DYNAMICS OF NUTRIENTS AND PHYTOPLANKTON PRODUCTION IN THE STRAIT OF GEORGIA ESTUARY, BRITISH COLUMBIA, CANADA

by

KEDONG YIN

B.Sc., Ocean University of Qingdao, 1982
M.Sc., The University of British Columbia, 1988

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Department of Oceanography)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

March 1994

© Kedong Yin, 1994
In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

(Signature)

Department of Oceanography

The University of British Columbia
Vancouver, Canada

Date March 29, 1994
ABSTRACT

Vertical profiles of temperature, salinity, NO3 and fluorescence were taken along the Fraser River estuary and during time series at a station near the river mouth to investigate entrainment of NO3. In late spring and early summer, the NO3-poorer estuarine plume in the Strait of Georgia invaded the river with the advancing salt wedge on the flood tide in the middle layer between the river water and the NO3-rich deep seawater, forming a three-layered system. Thus, upward entrainment of seawater into the riverine plume does not necessarily result in an upward entrainment of NO3. More NO3 was entrained during the spring tide than during the neap tide; more during a higher river discharge than during a lower river discharge; and more under windy conditions than weak winds. Under all the conditions investigated, the contribution of the entrained NO3 to the surface layer was (2-11 times) more than that of the river-borne NO3.

The spring bloom was underway in early April, 1991 in the Strait of Georgia estuary when it was interrupted by a wind event. Five days after the wind event, phytoplankton biomass and production were even lower. During the next four days, they gradually increased, and NO3 concentrations in the water column decreased slowly, which indicated a slow recovery of the spring bloom. Higher zooplankton abundance were responsible for the slow recovery.

The interaction between tidal ranges, river discharge and winds in the Strait during spring controls the stability of the water column and hence, the development of the spring bloom. In 1988, nutrients, phytoplankton biomass, production and species composition during early June indicated the delayed spring bloom, due to a later initiation of the annual freshet and strong winds during March-mid-April. Whereas in 1992 (an El Niño year), an earlier initiation of the freshet and calm weather in March appeared to result in an earlier onset of the spring bloom. The observations in all those years strongly suggest that massive recruitment of the copepod Neocalanus plumchrus to the surface, due to its ontogenic migration from deep waters, regulates the development of the spring bloom.
Thus, the interannual variability in the timing of the spring bloom determines the matching (phasing) between phytoplankton and zooplankton.
TABLE OF CONTENTS

ABSTRACT ........................................................................................................ II

TABLE OF CONTENTS .................................................................................. IV

LIST OF TABLES .......................................................................................... VII

LIST OF FIGURES ......................................................................................... VIII

ACKNOWLEDGMENTS .................................................................................. XVI

OVERVIEW ..................................................................................................... 1

GENERAL INTRODUCTION ........................................................................ 3

I. Dynamics of Nutrients and Phytoplankton Production .......................... 3
   Hydrodynamics and Phytoplankton Blooms ............................................. 3
   Dilution Model ......................................................................................... 4
   Strait of Georgia ...................................................................................... 5
      General Features .................................................................................. 5
      Influence of the Fraser River ............................................................... 9
      Effects of Tides on the Formation of the Riverine and Estuarine Plumes 13
   Other Estuaries ...................................................................................... 17
      River Flow-Controlled Dynamics ....................................................... 17
      Tidal Effects ....................................................................................... 22
      Winds .................................................................................................. 23
      Interactions Among River Discharge, Winds and Tides ..................... 25

II. Effects of Physical Forcing on Trophodynamics of Pelagic Food Webs.. 25
   Zooplankton ............................................................................................ 25
   Juvenile Fish ........................................................................................... 28

III. The Strait of Georgia Study — Issues to Investigate ............................. 30

HYPOTHESES AND OBJECTIVES .............................................................. 31

GENERAL MATERIALS AND METHODS .................................................. 33

   Definition of the Riverine and Estuarine Plumes ................................. 33
   Station Locations .................................................................................... 33
   Sampling and Data Processing ............................................................... 34
   Nutrient Analysis .................................................................................... 35
   14C Uptake ............................................................................................. 36
   Chl a, Particulate Organic Carbon and Nitrogen .................................. 37
   3H Uptake by Bacteria .......................................................................... 37
   Microflagellate Counts .......................................................................... 38
Chapter 1 Entrainment of Nitrate in The Fraser River Plume and its Biological Implications: Effects of the Salt Wedge

INTRODUCTION

MATERIALS AND METHODS

CONCEPTUAL MODEL

RESULTS AND DISCUSSION

1. Transect Results
   - Salinity, T-S diagram, Proportion and Equivalent Thickness
   - NO3
   - Fluorescence Maximum

2. Effects of Tides (Flood vs Ebb, Spring vs Neap) on Entrainment
   - Neap Tide
   - Spring Tide

3. Biological Significance

Chapter 2 Entrainment of Nitrate in The Fraser River Plume and its Biological Implications: Effects of Spring vs Neap Tides and River Discharge

INTRODUCTION

MATERIALS AND METHODS

RESULTS

1. Effects of Tides on Entrainment (Spring vs Neap)
   - Neap Tide
   - Spring Tide
   - Comparison between the neap and the spring tides

2. Effects of River Discharge
   - Lower Discharge
   - Higher Discharge

DISCUSSION

Spring vs Neap tides

Higher vs Lower River Discharge

Entrainment and Its Biological Significance

CHAPTER 3 Entrainment of Nitrate in The Fraser River Plume and its Biological Implications: Effects of Winds

INTRODUCTION

MATERIALS AND METHODS

RESULTS AND DISCUSSION
LIST OF TABLES

Table 2.1 Comparisons between the neap tide on June 12-13 and the spring tide on June 19-20, 1989. All the parameters are time-averaged over the time series. 105

Table 2.2 Comparisons between the low discharge on May 29-30, and the higher discharge on June 7-8, 1990. All the parameters are time-averaged over the time series. 115

Table 3.1 Comparisons between the weak wind condition on Aug. 23-24, 1990 and the strong wind condition on Aug. 7-8, 1991. All the parameters are time-averaged over the time series. 154

Table 5.1 Average (Avg) NH4 concentrations (μM) over the sampling depth (m) at four stations along the transect (see Figure 5.1) in the Strait of Georgia during May 31-June 9, 1988. n = the number of concentrations at different depths being averaged. min = the minimum concentration. max = the maximum concentration. See Appendix 3 for the actual concentrations. 215

Table 5.2 Average chl a (mg m⁻²), primary production (P.P.), and bacterial production (Bact. P.) at 4 stations during May 31 to June 9, 1988. Averaged total microflagellates during the same period are included (the values are depth-weighted averages first, and then averaged over a few days). n = the number of days which were averaged. The values in the bracket are the minimum and maximum. See Appendix 4 for the actual data. 216

Table 5.3 Table 5.3 Average abundance (10³ cells ml⁻¹) and relative biovolume (% of total phytoplankton biovolume) of major phytoplankton genera: Skeletonema costatum, Thalassiosira spp. and Chaetoceros spp. at the surface or at a depth of 1-2 m at 4 stations during May 31 to June 9, 1988. n = number of days which were averaged. See Appendix 5 for the actual data. 217

Table 5.4 Total number (per m⁻³) of calanoid copepods, Neocalanus plumchrus, and the most dominant genera of copepod during a time series at Stn 4 on June 8-9, 1988. Relative abundance is given as % of total number of copepods. See Appendix 6 for more data. 218

Table 5.5 Chl a and nutrients at 9 stations (see Figure 5.1) in the Strait of Georgia during April 19-22, 1993. 242

Table 5.6 Total zooplankton abundance and relative abundance of major zooplankton species (% of total zooplankton abundance) at 8 stations in the Strait of Georgia during April 19-22, 1993. 244
LIST OF FIGURES

