (0 to 25 m) of temperature, salinity, *in vivo* fluorescence and selected nutrients (nitrate+nitrite, phosphate) was obtained. The vertical profiling system has been described in detail by Jones et al. (1991) and Yin et al. (1995a). Basically, a hose connected to a water pump on deck was attached to a CTD (conductivity/temperature/depth) probe or an S4 (InterOcean®), which has the dual function of a CTD probe and a current meter. Water was pumped into a fluorometer and an AutoAnalyzer® on board ship for *in vivo* chlorophyll *a* (chl *a*) fluorescence and nutrient measurements, respectively, while the CTD probe was lowered slowly into the water at 1 m min⁻¹. Each sampling produced a high-resolution continuous vertical profile of physical and biological parameters and thus the relationship between these parameters in the water column can be easily recognized. Data from a vertical profile were smoothed over 0.5 min intervals. This smoothing reduced the fluctuations caused by the ship's motion.

The Practical Salinity Scale was used in the text and figures for salinity measurements. Therefore, the salinity values have no units, but they are equivalent to ‰ (Pond & Pickard 1978).

Nutrient analysis. All nutrients were determined using a Technicon AutoAnalyzer II. Salinity effects on nutrient analyses were tested on board ship and were found to be small. Therefore, no correction was made for salinity effects.

Nitrate (plus nitrite) and phosphate were determined following the procedures of Wood et al. (1967) and Hager et al. (1968), respectively.

Primary production and chl *a*. The measurement of incident solar irradiance (photosynthetically active radiation, PAR) and subsurface light intensities and the collection of water samples for ¹⁴C uptake experiments and nutrients were described by Harrison et al. (1991). The ¹⁴C uptake experiments and the calculation of primary production as well as chl *a* measurement were described in the same paper. Briefly, water samples for ¹⁴C uptake experiments and chl *a* were taken from depths based on light penetration (usually 100, 55, 30, 10, 3 and 1% of surface irradiance). The incubation period for ¹⁴C uptake was 4 h. The daily primary productivity in the water column was calculated based on the ratio of irradiance during the incubation to the daily total irradiance and integrated through the 6 sample depths. Chl *a* was analyzed on board ship and integrated through the same sample depths.

Data on tides, winds and river discharge. Observed hourly tidal heights at Point Atkinson for the Strait of Georgia were provided by the Tides and Current Section, Institute of Ocean Sciences, Sidney, BC, Canada. The discharge data for the Fraser River at Hope were obtained from the Water Survey of Canada. The wind data were recorded at the Sand Heads of the mouth of the Fraser River and provided by the Atmospheric Service, Environment Canada.

RESULTS

Between August 6 and 14, the Fraser River discharge increased rapidly from ca 4000 to 5000 m³ s⁻¹, forming a sub-peak in discharge after the annual maximum in June–July (Fig. 2). The tidal range indicates that there was a spring tide on August 8 and a neap tide on August 14 (Fig. 2). Winds were stronger during August 6–10 (except August 9) than during August 11–16 (Fig. 2). In particular, a wind event occurred on August 7. These changes in river discharge and winds exerted a marked influence on physical and biological processes during the period, which will be shown below in vertical profiles of salinity, fluorescence and nutrients (nitrate+nitrite, phosphate).

Effect of winds

Pre-wind event conditions

The tidal cycle during sampling times for the 24 h time series at Stn S3 during August 6–7 went through high water between T1 (time 1) (12:00 h) and T5 (24:00 h) and the ebb tide and lower low water thereafter (Fig. 3). The salinity contours show the well-developed stratification in the water column of the estuarine plume (Fig. 3A). Salinity at the surface was above 20 throughout the period (Fig. 3A). The surface mixed layer (defined as the layer in which the difference in salinity is <1) was lacking in the water column except for the shallow layer (4 m) at T8. The water column was stratified by an increase in salinity of 1 at roughly 1 to 2 m intervals down to 20 m. The effects of the tidal cycle on the structure of salinity were obvious from the contours of salinity >24 ; the contours of 27 and 28, in particular, moved up and down twice with the tidal cycle with some time lag. This deep water movement was apparent in the nitrate contours (Fig. 3B). Nitrate was undetectable at the surface layer during the time series and the nitracline was below 10 m (using $1 \mu\text{M}$ as the top of it) during T1–T4 and be-

low 7 m during T5–T8 (Fig. 3B). Nitrate concentrations at 20 m increased from $10 \mu\text{M}$ during T1–T3 to $>17 \mu\text{M}$ during T6–T8. In particular, at T7 at the end of the ebb tide, a parcel of water with high concentrations moved up to 11 m (using $11 \mu\text{M}$ as the tracer). Hourly wind speeds increased to 6 m s^{-1} during this sampling period of 00:00 to 10:00 h on August 7. The upward movement of this parcel of high nitrate water to shallower depths due to the tidal cycle would reduce the energy required for wind to mix nitrate into the upper layer.

Post-wind event conditions

After the wind event of August 7, the water column between Stns S3 and S7 along the transect was largely mixed on August 8 (Figs. 4 & 5). There were 2 fronts along the transect: one was the riverine front between Stns S2 and S3 and the second was the estuarine front between Stns P7 and S1 (Fig. 4). The estuarine plume was between the 2 fronts. Salinity at the surface increased to 25 in the estuarine plume and the halocline was weak (Fig. 4). At Stn S2 salinity was 20 at the surface due to the presence of the riverine plume near the river mouth and the salinity gradient was strong. In contrast, the water column was almost homogeneously mixed at Stn S1 beyond the estuarine front (Fig. 4). Although there was stratification in the estuarine plume, the water column had become one water mass as shown by the straight lines in the temperature-salinity (T-S) diagrams (Fig. 5).