Figure 1  Map of the Strait of Georgia showing the three sections: 1) the Southern Strait, 2) the Central Strait, and 3) the Northern Strait, separated by dotted lines. ................................................................. 6

Figure 2  An annual cycle of the estuarine plume development in relation to the Fraser River discharge. The volume of discharge is low during winter, medium during spring and highest during late spring and summer. .............. 11

Figure 3  Effects of tidal cycles on the formation of the riverine plume in relation to the estuarine plume. ................................................................. 14

Figure 4  T-S diagrams from a time series of vertical profiles taken on May 31-June 1, 1990 were plotted in one graph to determine the characteristic salinity and temperature (S2, T2). The same procedure was used for the transect sampled on August 7-8, 1991. ....................................................... 41

Figure 5  Vertical profiles of salinity and temperature showing a depth D1 with salinity and temperature (S1, T1); B) the vertical distribution of proportion of freshwater (FW), the estuarine plume (EP), and the deep water (DW) calculated from the equations (1), (2) and (3) in the text, showing the calculated proportion V1i, V2i and V3i at D1 for for FW, EP and DW, respectively. Integrating V1, V2 and V3 over depth to D0 is the equivalent thickness of FW, EEP and EDW, respectively.......................... 43

Figure 1.1  Map of the study area at the mouth of the Fraser River, British Columbia, Canada and the stations R1, R2, R3, R4, R5, R6, R7 and Stn 2 along the transect. Station depths: R1 = 15 m, R2 = 20 m, R3 = 12 m, R4 = 15 m, R5 = 45 m, R6 = 96 m, R7 = 146 m and Stn 2 = 200 m. The dotted line shows the edge of the shallow banks which are exposed at lower low water. ................................................................. 49

Figure 1.2  The conceptual model illustrating the riverine plume, the estuarine plume and the deep seawater: A) a salt wedge invades the river during a flood tide and the estuarine plume dams the river outflow at the river mouth during HHW, and B) the riverine plume is formed as the salt wedge retreats during an ebb tide. Zone I illustrates a wall-like structure of deep seawater. ................................................................. 52

Figure 1.3  Change in tidal height with time during the sampling period along the transect on August 13-14, 1991. The arrows indicate the sampling time at which the station was visited and "-2" denotes the second visit............. 56

Figure 1.4  Vertical profiles of salinity, NO3 and fluorescence (in relative units) at R1, R2, R3, R4, R5, R6, R7, and Stn 2 (Figure 1.1) along the transect on August 13 and 14 (Figure 1.2)........................................... 58
Figure 1.5 Temperature-salinity (T-S) diagrams for the vertical profiles at the same stations along the transect as in Figure 1.4. ............................................................... 60

Figure 1.6 Vertical distribution of the proportions of the riverine plume, estuarine plume and deep water for the vertical profiles at the same stations along the transect as in Figure 1.4. ............................................................... 62

Figure 1.7 Dependence of: A) depth-integrated entrained NO₃ on entrained deep seawater (EDW), and B) depth-integrated fluorescence (Int. Flu.) in the water column on the equivalent thickness of the estuarine plume (EP), for the vertical profiles at the same stations along the transect as in Figure 1.4.  67

Figure 1.8 Uptake of nutrients over a range of irradiances for a sample taken at the chl maximum at 10 m at Stn 2 on June 12, 1989. The initial concentrations of nutrients were saturating ($\text{NO}_3 = 7.9 \mu\text{M}$, $\text{SiO}_4 = 13.0 \mu\text{M}$, $\text{NH}_4 = 1.32 \mu\text{M}$, and $\text{PO}_4 = 1.5 \mu\text{M}$). ............................................................... 70

Figure 1.9 Change of the tidal height with time for the neap tide on June 11-12 and the spring tide on June 19, 1989. The arrows indicate the sampling times at which the vertical profiles were taken for Figures 1.10 and 1.11. ...................... 73

Figure 1.10 Vertical salinity profiles with their corresponding T-S diagrams at R3 and R4 during the flood and ebb of the neap tide on June 11-12, 1989. ...... 75

Figure 1.11 Vertical salinity profiles with their corresponding T-S diagrams at R3 and R4 during the flood and ebb of the spring tide on June 19, 1989. ...... 78

Figure 1.12 Vertical distribution in proportion of freshwater (FW), the estuarine plume (EP) and the deep water (DW) for the vertical profiles at R3 and R4 during the neap tide (June 11-12) shown in Figure 1.10 and during the spring tide (June 19, 1989) shown in Figure 1.11. ................................. 81

Figure 1.13 Equivalent thickness of the freshwater (FW), the entrained estuarine plume (EEP) and the entrained deep seawater EDW for vertical profiles sampled at R3 and R4 during floods and ebbs in the spring and neap tides in June, 1989. The sum of these three equivalent thicknesses is the depth at which the proportion of freshwater drops to zero. See discussion in the text. ................................................................. 83

Figure 1.14 The relationship between the equivalent thickness of the entrained deep water (EDW) and the equivalent thickness of the estuarine plume (EP) for the vertical profiles A) along the transect on August 13-14, 1991, B) at R3 and R4 during the neap tide on June 11-12, 1989, and C) at R3 and R4 during the spring tide on June 19 and June 22, 1989. Some vertical profiles shown in Figure 1.4 are not included in (A) because they were not deep enough for the calculation of the equivalent thickness of the estuarine plume. ................................................................. 86
Figure 2.1 Depth contours of salinity and NO₃ for the time series at Stn 2 on June 12-13, during the neap tide (A, B) and June 19-20, 1989 during the spring tide (C, D). The arrows indicate the times when the vertical profiles were completed since it usually took 0.5 h to complete a vertical profile.

Figure 2.2 Time series of the T-S diagrams for A) the neap tide, and B) the spring tide. See Figure 2.1A for the sampling times and their relation to the tidal cycles. Successive T-S curves are offset by 5 on the salinity axis.

Figure 2.3 Time series of the equivalent thickness of freshwater, the entrained estuarine plume and the entrained deep water during A) a neap tide, and B) a spring tide. See Figure 2.1A and B for the sampling times.

Figure 2.4 Linear regressions between the amount of the entrained NO₃ and the equivalent thickness of the entrained deep water (EDW) (A,C) and the depth-integrated fluorescence and the equivalent thickness of the estuarine plume (EP) (B,D) for the neap tide of June 12-13 and the spring tide: June 19-20, 1989. The slopes of A and C are indicated by b (3.1 and 15.2 μM for the neap and spring tides, respectively). T1, T2 and T5 are not included in the regression in C because NO₃ concentrations were not measured or were not deep enough for the calculation of entrained NO₃. T1 and T5 are not included in the regression in D for the same reason.

Figure 2.5 Depth contours of salinity and NO₃ (μM) for the time series at Stn 2 on May 29-30, during a day of lower river discharge (A, B) and on June 7-8, 1990 during a day of higher river discharge (C, D). The contours in A and B were plotted using more vertical profiles than the arrows indicated. Those arrows indicate only the sampling times (when the vertical profiles were completed) for the time series of T-S diagrams and the equivalent thickness shown in Figures 2.6A and 2.7A. Therefore, the contours in A and B present more features than the number of the vertical profiles indicated by the arrows (for example, around T4 when another vertical profile with a minimum of NO₃ at an intermediate depth is contoured close to T4 in time, two sets of circular contour lines next to each other are formed). The axis of Hour for the NO₃ contour D is longer than in C, because the salinity instrument for the last vertical profile was broken and not plotted in D.

Figure 2.6 Time series of the T-S diagrams for A) the smaller discharge on May 29-30, and B) the larger discharge on June 7-8, 1990. See Figure 2.5A for the sampling times. Successive T-S curves are offset by 5 on the salinity axis.

Figure 2.7 Time series of the equivalent thickness of freshwater, the entrained estuarine plume and the entrained deep water during A) the lower discharge, and B) the higher discharge. See Figure 2.5 for the sampling times. T5 and T6 in B are missing because the vertical profiles at these times were not deep enough for the calculation.
Figure 2.8 Linear regressions between the amount of the entrained NO$_3$ and the equivalent thickness of the entrained deep water (EDW) (A,C) and the depth-integrated fluorescence and the equivalent thickness of the estuarine plume (EP) (B,D) for the low discharge on May 29-30, and the higher discharge on June 7-8, 1990. The slopes of A and B are indicated by b (16.8 and 25.1 $\mu$M for the lower and high discharge, respectively). T5 and T6 are not included in the regression in C and D for the same reason as stated in Figure 2.7 .......................................................... 113

Figure 2.9 The conceptual model illustrating how Zone I (the area of the deep seawater exposed to the riverine plume seaward of the river mouth) changes with the riverine plume, the estuarine plume and the deep water at different stages of tidal cycles and river discharge. The dashed line indicates a condition during a neap ebb or smaller discharge and the solid line indicates a spring ebb or larger discharge condition ............................................. 118

Figure 2.10 Vertical profiles of salinity (S), nitrate (N) and fluorescence (F) with their corresponding temperature-salinity diagram and NO$_3$-salinity and fluorescence-salinity diagrams, at T2 (A, B) and T3 (C, D) (see Figure 2.1 for sampling times) during the neap tide of June 12, 1989. These graphs demonstrate the entrainment of NO$_3$ accompanied by a second shallower fluorescence maximum entrained from the deeper fluorescence maximum... 122

Figure 2.11 A riverine front (shown in Figure 2.9) crossed a station, 35 km away from the river mouth on June 14, 1989. Two vertical profiles were taken within 30 min, one (dotted line) was 50 m away from the riverine front (seaward of the riverine plume) and the other (solid line) after the riverine front passed the station 20 m away (within the riverine plume). The movement of the riverine front induced entrainment of NO$_3$ and double chl a maxima................................................................. 125

Figure 3.1 Tidal height (A) and wind speed (B) for the two time series at Stn 2, 8 km seaward of the mouth of the Fraser River. The solid line represents the time series on August 7-8, 1991 with 8 solid filled triangles indicating the sampling times. The dotted line represents the time series on August 23-24, 1990 with 6 open inverted triangles indicating the sampling times............. 131

Figure 3.2 Time series of six vertical profiles of salinity, NO$_3$ and fluorescence under weak winds for August 23-24, 1990 (see Figure 3.1 for the sampling times) .............................................................. 134

Figure 3.3 Time series of T-S diagrams under weak winds on August 23-24, 1990 (see Figure 3.1 for the sampling times) .............................................................. 136

Figure 3.4 Time series of vertical distribution in proportion of freshwater (FW), the estuarine plume (EP) and the deep water (DW) under weak winds on August 23-24, 1990 (see Figure 3.1 for the sampling times). .......................... 138
Figure 3.5 Time series of eight vertical profiles of salinity, NO$_3$ and fluorescence under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times). ............................................................... 140

Figure 3.6 Time series of T-S diagrams under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times) ............................................................... 142

Figure 3.7 Time series of vertical profiles of velocity (solid line) and Richardson number (circles) under windy conditions on August 7-8, 1991. The velocity shown is the component in the direction of the surface flow, which changes somewhat between the vertical profiles. The component perpendicular to the surface component is generally small. The vertical dotted line delineates zero in velocity. The filled circles indicate Richardson numbers that are < 0.25. Salinity is also plotted for comparison ........................................... 146

Figure 3.8 Time series of vertical distribution in proportion of freshwater, the estuarine plume and the deep seawater under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times) .................................................. 149

Figure 3.9 Time series of equivalent thickness of freshwater, the entrained estuarine plume and the entrained deep seawater under: A) a weak wind condition on August 23-24, 1990, and B) a strong wind condition on August 7-8, 1991 (see Figure 3.1 for the sampling times) ........................................ 151

Figure 3.10 Vertical profiles of chl a and primary production at the beginning (T1) and the end (T8) of time series of August 7-8, 1991 (see Figure 3.1 for the sampling times) ........................................ 156

Figure 4.1 Map of the stations in the Strait of Georgia for the cruise conducted during April 2-19, 1991 ................................................................. 161

Figure 4.2 A) Fraser River discharge for 1991 at Hope; B) Fraser River discharge and daily averaged wind speed, and C) tidal ranges during April 1-19, 1991 163

Figure 4.3 Temporal and spatial changes in chl a (mg m$^{-2}$) and primary production (mg C m$^{-2}$ d$^{-1}$) along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 4-18, 1991. Note that the Y axis scale for April 4-5 differs from those of the other periods ................................................................. 166

Figure 4.4 Vertical profiles of salinity along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9 ................................................................. 168

Figure 4.5 Vertical profiles of salinity along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 15-19 ................................................................. 171

Figure 4.6 Vertical profiles of NO$_3$ along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9 ................................................................. 174
Figure 4.7 Vertical profiles of NO₃ along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 15-19. ................................................................. 176

Figure 4.8 Vertical profiles of temperature along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9. ................................................................. 179

Figure 4.9 Zooplankton abundance in the top 25 m at some stations along the transect during April 4-18. A) Neocalanus plumchrus, showing the portion of copepodite stages C1 through C5, B) Peudocalanus minutus, and C) other zooplankton including Calanus sp., Acartia longiremis, Eucalanus sp. and Centropages sp. ................................................................. 183

Figure 4.10 Vertical profiles of NH₄ concentrations along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9. ................................................................. 186

Figure 4.11 Vertical profiles of NH₄ concentrations along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 15-18. ................................................................. 188

Figure 4.12 Vertical profiles of total nitrogen (TN) during April 4-9, 1991. Triangle symbol indicates the sampling next day at the same station (Stn 2 and Stn 3). ................................................................. 191

Figure 4.13 Regression of particulate nitrogen (PN) over chl a a during April 4-9, 1991. PN=0.859*Chla + 3.396 (R²=0.835, p<0.0005). The two dotted lines are 95% confidence intervals. ................................................................. 193

Figure 4.14 Vertical profiles of total nitrogen (TN) along the transect from Stn 2 to Stn 1 (Figure 4.1) on April 15-18. PON is calculated using the regression in Figure 4.12. ................................................................. 195

Figure 5.1 Map of the study area indicating stations for 1988 (X), 1992 (●), and 1993 (△). The stations in 1992 were the same as in 1991, but some stations in 1991 were not visited in 1992. ................................................................. 202

Figure 5.2 A) and B) The Fraser River discharge, C) wind speed and tidal ranges for the cruise period: May 31-June 9, 1988 ................................................................. 204

Figure 5.3 Vertical profiles of salinity along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988. ................................................................. 206

Figure 5.4 Vertical profiles of fluorescence along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988. ................................................................. 208

Figure 5.5 Vertical profiles of NO₃ along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988. ................................................................. 210
Figure 5.6 Vertical profiles of SiO4 along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988. ........................................ 213

Figure 5.7 A) The Fraser River discharge, B) wind speed and C) tidal ranges for the cruise period: January 1- April 30. Circles indicate the period of the cruise during April 6-15, 1992 and triangles represent April 19-22, 1993. ... 220

Figure 5.8 Vertical profiles of salinity along the transect (see Figure 5.1) during April 6-15, 1992. A dotted line indicates a profile sampled at a different time of the day. ........................................ 222

Figure 5.9 Vertical profiles of temperature along the transect (see Figure 5.1) during April 6-15, 1992. A dotted line indicates a profile sampled at a different time of the day. ........................................ 224

Figure 5.10 Vertical profiles of silicate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 227

Figure 5.11 Vertical profiles of nitrate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 229

Figure 5.12 Vertical profiles of phosphate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 231

Figure 5.13 Vertical profiles of ammonium along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 233

Figure 5.14 Vertical profiles of urea along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 235