Nitrate concentrations also responded to the change in the water column structure (Fig. 5). Nitrate in the surface layer was about $10 \mu\text{M}$ at Stn S3, decreased seaward at Stns P3 to P4 and became undetectable at Stns P5 to P7. Beyond the estuarine plume at Stn S1, nitrate increased to $15 \mu\text{M}$. Nitrate concentrations at 20 m were above $20 \mu\text{M}$ along the transect.

Chlorophyll fluorescence reflected the spatial and vertical distribution in nitrate concentration (Fig. 5). Fluorescence of the surface layer in the estuarine plume increased seaward from Stns S3 to P6. In fact, the pattern indicated that a bloom was developing in the estuarine plume on August 8.

The time series at Stn S1 showed that the stratification of the water column gradually increased with time because of a decrease in salinity at the surface (Fig. 6A). This indicated that the estuarine plume was moving across the station during the time series. Superimposed on the movement of the estuarine plume, the effects of the tidal cycle were visible on the contours, although the salinity contours did not appear to be in phase with the tidal curve. Nitrate concentrations at the surface decreased from $15 \mu\text{M}$ at T1 to $<3 \mu\text{M}$ at T4 and further to $<1 \mu\text{M}$ during T8–T12, but

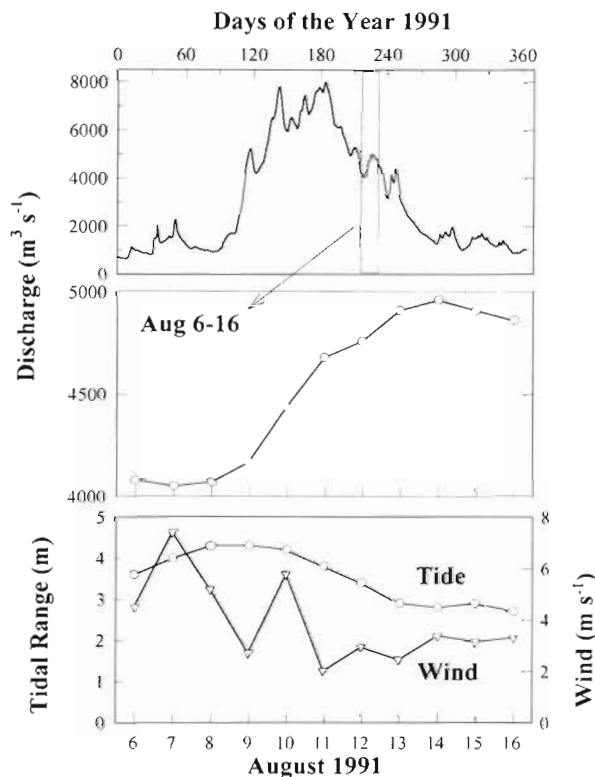


Fig. 2. Daily averaged river discharge, wind speed, and tidal ranges during August 6–16. Annual river discharge for 1991 at Hope is included

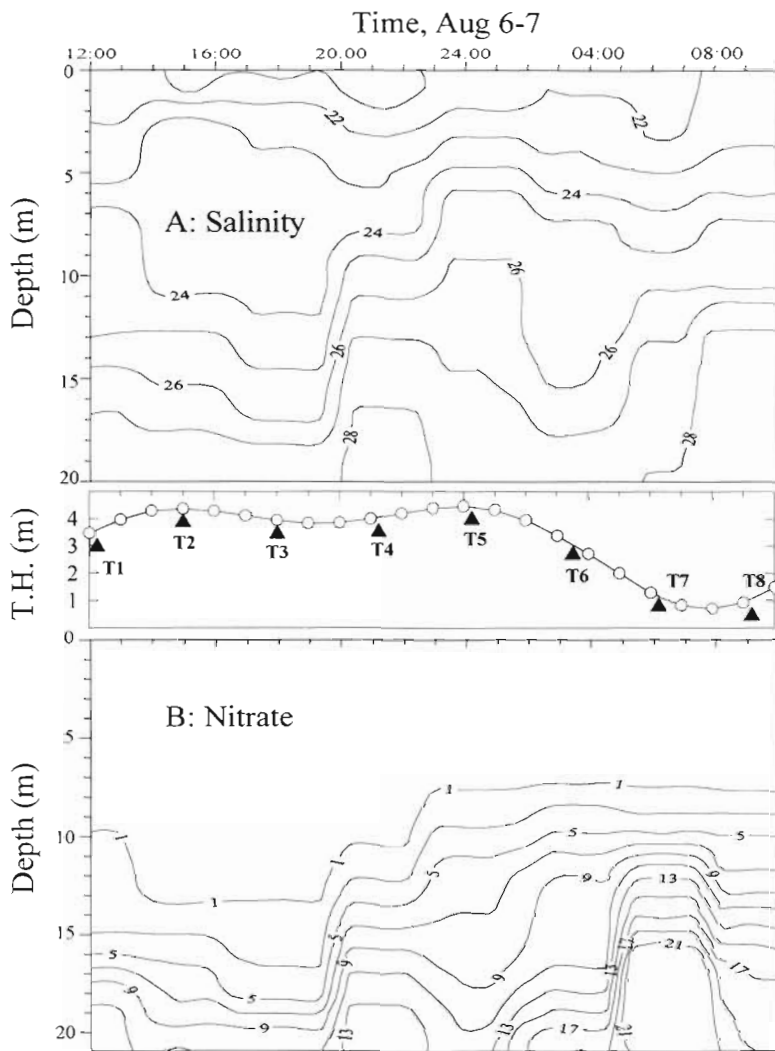


Fig. 3. Time-depth contours of (A) salinity and (B) nitrate at Stn S3. The middle panel is the tidal height (T.H.) during the same period, i.e. when vertical profiles were taken. Arrows indicate sampling times (T)

nitrate at 20 m remained above 20 μM throughout most of the time course. The depletion of nitrate during T8–T12 was limited to the top 4 to 7 m (Fig. 6B). This depletion was due to the advection of the estuarine plume from Stn P7. As a result, the high nitrate water present at the beginning of the time series was pushed away. The movement of the estuarine plume was further driven towards Stn S1 as river discharge increased during August 9–14.