Figure 5.15. Vertical profiles of chl a along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day. ........................................ 237

Figure 5.16. Vertical profiles of primary production along the transect (see Figure 5.1) during April 6-15, 1992. ........................................ 239

Figure 5.17 Tidal ranges (m) at Point Atkinson in the Strait of Georgia for 1988, 1989, 1990, and 1991. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study. ........................................ 246
Figure 5.18 Daily discharge (m$^3$ s$^{-1}$) of the Fraser River at Hope for 1988, 1989, 1990, and 1991. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study. ................................................................. 248

Figure 5.19 Daily average wind speed (m s$^{-1}$) at the Vancouver International Airport (VIA) for 1988, 1989, 1990, and 1991. VIA is very close to the Fraser River mouth. The wind direction was not taken into account. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study. ........... 250
ACKNOWLEDGMENTS

I am deeply indebted to my supervisor, Dr. Paul J. Harrison, for his advice, guidance and support throughout my study period at UBC. In particular, his kindness and patience has impressed me in both my academic and personal life. His determination to continue this research project in the Strait of Georgia without full funding has made my thesis possible. Appreciation also goes to his family, with which I have enjoyed many holidays together and from which I have leaned a lot about the Canadian way of life.

This dissertation is the result of many years of cruises which were the concerted efforts of Dr. Paul J. Harrison as chief scientist, Dr. Mike St. John who coordinated cruises, Peter Clifford who did the cruise preparation and conducted $^{14}$C-uptake experiments and other measurements, Robert Goldblatt who took zooplankton samples and provided zooplankton data for Chapter 4, and many other participants such as John Berges and Heidi Sawyer. Technical assistance by David Jones, who set up the electronic cruise equipment and wrote the computer programs, made electronic data logging possible. Thanks are given to the Department of Fisheries and Oceans for providing ship time and the officers and crew of C.S.S. Vector, C.S.S. W.E. Richer, and C.S.S. Caligus for their assistance during the cruises.

Discussions with Drs. Tim Parsons and Keith Thomson and especially Steve Pond were very useful. Comments by Robert Goldblatt on Chapters 4 and 5 were also helpful. Dr. Harrison's lab seminar series has been a beneficial place for me to organize data, express my ideas and receive feedback, criticisms and comments.

Special thanks are given to my colleagues, Drs. Maurice Levasseur and William Cochlan as well as other people in Dr. Harrison's lab who created a friendly working environment and kindly received my frequent plaguing for help. Encouragement during my doctoral study was given by my late sister in Germany, and my parents and brothers in China. They have provided me with strong moral support. I am also grateful to the Fountain family (at 3895 W 24th Avenue, Vancouver) who treated me as part of their
family since I lived there in 1987. I want to thank my wife, Manli Lu, who has been very supportive and patient with me during my endless study, and my son, Henry, who has given me great joy since his birth in 1989.

My financial support in the past three years was kindly provided by Pacific Biological Station, Biological Science Branch, Department of Fisheries and Oceans, Nanaimo, B.C.

This research was partially funded by a Natural Science and Engineering Research Council of Canada (NSERC) strategic grant to Dr. Paul J. Harrison.
OVERVIEW

Recently, many field studies in biological oceanography have focused on the coupling between biological and physical processes over a variety of spatial and temporal scales. However, data on nutrients, phytoplankton biomass, primary production and related physical parameters over short time scales (days) are definitely lacking for the Strait of Georgia estuary.

The GENERAL INTRODUCTION reviews how physical driving forces such as river outflow, winds and tidal cycles controls the dynamics of nutrients and phytoplankton blooms in estuaries. A conceptual model for the Strait of Georgia is introduced to describe: i) how the riverine plume is formed and modulated by tidal cycles, ii) how the estuarine plume is formed from river discharge which changes over seasons, iii) the relationship between the two plumes, and iv) the relationship between the dynamics of nutrients, phytoplankton biomass and production, and the two plumes.

An important feature in this study is the use of high resolution vertical profiles of salinity, temperature, current velocity, *in vivo* fluorescence and the nutrients, NO$_3$, NH$_4$, PO$_4$, and SiO$_4$, to resolve day-to-day variations and to infer responses of biological variables (nutrients and phytoplankton biomass and production) to changes in river discharge, winds and tidal cycles. This study is part of a larger project which was conducted between 1987-1993. The investigations were once (1-3 weeks) a year in 1987-89 and 1993, twice in 1992, and 3-4 times in 1990 and 1991, covering periods from spring to fall. The study area was in the riverine plume and the estuarine plume in the Central Strait of Georgia.

Although nitrogen is very low or undetectable at the surface layer in the Strait of Georgia in late spring and summer, phytoplankton productivity remains high. It has long been believed that entrainment of nitrogen is responsible for the supply of nitrogen during this period. The first three chapters are devoted to examining the processes of NO$_3$ entrainment. Chapter 1 starts with the effects of salt wedge dynamics on entrainment of
NO₃ in the river channel, and unfolds into the effects of spring and neap tidal cycles, different magnitudes of river discharge (Chapter 2) and winds on entrainment of NO₃ beyond the river mouth (Chapter 3). This is the first quantitative study of the entrainment of nutrients in the Strait of Georgia. These findings indicate that entrainment of nitrogen is more important than river-borne nitrogen.

The remainder of the thesis (Chapters 4 and 5) deals with another time period (the timing of the spring bloom) compared to Chapters 1, 2 and 3 where entrainment of NO₃ was studied during summer when phytoplankton are periodically N-limited.

In spring when the spring bloom starts, nutrients in the water column are high in the Strait of Georgia and entrainment of nutrients is not important due to the low river discharge. During the same period, the stability of the water column fluctuates due to tidal and wind mixing and the spring bloom develops in a sequence of steps. Chapters 4 and 5 deal with how the timing (initiation and development) of the spring bloom is coupled with the fluctuation of the stability of the water column. In Chapter 4, the spring bloom in 1991 was closely followed. It was underway when it was interrupted by a wind event. However, its recovery was slow, probably because of grazing from a massive amount of zooplankton which appeared in the surface layer due to the ontogenic migration of the copepod Neocalanus plumchrus.

Last (Chapter 5), the interannual variability in the timing of the spring bloom was examined for 1988, 1992 and 1993. Based on the evidence of the wind effects (Chapters 3 and 4) and daily variations in river discharge, winds, and tidal ranges for 1988-1993, the river discharge and the reduced tidal mixing in March appears to determine the onset of the spring bloom in spring, and winds and the ontogenic migration of zooplankton regulate the course of development of the spring bloom. The interaction between physical and biological processes has important implications for pelagic food webs and fisheries in the Strait of Georgia.
GENERAL INTRODUCTION

I. Dynamics of Nutrients and Phytoplankton Production

Hydrodynamics and Phytoplankton Blooms

It is well known that biological processes are closely coupled with physical processes over various time scales (Legendre and Demers 1984, Denman and Powell 1984, Legendre et al. 1988). The linkage of biological dynamics to hydrodynamics was first explicitly established by Gran and Braarud (1935), who invoked the lack of vertical stability of the water column to explain the low phytoplankton numbers observed in the Bay of Fundy. Since then the concept of the mixed layer depth and the critical depth has been developed (Bigelow et al. 1940, Riley 1942, Sverdrup 1953) and has received wide acceptance. It states that the relationship between the mixed layer depth and the critical depth determines the initiation of the spring bloom. Basically, when the mixed layer depth is deeper than the critical depth, the phytoplankton spend too much time at light levels below the compensation light intensity and there is no net production in the water column; when the opposite occurs, then net production is achieved. In fact, the vertical stability of the water column defines the light fields and determines if a phytoplankton bloom can occur. Winter blooms can occur, for example, in Narragansett Bay (Pratt 1965), the Peel-Harvey estuary (McComb et al. 1981), the Pamlico River (Hobbie et al. 1975) and the Niantic River estuary (Marshall and Wheeler 1965). It is worth pointing out that the model is based on the daily scale (Sverdrup 1953), which is necessary for daily net phytoplankton production. However a bloom requires a longer time scale to develop.