Effect of river discharge

On August 10, the stratification of the water column appeared to recover from the wind event. The riverine plume invaded Stn S3 as indicated by the sharp halo-

cline in the top 4 m (Fig. 7). There was a shallow surface mixed layer at Stns P5 and P6, which disappeared on August 11 (Fig. 7). On August 11, the halocline occupied almost the entire upper 20 m and consisted of a top and bottom segment which were separated at about 10 m. The gradient was much stronger in the top than in the bottom segment. During August 12–14, the riverine plume remained distinct at Stn S3. At Stns P3 to P6, salinity in the top segment decreased while the bottom segment increased its gradient (Fig. 7), indicating the effect of entrainment into the estuarine plume as the increased river outflow mixed with and pushed the estuarine plume.

The change in the water column structure affected nitrate concentrations and fluorescence in the water column. Nitrate in the top 5 m was undetectable along the transect on August 10 (Fig. 8). On August 11, nitrate concentrations increased in the top 5 m at Stns S3 and P6, while the nitracline occupied the entire water column, indicating the entrainment of nitrate. The entrainment of nitrate was also shown by an increase in nitrate between 5 and 10 m at Stns P5 and P6 on August 13. By August 14, nitrate was depleted in the top 7 m at Stns P5 and S1 and 10 m at Stn P6 (Fig. 8). Vertical profiles of phosphate showed a change similar to that for nitrate (Fig. 9). The increases in phosphate concentration corresponded to the

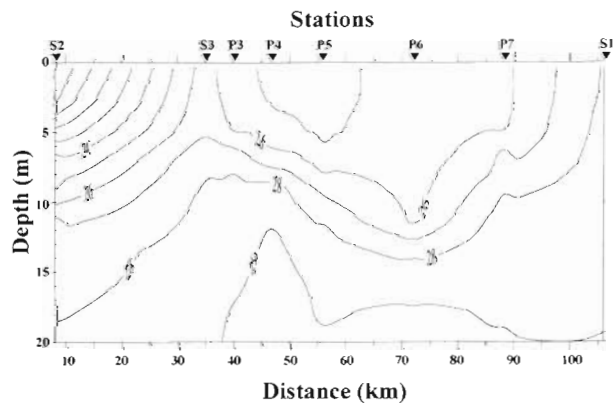


Fig. 4. Depth contour of salinity along the transect on August 8. Arrows indicate the positions of the stations where vertical profiles were taken

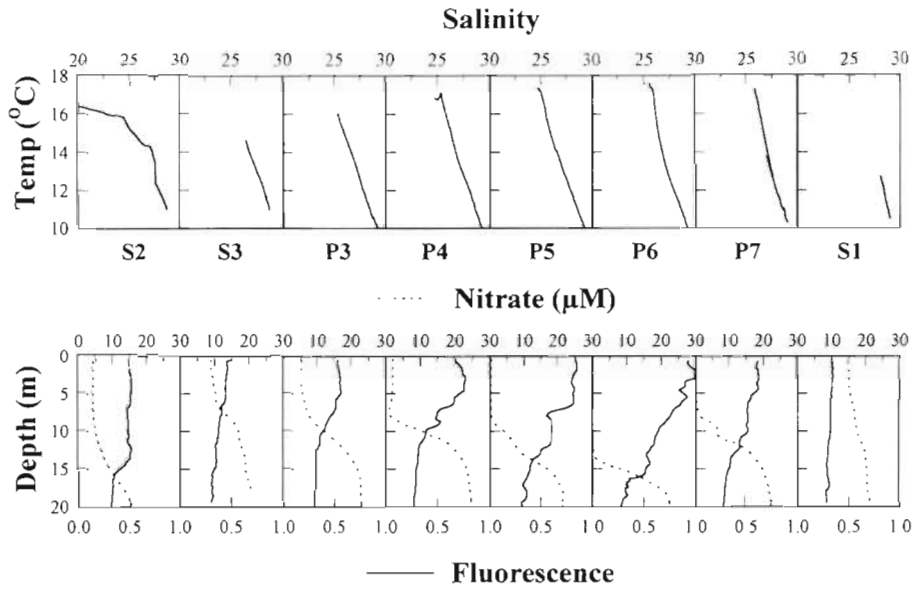
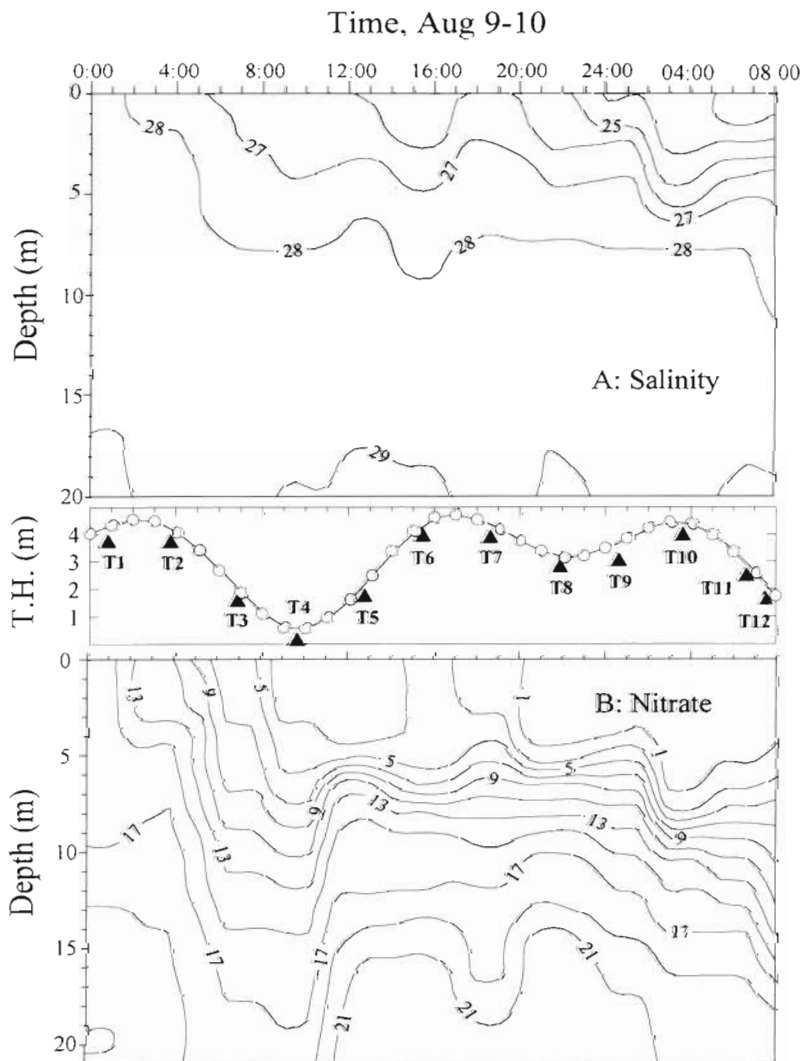


Fig. 5. Temperature-salinity (T-S) diagrams (top panel) and NO₃-fluorescence profiles (bottom panel) showing a wind-induced bloom on August 8, 1991 along the transect. Fluorescence given in relative units



increases in nitrate and were even more evident. This is believed to be due to the different physiological response by phytoplankton to nitrate and phosphate. An *in situ* microcosm experiment conducted during the same cruise showed that when exposed to both nutrients, nitrogen-limited phytoplankton tended to take up nitrogen before phosphorus (authors' unpubl. data). Thus, phosphate remained in the water column, because nitrogen is most likely limiting in the Strait of Georgia (Harrison et al. 1983). The same phenomenon was observed during the June cruise (Yin et al. 1997).

Vertical profiles of fluorescence along the transect showed that fluorescence was maximal at the surface on August 10, formed a maximum at 5 m on August 11 (at Stns P5 and S1) and 12, and formed the subsurface maximum at 10 m on August 13 (Fig. 8). By August 14, the maximum decreased at Stns P5 and S1 and was diminished at the other stations. The subsurface maximum was located just above the nitracline.

Fig. 6. Time-depth contours of (A) salinity and (B) nitrate at Stn S1. The middle panel is the tidal height (T.H.) during the same period, i.e. when vertical profiles were taken. Arrows indicate sampling times (T)

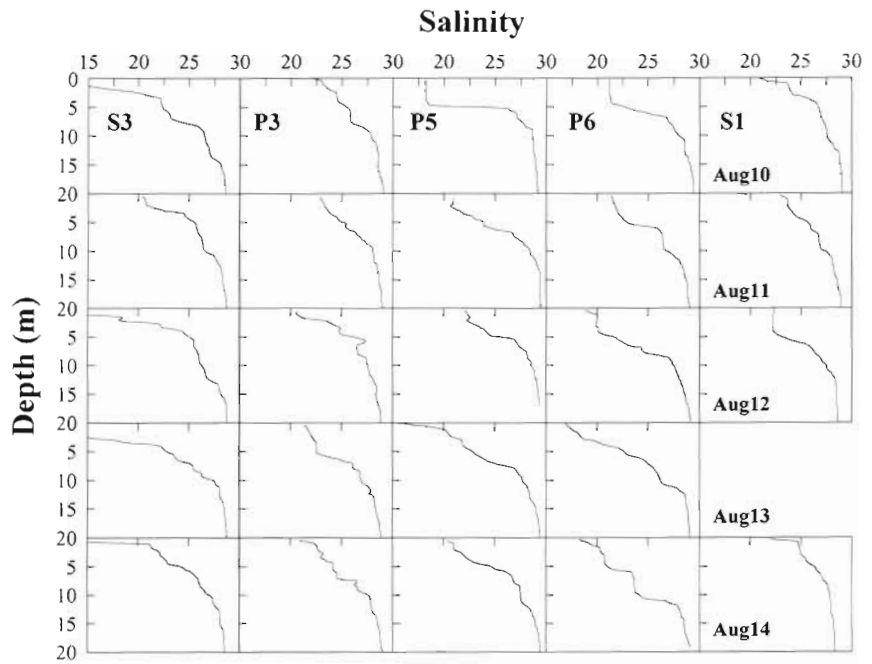


Fig. 7. Vertical profiles of salinity along the transect during August 10–14, 1991. No data were obtained on August 13 at Stn 1

Phytoplankton biomass and production

Chlorophyll *a* in the water column on August 8 increased seaward from 10 mg m⁻² at Stn S2 to 40 mg m⁻² at Stn P4, and it decreased seaward from 63.6 mg m⁻² at Stn S3 to 27.5 mg m⁻² at Stn S1 on August 10

(Fig. 10). Between Stns P3 and P7, chl *a* was high (>40 mg m⁻²) during August 11–13 and was reduced on August 14. The distribution of phytoplankton production was very similar to chl *a* and the daily productivity ranged from <300 to 2500 mg C m⁻² d⁻¹ during August 8–14.