In estuarine environments where physical processes are more variable due to river discharge, winds, and tidal cycles, the timing of the spring bloom varies. There is usually intensive horizontal advection and vertical mixing in estuaries. The critical depth model which is based on vertical structure and a daily scale becomes insufficient to explain temporal and spatial distribution of nutrients and phytoplankton over various scales in estuaries. For example, when river flow is high there is no spring bloom in the upper estuary in spite of a highly stratified water column and high nutrients in some estuaries.
including the St. Lawrence estuary (Sinclair et al. 1981, Therriault and Levasseur 1985), the Hudson River estuary (Malone 1977), and the Delaware estuary (Pennock 1985, Pennock and Sharp 1986). Therefore, dilution rate (or flushing rate) or residence time of water in the euphotic zone is invoked to explain the observations of regional and temporal conditions for blooms in those estuaries and the regulation of the occurrence of the spring bloom (Malone 1977, Côte and Lacroix 1979, Malone and Chervin 1979, Sinclair et al. 1981, Therriault and Levasseur 1985).

Another assumption of the critical depth model is that nutrients in the water column are not limiting (Sverdrup 1953). This holds true during the beginning of the spring bloom. At the end of the bloom, nutrients are depleted in the euphotic zone. It is the dynamics of the limiting nutrients that regulates the dynamics of phytoplankton production. During this time, pulses of supplied nutrients are utilized rapidly. Any physical process which changes the concentration of the limiting nutrient is reflected in phytoplankton production. When the magnitude of the physical process is large enough such as during a spring tide or a wind event, a bloom may result. Reports of a phytoplankton bloom following an event such as a wind storm or a spring tide are not uncommon (e.g. Takahashi et al. 1973, Iverson et al. 1974, Walsh et al. 1978, Walsh 1981, Haas et al. 1981a an b, Legendre et al. 1982).

**Dilution Model**

In order to describe the effects of physical processes on biological production as discussed above, a conceptual model which is similar to the semi-continuous culture can be developed. In a section of an estuary, the culture volume (thickness) is defined by the euphotic zone depth which is determined by light intensity and light penetration in the water column. Therefore, the volume varies with light. Only two parameters are required to express the dynamics of the culture: dilution rate of the culture and growth rate of phytoplankton. The dilution rate is defined by the ratio of inflow rate to the volume of the culture. The growth rate is determined by light and nutrients at a certain temperature.
Here both the dilution rate and the growth rate are an average over the euphotic zone. The culture behaves like a turbidostat under a nutrient-saturated condition, and shifts to a chemostat when a nutrient becomes limiting. When there is no dilution, the culture is like a batch culture. If the dilution rate is too high, the culture is washed out. The dilution rate is determined by both the euphotic zone depth (volume) and horizontal advection and vertical mixing across the euphotic zone depth. If the river flow and vertical mixing due to tidal mixing increases, the dilution rate increases. On the other hand, under the same flow rate or mixing conditions, the culture volume is smaller when light intensity is low or water turbidity is high. The effects are two fold: the growth rate is reduced and the dilution rate becomes higher. A bloom usually occurs when growth rate in the euphotic zone exceeds the dilution rate over a sufficient time period (several days). This is essentially consistent with the idea that a phytoplankton bloom only occurs when there is matching or resonance of physical scales with biological scales (Legendre et al. 1988). In the following discussion of the effects of river discharge, tidal cycles and winds on the dynamics of nutrients and phytoplankton production, the dilution rate and the growth rate can be considered as proximal parameters which can be used to express the complex physical processes on the dynamics over various time scales.

**Strait of Georgia**

**General Features**

**Geography** The Strait of Georgia is a coastal basin which lies between Vancouver Island and the mainland of British Columbia (Figure 1). It covers a surface area of 6900 km² with an average depth 156 m. There are two connections with the Pacific Ocean to the north and south. At the southern end, the strait is connected through some narrow channels and shallow sills to the Strait of Juan de Fuca which leads to the Pacific Ocean. At the northern end, it passes through Johnstone Strait to the Pacific Ocean.
Figure 1  Map of the Strait of Georgia showing the three sections: 1) the Southern Strait, 2) the Central Strait, and 3) the Northern Strait, separated by dotted lines.
According to Waldichuk (1957), the Strait of Georgia can be divided, as shown in Figure 1, into three sections: 1) the Southern Strait covers the region from the northern boundary of the San Juan Archipelago to a line between Point Roberts and Active Pass; 2) the Central Strait extends from the Southern Strait to the southern end of Texada Island; and 3) the Northern Strait extends from the Central Strait to the mouths of the northern channels. These sections approximately delineate the region of intensive tidal mixing in the south, the region of major influence of the Fraser River in the central part, and the northern region which receives the combined influence of the northern inlets and the Fraser River. The Strait is generally bounded by steep rocky shores (Levings 1983). This study was mainly in the Central Strait.

**Environmental** Although the Strait of Georgia is still comparatively free of major pollution problems, local environmental degradation in waters on its periphery adjacent to urban communities and industries, such as pulp mills has taken place (Waldichuk 1983). The Strait of Georgia receives pollutants from rivers and runoff, outfalls (sewage, and pulp and paper mills), ocean dumping, and shipping.

**Fisheries** The Strait of Georgia is a very productive region for several important commercial fisheries and recreational fishing as well. The dollar value from fisheries is close to 1 billion. It is a rearing site for juvenile fish, including Pacific salmon, particularly coho and chinook, which spend several months in the Strait of Georgia before they migrate to the Pacific Ocean (Healey 1978, Fraser et al. 1982). Other juvenile fish include herring, hake and lingcod which spawn and spend time in the Strait (Ketchen 1983).

**Oceanography** The general oceanography of the Strait has been described in comprehensive reviews of biological aspects by Parsons et al. (1970) and Harrison et al. (1983), and physical aspects by Waldichuk (1957) and LeBlond (1983). Both physical and biological processes in the Strait are influenced by runoff, tides and winds.
Influence of the Fraser River

The freshwater adds a stabilizing agent to the water column which favors phytoplankton blooms on one hand, while on the other hand, it introduces turbidity which decreases light penetration through the water column and reduces photosynthesis. The balance between dilution rate and growth rate varies daily due to horizontal advection of water masses and vertical mixing processes. Net primary production may vary greatly from one day to the next. Fluctuations in river discharge generate large temporal and spatial variations in phytoplankton blooms. A maximum of phytoplankton biomass and removal of nutrient usually occurs in an appropriate region depending on the river outflow, geography and topography of the estuary (Carpenter and Dunham 1985). In early spring, because of the freshwater addition to the water column in an estuary, stratification occurs earlier and is stronger than in adjacent waters, and the bloom occurs earlier than in the adjacent water masses (Sinclair et al. 1981, Smayda 1983, Mann & Lazier 1991).

Based on previous studies (Parsons et al. 1969a, Stockner et al. 1979) and the 6 year series of data reports (Clifford et al. 1989, 1990, 1991a, 1991b, 1992), a conceptual framework was developed for the discussion of the coupling of physical with biological processes in the central Strait.