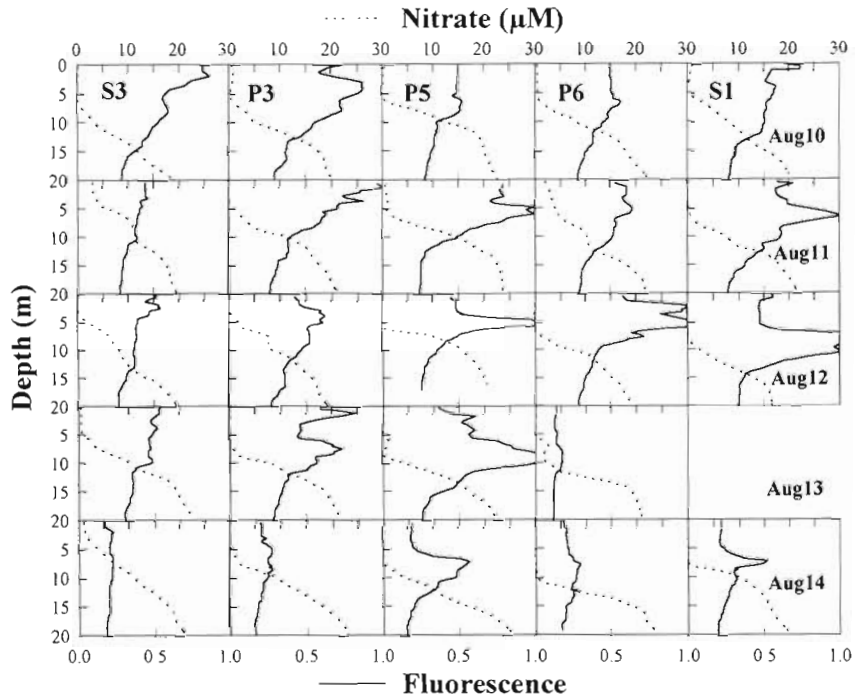


Fig. 8. Vertical profiles of nitrate and fluorescence along the transect during August 10–14, 1991. Fluorescence given in relative units. No data were obtained on August 13 at Stn 1

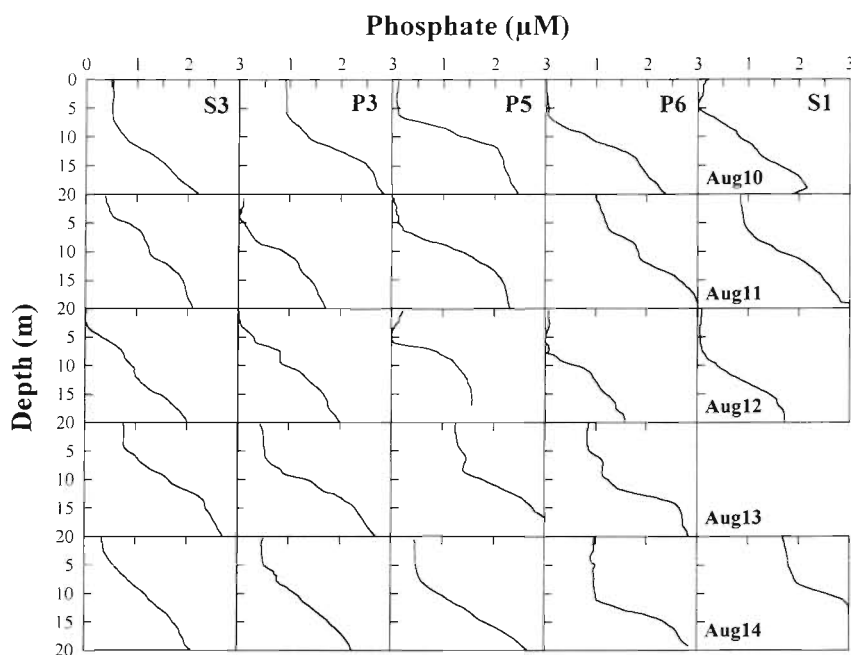


Fig. 9. Vertical profiles of phosphate along the transect during August 10–14, 1991
No data were obtained on August 13 at Stn 1

DISCUSSION

Our results show that the water column was well stratified and nitrate was depleted in the top 7 to 13 m in the estuarine plume (using Stn S3 to represent the conditions) on August 6. A wind event on August 7 mixed the water column, increased nitrate concentrations and caused a bloom in the estuarine plume. An increase in river discharge resulted in the continuation of the bloom in the estuarine plume during August 10–14. The tidal effects were superimposed on these processes. The mechanism for enhancing primary production was to increase concentrations of nitrate at a shallower water depth within the euphotic zone through vertical mixing or entrainment.

Part of the nitracline was positioned within the euphotic zone. This must have been due to frequent vertical mixing within the 20 m water column in the central Strait of Georgia based on the structure (shape and magnitude) of the halocline and the nitracline. The water column was stratified because there was a step-wise increase in salinity in the water column down to 20 m. The euphotic zone was usually 15 m deep at this time (Clifford et al. 1992), which is deeper than the major halocline. It is expected that the nitracline should have been below the euphotic zone if the stratification had been stable. However, the nitracline was rather shallow and the large sloping portion of it was within the lower part of the euphotic zone. This indi-

cates that nitrate was taken up in the nitracline within the euphotic zone, but the water column was not stable long enough for nitrate to be depleted due to limiting irradiances in the lower portion of the euphotic zone. Apparently, vertical mixing (relative to biological uptake) was fast enough to maintain the sloping nitracline in the bottom part of the euphotic zone. The main driving force for vertical mixing across the halocline must have come from horizontal movement of the estuarine plume. This is supported by vertical profiles of salinity. In the central Strait, the water column of the euphotic zone could be divided into an upper and a lower layer. The upper layer was not homogeneously mixed because of the tide-modulated river outflow and wind mixing. When freshwater was discharged, it would be mixed by winds from the surface and by tides from the

bottom as it moved away, and thus new freshwater was added to the water column before a mixed layer was formed. Such a process was shown as a feature of step-wise increases with depth in the vertical salinity structure in this study and a previous study (Yin et al. 1997). This upper layer was the main body of the estuarine plume and its lower boundary was the bottom of the major halocline. In contrast, the lower layer was relatively well mixed. In particular, the salinity at 20 m during this cruise was near 28 to 30, which was very close to the salinity in April at the same depth (Yin et al. 1996). Considering a large amount of freshwater input from the river discharge over 4 mo, the salinity should have been reduced at depth if there was only vertical mixing. Therefore, a balanced exchange between the central Strait of Georgia and Juan de Fuca Strait must have taken place in order to maintain the same salinity at depth. This indicates that the estuarine plume was advected at the surface out of the Strait of Georgia through these narrow and shallow channels and the seawater (high salinity) moved in at depth as a return flow (Waldichuk 1957, LeBlond 1983). The movement of the estuarine plume resulted in entrainment of deeper water. This entraining process was amplified when the estuarine plume front crossed Stn S1 (Fig. 11). The front was seen as a sharp color line due to the turbidity in the estuarine plume. As the color line passed the ship, the lower part of the sharp halocline between the surface and 5.5 m was