The Estuarine Plume

The Fraser River is one of the largest rivers on the west coast of North America. Its discharge contributes 85\% of the runoff into the Strait of Georgia (Waldichuk, 1957). The mean monthly discharge in the Fraser River from 1913-1976 shows a minimum in March (ca. 700 m$^3$ s$^{-1}$) and maximum in June (ca. 10,000 m$^3$ s$^{-1}$) (Fraser et al. 1982). The spring freshet starts in the beginning of April in a normal year. In winter, when river discharge is small, tidal and wind energy are large enough to mix the discharged freshwater with seawater almost completely. With increasing freshwater discharge during the start of the annual freshet in spring, a stratified water column develops due to the accumulation of the outflowing freshwater. In this study, this stratified layer will be referred to as the estuarine plume following Garvine (1986). At this
time, the estuarine plume is small and near the river mouth. In June and July when the Fraser River discharge reaches its annual maximum, the estuarine plume expands seaward and covers most of the Central and Southern Strait and it also increases in thickness. This seasonal development is illustrated in Figure 2. The vertical extent of the estuarine plume can be defined by a salinity of 28 as the bottom boundary, but the surface salinity in the estuarine plume varies, usually between salinities of about 15 and 25.

**Seasonal Development of Phytoplankton Blooms in the Estuarine Plume** In the Fraser River, phytoplankton growth is very low due to high turbidity and a fast flushing rate, and no bloom occurs throughout the year. Once the freshwater flows out into the wide open receiving area in the Strait, both dilution rate and turbidity become rapidly reduced as freshwater is mixed with seawater. Earlier observations by Parsons *et al.* (1969a) and Stockner *et al.* (1979) indicate that the spring bloom starts earlier in the estuarine plume (termed the Fraser River plume in their paper) when the plume is small near the river mouth. At the same time, nutrients (nitrate) decrease in the estuarine plume compared with the adjacent seaward water. With the expansion of the estuarine plume as the Fraser River discharge increases, the spring bloom moves seaward and nitrate becomes depleted in April and May. In spite of periods of undetectable concentrations of nitrate in the estuarine plume, primary production and biomass remain high during the period when the Fraser River discharge reaches its annual maximum in June and July (Clifford *et al.* 1989, 1990, 1991a, 1991b, 1992). This maintenance of high primary production in the estuarine plume is in contrast to the study by Parsons *et al.* (1970, their Fig. 2) in which primary production declined rapidly during this period of time. Their estimate was based on samples collected at different sites representing the entire Strait, whereas the sampling in this study was in the estuarine plume. Thus, the contrast between the study of Parsons *et al.* (1970) and my study actually suggests that the estuarine plume is very productive during the maximum river discharge. The regional maximum in phytoplankton biomass and production occurs near the edge of the estuarine plume (Harrison *et al.* 1991).
Figure 2 An annual cycle of the estuarine plume development in relation to the Fraser River discharge. The volume of discharge is low during winter, medium during spring and highest during late spring and summer.
High biomass and production are believed to be due to entrainment of NO₃ from deeper NO₃-rich water during the maximum river discharge since nitrate in the river is reduced to less than 10 μM during the same period (Drinnan and Clark 1980, Clifford et al. 1992). The entrainment of NO₃ occurs between the riverine plume and deep water near the river mouth and between the estuarine plume and the deep water, which will be discussed further in Chapter 1.

**Effects of Tides on the Formation of the Riverine and Estuarine Plumes**

In the Strait of Georgia, tides are mixed, with the M2, semi-diurnal constituent being dominant. The variation in tidal range is due to the change in lower low water levels (LLW) and the range is as high as 5 m. The Fraser River outflow is modulated by the tidal cycle, as illustrated in Figure 3. During higher high water (HHW), the Fraser River outflow is dammed at the river mouth and the river water accumulates in the river basin. During the ebb tide, the accumulated river water is released and spreads over the estuarine plume. This released outflow forms a distinct surface layer which is referred to as the riverine plume in this study following Garvine (1986). The riverine plume in the Strait of Georgia is not defined by salinity but by a sharp halocline usually occurring in the top 5 m. During the next flood tide, the riverine plume remains in the Strait of Georgia, and, it is subjected to wind and tidal mixing. The riverine plume is usually turbid and shallow (2-5 m) with low salinity (<15). Before it loses its distinct features (low salinity, brownish color, sediments and high silicate) depending on the degree of mixing, the aged riverine plume may be covered by the newly formed riverine plume during the next ebb tide. Thus, the water column structure is often multi-layered. Horizontal mapping of salinity and vertical profiles of salinity and nutrients clearly show the two plumes in the water column based on two distinct sharp haloclines in one vertical profile (Harrison et al., 1991). A distinct mixed layer like the one usually found in the open ocean may be absent. The dynamics of the riverine plume has received
Figure 3  Effects of tidal cycles on the formation of the riverine plume in relation to the estuarine plume.
little study, although it is a highly visible feature in the Strait (LeBlond 1983). Because of
its silt-laden sediments, light penetration is greatly reduced when it spreads over the water
column. Therefore, it has pronounced effects on phytoplankton production.

The movement and extent of the riverine plume depend on the winds and tidal
cycles. During a spring tide when the water level drops to LLW, the riverine plume shoots
out over a large area. With the rise of LLW in the Strait following the spring tide, the
extent of the riverine plume is gradually reduced. When neap tides occur, the extent of the
riverine plume is minimal. During the transition period from the spring to neap tide, the
old riverine plumes are mixed with seawater, and turbidity is reduced as sediment rapidly
settles. These old riverine plumes become part of the estuarine plume.

At the same time, nutrients are carried from the river into the Strait. Although
concentrations of limiting nutrients (nitrogen) in the river are not high (< 10 \( \mu \text{M nitrate} \))
during the annual freshet, entrainment of nitrate as a consequence of the movement of the
riverine plume can be substantial. In addition, strong mixing during the spring tide
transports nutrients upwards. Thus, with a supply of nutrients during the spring tide and
the gradual reduced mixing during the transition period, a phytoplankton bloom may
develop during the neap tide. Such a neap tidal bloom sequence has been observed in the
Strait (Harrison et al. 1991).

Tidal fronts also exist near the shallow banks in the Strait and there is evidence to
suggest high production of phytoplankton at the fronts, although the signal is often smeared
by heavy runoff (Parsons et al. 1983). The physical and biological dynamics of the front
have seldom been studied in the Strait of Georgia, let alone how pelagic-benthic exchange
at the shallow regions during tidal mixing is related to the pelagic biological production in
deeper regions across the fronts (Levings et al. 1983).
Other Estuaries

River Flow-Controlled Dynamics

There is often a spatial and temporal progression of high biomass and production along an estuary. The progression downstream or downplume is mainly due to vertical mixing and turbidity (light). Because of high turbidity in the riverine plume, the euphotic zone is shallow (e.g. 3 m). In any downstream section, the water column can be considered to be stratified to some depth as a result of partial mixing of freshwater with seawater. However, phytoplankton cells at the section can not stay within the (3 m) euphotic zone for a sufficient length of time to generate a bloom, due to horizontal advection and vertical mixing resulting from continuous flow in addition to tidal and wind mixing. When the plume moves downstream, turbidity is reduced and the euphotic zone becomes deeper. As a result, the dilution rate decreases and phytoplankton cells remain in the euphotic zone longer. Wherever the growth rate of phytoplankton exceeds the dilution rate for a sufficient period of time, a phytoplankton bloom will occur. When a river flows out into a relatively open area such as in the Strait of Georgia or the Northern Gulf of Mexico, the dilution rate is rapidly reduced. A bloom can start earlier near the river mouth and progresses seaward with the increasing river discharge. Such blooms have been observed in the Strait of Georgia (Parsons et al. 1969, Stockner et al. 1979) and the Mississippi River areas (references cited below), and in other coastal estuaries (references cited below). In the Columbia River plume along the Oregon coast, the horizontal distribution of nutrients in the upper 10 m showed lower concentrations near the river than in the adjacent areas (Stefansson and Richards 1963), indicating an early onset of the spring bloom. In the Northern Adriatic Sea, low salinity water from Po River discharge in the western part of the sea often took about 2 months to reach the easternmost stations. During the spring, an eastward progression in the chl a standing crop was correlated with this progression in salinity (Revelante and Gilmartin 1976).
**Mississippi River**  In the Mississippi River, the mean monthly discharge is minimal in September, starts to increase rapidly in Jan-Feb and reaches a maximum in April (Ho and Barrett 1977). There is a "downplume" progression of phytoplankton biomass and production with the displacement of the plume further away from the river mouth (downplume) as the river discharge increases. In October 1983 when the river flow was very low, the chl a maximum occurred in the Mississippi estuary (Fox et al. 1987). In the spring (Feb 19-March 10, 1991), the chl a biomass maximum was located downplume of the NO3 maximum, near the river mouth (Hitchcock and Whiteledge 1992). The primary production maximum in April 1988 was also near the river mouth. In the summer (July 17-August 10) of 1990, however, the maximum (higher than in 1988) of the Mississippi River discharge persisted from early April to late June (Lohrenz et al. 1992), causing the river plume to be displaced further southwest (downstream) along with the maximum in NO3 and chl a biomass (Hitchcock and Whiteledge 1992) and primary production (Lohrenz et al. 1992). In the same year, the uptake of nitrate and ammonium was also high at the chl a maximum (Dortch et al. 1992).

In other estuaries, blooms usually start earlier somewhere in the lower part and progress upstream. In those estuaries, their channels or basins are confined and are quite long before they enter the coastal sea. When the river flows downstream, the river channels and the upper estuary are usually so narrow that the dilution rate exceeds the phytoplankton growth rate in spite of a highly stratified water column. As water moves downstream, the estuarine channels increase their width and turbidity decreases. The dilution rate decreases due to both the slow flow rate as a result of the widened channel and the deeper euphotic zone which increases the culture volume as indicated in the model (Fig. 2). In some sections of the river, the growth rate of phytoplankton will exceed the dilution rate. As the river discharge increases during the annual freshet, however, the condition of the dilution rate exceeding the growth rate can not persist long in that section and moves to the next section further downstream. The downstream displacement will not
stop until the river discharge reaches its annual maximum. Where this end section occurs largely depends on the river flow, geography and topography. There, a bloom may occur. The bloom area and its downstream boundary are limited by nutrients from the river since the dilution rate downstream of the bloom area are further reduced. With the decrease in river discharge, the spring bloom progresses upstream since the dilution rate decreases upstream. The upstream progression of the bloom has been shown in estuaries including the St. Lawrence, Chesapeake Bay, San Francisco Bay and the Hudson River estuary.

**St. Lawrence River** Biological studies in the St. Lawrence estuary and the Gulf of St. Lawrence have been conducted extensively (de Lafontaine et al. 1991). The two systems are forced at various temporal and spatial scales by tides, local and large-scale meteorological seasonal and transient events, freshwater runoff and heat flux and perturbations at the edge of the continental shelf (Budgen et al. 1982, de Lafontaine et al. 1991). Biological processes are driven by these physical processes. The runoff in the region is minimum in February and reaches a maximum in May-June, with occasional pulses of considerable magnitude (1000 m$^3$ s$^{-1}$). The spring bloom starts at the end of April in the Southern Gulf, while the bloom in the Gaspé Current region (upstream) does not start until the end of May and persists until the end of June (Steven et al. 1973a, b, c). In the lower St. Lawrence estuary which is further upstream of the Gaspé Current region, the spring bloom is even delayed until June, due to high river flow and high turbidity which result in a high dilution rate and low growth rate of phytoplankton during spring (Steven 1974, 1975, Sinclair et al. 1978, Levasseur et al. 1984). It is suggested that the regional difference in phytoplankton dynamics is probably related to the establishment of stratification following the ice break-up and the timing of freshwater runoff (de Lafontaine et al. 1991). This idea essentially agrees with the culture model. Nutrient distribution shows an increase in nutrients with distance into the Gulf from Cabot Strait during May-August (Coote and Yeats 1979), which agrees with the regional pattern in the development of the spring bloom.
**Chesapeake Bay** In the Chesapeake Bay estuary, the mean annual cycle of freshwater flow from the Susquehanna River is characterized by a spring maximum during March-April and a summer minimum during August-September (Schubel and Pritchard 1986). It is reported that chl a and productivity maxima usually occur seaward of the turbidity maximum where light penetration increases and sufficient nutrients are present to support high phytoplankton growth rates (Harding et al. 1986). Upstream production is low due to high turbidity and rapid flushing rates. The chl a and productivity maxima were found to move with seasons (Fisher et al. 1988, Malone et al. 1988). Fisher et al. (1988) used a mixing diagram to illustrate that phytoplankton accumulation was associated with inorganic nutrient removal. The chl a maximum was associated with a salinity of 15 in March, and with a salinity of 7 in June. The nitrate depletion region occurred at the seaward edge of the chl a maximum and also moved from downstream in March to upstream in June. Malone et al. (1988) showed that seaward of the turbidity maximum, concentrations of dissolved inorganic nutrients decreased rapidly as phytoplankton biomass increased along the salinity gradient. In their study, seasonal variations in biomass were correlated with riverine nitrate input. They also showed that such a upstream progression of the bloom varied with the interannual variation in the river discharge (timing, magnitude and duration). A low discharge occurred in 1985 while a high discharge occurred in 1986. The spring freshet peaked during March 12 - April 9 in 1985 and during a shorter period (March 11-25) with a higher discharge in 1986. The spring bloom peaked in mid-April 1985 compared to mid-May 1986. There was evidence of the bloom progression upstream. The 1985 spring bloom peaked in mid-March at the southern end of the study area and progressed upstream and peaked in late April at the northern end of the study area. A similar progression occurred during 1986, but began in mid-April and ended in mid-May. The delay of the 1986 spring bloom may be interpreted to reflect more rapid flushing of the surface layer in response to higher freshwater flow. It was possible that the spring
bloom in 1986 occurred further downstream of the study area and progressed upstream, which would have accounted for the observed later bloom in the same region as in 1985.

**San Francisco Bay**  San Francisco Bay comprises several different estuarine habitats: Suisan Bay (the upper estuary), San Pablo Bay (middle estuary) and South Bay (lower estuary). Maximal river discharge occurs from December to March (Schemel and Hager 1986). The phytoplankton biomass reaches a seasonal maximum during spring in South Bay, during early summer in San Pablo Bay, and during late summer in Suisan Bay (Cloern et al. 1985). Particularly in the Northern San Francisco Bay, river discharge controls the dynamics of nutrients (Peterson et al. 1985) and phytoplankton (Cloern et al. 1983). During the summer of wet years, the effects of increased river flow often dominate the nutrient distribution (i.e. by conservative mixing), whereas in the summer of dry years, phytoplankton productivity dominates (Peterson et al. 1985), reflecting a relationship between the dilution rate and phytoplankton growth rate in the system.

**Hudson River estuary**  Freshwater transport into the Hudson River estuary is maximal during spring and minimal during summer. The estuary is divided into the upper bay and the lower bay which is connected to the New York Bight in the coastal sea. Although major nutrient concentrations are consistently high, net plankton growth rates are apparently less than flushing rates and therefore, too low to generate blooms in the estuary (Malone 1977). In the same study, a spatial and temporal pattern was observed: in February, chl a increased downstream as far as station (P1) between the lower Bay and the New York Bight, but in late April, the regional maximum moved to the lower part of the upper bay. In July, it progressed further upstream above the upper bay. Unutilized high nutrients in the estuary are transported into the coastal plume in the New York Bight where a higher biomass forms, as was observed in February-March (Malone and Chervin 1979) and also in August (Bowman and Iverson 1978).
**Tidal Effects**

**Tidal Mixing** Tidal mixing acts as a stirring force at the bottom of the water column as it shoals. A tidal front along the coast is a typical example of such mixing. The dilution rate on the mixed side exceeds the growth rate over a tidal cycle whereas phytoplankton production rate is limited by nutrients on the stratified side. The tidal front becomes an ideal region for a balance between mixing and nutrient supply (Le Fèvre 1986). In an estuary, the degree of tidal mixing varies with the channel width and bottom depth in addition to tidal ranges. As a result, the water column in some sections of the estuary is subject to periodic destratification and restratification, which is particularly magnified with spring and neap tidal cycles (Haas et al. 1977, 1981a).