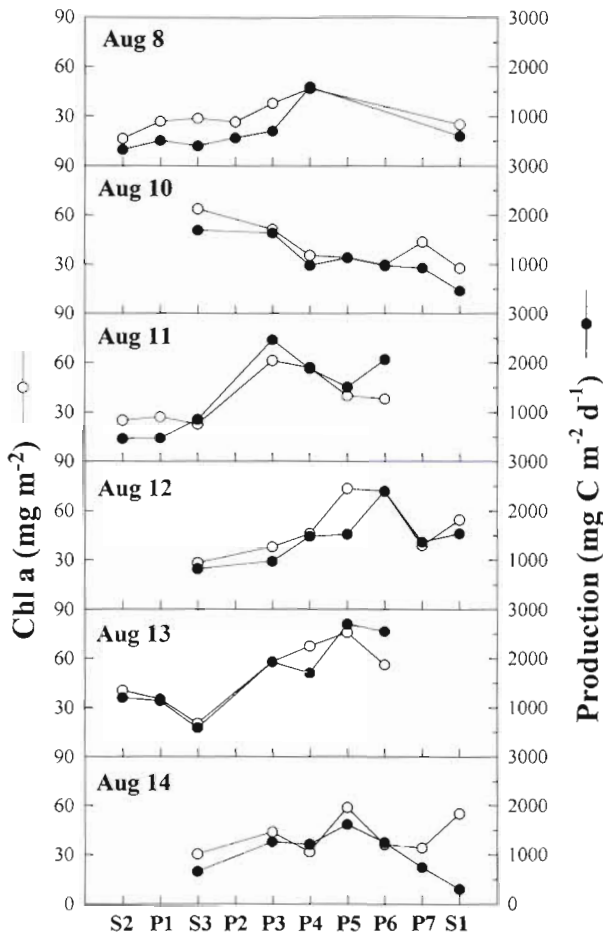


Fig. 10. Water column chl a and primary productivity along the transect during August 10–14, 1991

lifted as the salinity of the upper part decreased. This elevation was the result of entrainment. The internal waves may also cause turbulent eddies at the pycnocline, which are subject to vertical mixing by winds after they break down. The time scales of this horizontal movement process must be short enough to maintain the nitracline above the euphotic zone. Such a short residence time of the estuarine plume could result in a rapid renewal of the deep seawater underneath the estuarine plume. In fact, it is surprising that the deep sea water below the estuarine plume did belong to the same water mass. This was confirmed by the linearity of T-S diagrams for which the data points were taken either at 20 m at one station (Stns S3 and S1) over a time series, or from different stations along the transect during the same day (Table 1). This same water mass was consistent with the intermediate water mass described by Waldichuk (1957). Due to mixing in this same deep water mass, high nitrate concentrations were maintained in the deep seawater. These high

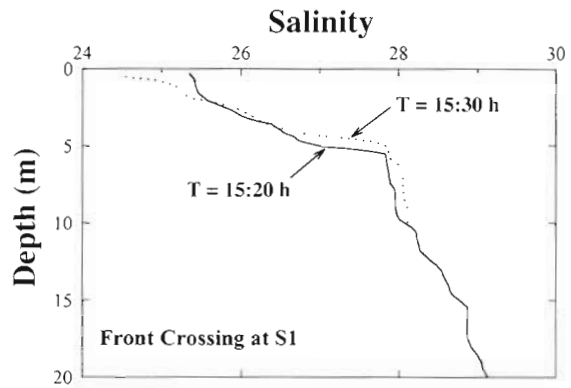


Fig. 11. The estuarine plume front crossed Stn S1 and clearly demonstrated the entrainment process. Vertical profiles represented by the dashed and solid lines were taken 10 min apart when the front crossed the station. T: time

nitrate concentrations at 20 m in summer were similar to those in April (Yin et al. 1996) and in June (Yin et al. 1997) and were within reach of wind mixing and upward entrainment.

Because of the positions (relative to the euphotic zone) of the halocline and nitracline in the water column, the distribution of nutrients and chl a fluorescence, which is a result of the interaction between physical and biological processes, was very responsive to the interaction. The nitracline was in a delicate balancing position of time scales between biological utilization of nutrients and physical mixing. A decrease or an increase in the rates of mixing could lead to a depletion or an elevation of nutrients in the distribution of nutrients and fluorescence. On the other hand, continuous sunshine or cloudiness during the day could result in a similar fluctuation. Tidal cycling changes the position of the nitracline, as shown in this study (Fig. 3), providing nutrients for photosynthesis when

Table 1. Linear regressions of temperature-salinity (T-S) diagrams using (T, S) data points at 20 m from a time series at Stns S3 and S1 and from different stations along the transect on the same day

Time series or transect	Number of data points (T, S)	R ²	Significance (p)
S3 time series	8	0.99	<0.0001
S1 time series	10	0.99	<0.0001
August 8 transect	8	0.98	<0.0001
August 10 transect	9	0.97	<0.0001
August 11 transect	9	0.97	<0.0001
August 12 transect	9	0.94	<0.0001
August 13 transect	8	0.95	<0.0001
August 14 transect	9	0.95	<0.0001

the nitracline is lifted upwards (Demers et al. 1986). Tidal mixing is a continuous process, also providing nutrients. Wind, river discharge and tides usually act in concert in vertical mixing, but signals of a force can be more distinct than others as the force becomes dominant. The vertical mixing or entrainment was manifested as observed in this study when wind speeds increased and/or a fluctuation in the amount of river outflow occurred. An increase of $1000 \text{ m}^3 \text{ s}^{-1}$ in river discharge over a week resulted in the visible signal of entrainment of nitrate in August (this study) and in June (Yin et al. 1997), and subsequent utilization of entrained nitrate often resulted in a subsurface fluorescence maximum. It is surprising to note that an average wind speed of 6 m s^{-1} over 36 h in summer mixed the water column to such a large extent (e.g. Stns S3 and S1) even under strong stratification before the wind event. The response of phytoplankton to increased nutrients was fast and the bloom observed on August 8 in the estuarine plume from Stns S3 to P7 appeared to take place during our sampling period from the morning (Stn S2) to the afternoon (Stn S1). Winds were highly variable in August (Fig. 12) and the frequent episodes of high wind speed between August 18 and 30 must have increased primary productivity. Due to active mixing processes by wind and river discharge, it appears that primary productivity in the central Strait was substantially fueled by nitrate instead of ammonium since ammonium concentrations in the water column along the transect were below $0.1 \mu\text{M}$ except at Stn S3 (Clifford et al. 1992). Nitrate utilized during this period was not likely to have been from the regeneration of organic matter produced in the previous season, which is the case in other estuaries such as Chesapeake Bay (Malone et al. 1988), since bacterial production was low in the Strait of Georgia at a salinity of >20 (Albright 1983, Harrison et al. 1991).

Phytoplankton biomass and productivity in the central Strait of Georgia observed in this study were reasonably high in summer due to vertical mixing, which supplied nutrients to the euphotic zone. The values were slightly lower than those during June (Yin et al. 1997) and early April (Yin et al. 1996), but higher than Parsons et al.'s (1970) and Stockner et al.'s (1979) values for August. Our values in the central Strait are higher than or comparable to many other estuaries. Summer chl *a* levels in the northwestern Gulf of St. Lawrence, Canada, were below 40 mg m^{-2} for most of the area, while in the lower St. Lawrence estuary, chl *a* was about 40 mg m^{-2} and primary productivity ranged between 1000 and $2000 \text{ mg C m}^{-2} \text{ d}^{-1}$ in July and

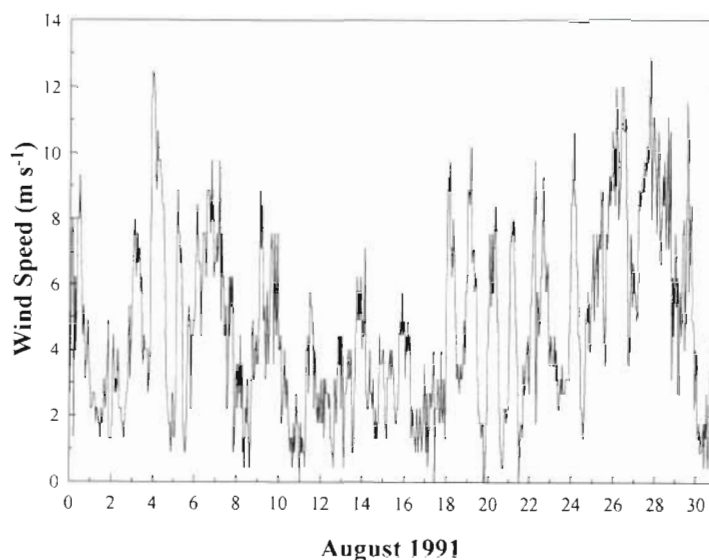


Fig. 12. Hourly wind speeds at Sand Heads at the mouth of the Fraser River during August 1991

August (Sinclair 1978, cf. Sevigny et al. 1979). In southern San Francisco Bay, daily primary productivity in summer was about $500 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Cole & Cloern 1984, 1987). Riegman & Colijn (1991) reviewed phytoplankton productivity for the North Sea, where typical summer values were $650 \text{ mg C m}^{-2} \text{ d}^{-1}$ for the northern part.

Previous estimates of annual primary production indicated that primary productivity in the central Strait of Georgia was low in summer (Parsons et al. 1970). However, our results are the first to show that during summer the interaction of winds and river discharge frequently provides nutrients, which increases primary production and decreases the periods of nitrogen limitation. Our results show that wind is very important in supplying new nitrogen (NO_3) to the surface layers through vertical mixing. Thus, during a summer with frequent wind events, primary productivity would be higher than previously thought, with much of the production coming from new nitrogen. These wind events are short-lived and require frequent monitoring to obtain reliable estimates of summer primary productivity.

Acknowledgements. Thanks are extended to the Department of Fisheries and Oceans for providing ship time and to the officers and crew of C.S.S. 'Vector' for their assistance. This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic grant. The Research Fellowship to support K.Y. was kindly provided by the Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada.

LITERATURE CITED

- Albright LJ (1983) Heterotrophic bacterial biomass, activities, and productivities within the Fraser River plume. *Can J Fish Aquat Sci* 40:216–220
- Bowman MJ, Yentsch CM, Peterson WJ (eds) (1986) Tidal mixing and plankton dynamics. Springer-Verlag, Berlin
- Boynton WR, Kemp WM, Keefe CW (1982) A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy VS (ed) Estuarine comparisons. Academic Press, New York, p 69–90
- Clifford PJ, Yin K, Harrison PJ, St. John MA, Goldblatt R, Varela D (1992) Plankton production and nutrient dynamics in the Fraser River plume, 1991. Manuscript report no. 59. Department of Oceanography, University of British Columbia, Vancouver
- Cloern JE (1996) Phytoplankton bloom dynamics in coastal ecosystem: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Rev Geophys* 34:127–168
- Cole BE, Cloern JE (1984) Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay, California. *Mar Ecol Prog Ser* 15:15–24
- Cole BE, Cloern JE (1987) An empirical model of phytoplankton productivity in estuaries. *Mar Ecol Prog Ser* 36:299–305
- Demers S, Legendre L, Therriault JC (1986) Phytoplankton responses to vertical tidal mixing. In: Bowman MJ, Yentsch CM, Peterson WT (eds) Tidal mixing and plankton dynamics. Springer-Verlag, Berlin, p 1–40
- Dortch Q, Postel JR (1989) Biochemical indicators of nitrogen utilization by phytoplankton during upwelling off the Washington coast (USA). *Limnol Oceanogr* 34:758–773
- Hager SW, Gordon LI, Park PK (1968) A practical manual for the use of Technicon AutoAnalyzer in seawater nutrient analysis. Final report to B.C.F., contract 14-17-0001-1759, October 1968, Reference 68-73
- Harrison PJ, Clifford PJ, Cochlan WP, Yin K, St. John MA, Thompson PA, Sibbald MJ, Albright LJ (1991) Nutrient and phytoplankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia. *Mar Ecol Prog Ser* 70:291–304
- Harrison PJ, Fulton JD, Taylor FJR, Parsons TR (1983) Review of the biological oceanography of the Strait of Georgia: pelagic environment. *Can J Fish Aquat Sci* 40:1064–1094
- Hitchcock GLM, Langdon C, Smayda TJ (1987) Short-term changes in the biology of a Gulf Stream warm-core ring: phytoplankton biomass and productivity. *Limnol Oceanogr* 32:919–928
- Horrigan SG, Montoya JP, Nevins JL, McCarthy JJ, Ducklow H, Goerick R, Malone T (1990) Nitrogenous nutrient transformations in the spring and fall in the Chesapeake Bay (USA). *Estuar Coast Shelf Sci* 30:369–392
- Iverson RL, Curl HC, O'Connors HB Jr, Kirk D Jr, Zakar K (1974) Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. *Limnol Oceanogr* 19:271–278
- Jones DM, Harrison PJ, Clifford PJ, Yin K, St. John MA (1991) A computer-based system for the acquisition and display of continuous vertical profiles of temperature, salinity, fluorescence and nutrients. *Water Res* 25:1545–1548
- LeBlond PH (1983) The Strait of Georgia: functional anatomy of a coastal sea. *Can J Fish Aquat Sci* 40:1033–1063
- Malone TC, Crocker LH, Pike SE, Wendler BW (1988) Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Mar Ecol Prog Ser* 48:235–249
- Mann KH, Lazier JRN (1991) Dynamics of marine ecosystem: biological-physical interactions in the oceans. Blackwell Scientific Publications, Boston
- Parsons TR, LeBrasseur RJ, Barraclough WE (1970) Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: a review. *J Fish Res Bd Can* 27:1251–1264
- Pitkanen H, Tamminen T, Kangas P, Huttula T, Kivi K, Kuosa H, Sarkkula J, Eloheimo K, Kauppila P, Skakalsky B (1993) Late summer trophic conditions in the north-east Gulf of Finland and the River Neva Estuary, Baltic Sea. *Estuar Coast Shelf Sci* 37:453–474
- Pond S, Pickard GL (1978) Introductory dynamic oceanography. Pergamon Press, Toronto
- Riegman R, Colijn F (1991) Evaluation of measurements and calculation of primary production in the Dogger Bank area (North Sea) in summer 1988. *Mar Ecol Prog Ser* 69:125–132
- Riegman R, Malschaert H, Colijn F (1990) Primary production of phytoplankton at a frontal zone located at the northern slope of the Dogger Bank (North Sea). *Mar Biol* 105:329–336
- Sevigny JM, Sinclair M, El-Sabh MI, Poulet S, Coote A (1979) Summer plankton distributions associated with the physical and nutrient properties of the northwestern Gulf of St. Lawrence. *J Fish Res Bd Can* 36:187–203
- Sinclair M (1978) Summer phytoplankton variability in the lower St. Lawrence estuary. *J Fish Res Bd Can* 35:1171–1185
- Stockner JG, Cliff DD, Shortreed KRS (1979) Phytoplankton ecology of the Strait of Georgia, British Columbia. *J Fish Res Bd Can* 36:657–666
- St. John MA, Marinone SG, Stronach J, Harrison PJ, Fyfe J, Beamish RJ (1993) A horizontal resolving physical-biological model of nitrate fluxes and primary productivity in the Strait of Georgia. *Can J Fish Aquat Sci* 50:1456–1466
- Waldichuk M (1957) Physical oceanography of the Strait of Georgia, British Columbia. *J Fish Res Bd Can* 14:321–486
- Wood ED, Armstrong FAJ, Richards FA (1967) Determination of nitrate in seawater by cadmium-copper reduction to nitrite. *J Mar Biol Assoc UK* 47:23–31
- Yin K, Harrison PJ, Beamish RJ (1997) Effects of a fluctuation in Fraser River discharge on primary production in the central Strait of Georgia, British Columbia, Canada. *Can J Fish Aquat Sci* 54:1015–1024
- Yin K, Harrison PJ, Goldblatt RH, Beamish RJ (1996) Spring bloom in the central Strait of Georgia: interactions of river discharge, winds and grazing. *Mar Ecol Prog Ser* 138:255–263
- Yin K, Harrison PJ, Pond S, Beamish RJ (1995a) Entrainment of nitrate in the Fraser River plume and its biological implications. I. Effects of salt wedge. *Estuar Coast Shelf Sci* 40:505–528
- Yin K, Harrison PJ, Pond S, Beamish RJ (1995b) Entrainment of nitrate in the Fraser River plume and its biological implications. II. Effects of spring vs neap tides and river discharge. *Estuar Coast Shelf Sci* 40:529–544
- Yin K, Harrison PJ, Pond S, Beamish RJ (1995c) Entrainment of nitrate in the Fraser River plume and its biological implications. III. Effects of winds. *Estuar Coast Shelf Sci* 40:545–558