**Responses of Phytoplankton to Tidal Mixing** The coupling of the dynamics of nutrients and phytoplankton production to hydrodynamics induced by tidal cycles has been recently reported (Demers et al. 1986). As they point out, tidal effects are through the proximal agency of light and nutrient fluctuations. Phytoplankton have a physiological capability to respond to the fluctuations. For example, it has been demonstrated, both in the laboratory and in the field, that photosynthetic activity is increased for phytoplankton exposed to cyclical changes in light intensity (Harris and Lott 1973, Jewson and Wood 1975, Harris and Piccinin 1977, Harris 1978, Marra 1978a, b, Demers et al. 1986). Nutrient uptake (especially NH$_4$ and PO$_4$) is enhanced when phytoplankton become nutrient-limited (Conway and Harrison 1977) and when phytoplankton are exposed to limiting nutrients supplied as pulses or continuously, phytoplankton species succession is affected (Turpin and Harrison 1979, 1980, Quarmby et al. 1982). Furthermore, recent studies show that photosynthesis and nutrient uptake can be uncoupled (Turpin et al. 1979), suggesting that phytoplankton take up nutrients at one time and carry out photosynthesis at other times, or visa versa. The possession of these physiological capabilities by phytoplankton gives them an advantage in utilizing tidal cycles by responding to tidal-induced mixing. It appears that the interrelationship between the rate of
tidal processes (dilution rate) and the rate of physiological responses governs phytoplankton growth rates and production. Depending on species specific responses, the physiological changes resulting from vertical mixing and advection can also influence species succession and abundance by altering the vertical position of cells in the water column with respect to light and nutrient fields (Riley et al. 1949, Hutchison 1967, Smayda 1970, Malone 1971, Huntsman and Barber 1977, Falkowski 1980, Harris 1980, Demers et al. 1986).

**Phytoplankton Blooms and Tidal Mixing**  The effects of tidal mixing are manifested with the spring and neap tidal cycles, being strongest during spring tides and least during neap tides. Thus, phytoplankton blooms can occur with a fortnightly cycle, especially when nutrients are depleted in the euphotic zone. The occurrence of intermittent summer blooms has been frequently reported and was suggested to be due to nutrient-supply mechanisms (e.g. Takahashi et al. 1977, Webb and D'Elia 1980, Haas 1981b, Balch 1982). More importantly, tidal-induced mixing and internal waves occur daily and can be a mechanism to maintain primary production after the depletion of nutrients due to the spring bloom.

**Winds**

**Wind Mixing**  Winds are probably the most universal physical factor affecting all aquatic ecosystems. Winds exert effects on various temporal and spatial scales: examples are: oceanic wind-driven surface currents, upwelling, Langmiur circulation and turbulent mixing. When winds act at the sea surface and result in turbulent mixing of the water column, the degree of stratification is reduced and the mixed layer is deepened (Imberger and Parker 1985, Mann and Lazier 1991). Wind events lasting from days to a week can also alter the stratification significantly, sometimes resulting in seiching (Tyler 1984), localized upwelling (Tyler and Seliger 1978, 1981) and intense vertical mixing (Chapter 3). Stronger winds result in more mixing and a greater dilution of phytoplankton, and it takes a longer time to recover. On the other hand, stronger stratification requires a stronger wind to mix the water column to a homogeneity.
Phytoplankton Blooms and Wind Events  It is worth pointing out that a bloom does not necessarily require stratification of the water column if there is no wind mixing. Winds increase the dilution rate of the euphotic zone by mixing. There are beneficial effects and detrimental effects of winds on phytoplankton biomass depending on the frequency, magnitude and duration of winds, as Millet and Cecchi (1992) found in a lagoon ecosystem. During the early period of the seasonal stratification (weak) in spring, the spring bloom cannot develop when a wind event occurs, particularly when strong winds persist. This mechanism was used to explain the delayed bloom in Puget Sound (Winter 1975). On the other hand, when stratification is strong, for example, during summer, a wind event of a similar magnitude can result in a bloom. Such a bloom following a wind event has been reported for Saanich Inlet (Takahashi et al. 1977), a coastal region (Walsh et al. 1978) and an Arctic embayment (Walsh 1981) and for even large oceanic rings (Hitchcock et al. 1987, McCarthy and Nevins 1986). For example, in Auke Bay, Alaska, Iverson et al. (1974) observed that high winds (7 m s\(^{-1}\)) in summer resulted in an increase in NO\(_3\) concentration in the photic zone and a decrease at depth (27 m). The chl a maximum lagged about 3 days behind the wind event (Iverson et al. 1974), which suggested that the productivity maximum might have proceeded the chl a maximum by responding immediately to wind mixing. In a Gulf Stream warm-core ring, a sustained gale force wind altered the surface layer of the ring by deepening the surface mixed layer (Hitchcock et al. 1987) and resulted in an increase in NO\(_3\) concentration (McCarthy and Nevins 1986). As a result, biomass, productivity and nutrient uptake greatly increased (Hitchcock, et al. 1987, McCarthy and Nevins 1986). The latter study found that integrated rates for NO\(_3\) uptake in the mixed layer increased seven-fold. Even from satellite imagery, a bloom was evident once stratification was reestablished after a storm event occurred on April 29-30 in the warm core ring along the Gulf Stream (Brown et al. 1985).
Interactions Among River Discharge, Winds and Tides

In the above section, I have discussed the effects of river discharge, winds and tidal cycles. In nature, these three different driving forces interact with each other. Therefore, it is the interaction that controls dynamics of nutrients and phytoplankton. However, one force can be dominant over another at different times and in different regions. For example, in the Chesapeake Bay, as the runoff pulse due to ice melt and the rise in temperature begins, a stratified system is set up in the upper bay, and the area over which the tide and wind are sufficient for complete mixing of the water column is confined to the much less stratified southern bay (Tyler and Seliger 1989). Thordardottir (1986) explained interannual variations in the timing of the onset of the spring phytoplankton bloom off the coast of Iceland by interactions between freshwater run-off and the wind regime. The bloom normally begins first in a region which receives surface runoff and is sheltered from winds on three sides. The bloom begins to progress along the shore where stratification is delayed by wind mixing and then is facilitated by freshwater runoff. Finally the bloom spreads into the open ocean (Thordardottir 1986). The proximal parameters that can express the outcome of the interactions are dilution rate and growth rate. Thus, temporal and spatial differences in nutrients and phytoplankton biomass and production are due to the balance between dilution and growth. Variations in the balance can be transmitted to higher trophic levels through trophodynamics of pelagic food webs. Thus, even an episode of events can result in an effect on food webs (Walsh et al. 1978, Tyler and Seliger 1989).

II. Effects of Physical Forcing on Trophodynamics of Pelagic Food Webs

Zooplankton

There are direct effects of physical processes on zooplankton biomass distribution. Structures in zooplankton biomass or species composition have been found to be mainly related to such local hydrodynamic features as coastal fronts, internal waves, or tides (Cassie 1963, Wiebe 1970, Fasham et al. 1974, Smith et al. 1976). In highly dynamic estuaries, variations in zooplankton biomass have been reported to be mainly related to
tidal advection processes (Lee and McAlice 1979, Gagnon and Lacroix 1981, 1982, 1983, Maranda and Lacroix 1983). Aggregation of zooplankton was reported to be associated with internal waves or frontal regions (Haury et al. 1979, Herman et al. 1981). Strong relationships between chl $a$ and zooplankton biomass were similarly ascribed to internal waves by Star and Mullin (1981) and Haury et al. (1983). In the Strait of Georgia, zooplankton was also observed to aggregate at the riverine front and at the interface between the riverine plume and the estuarine plume during ebb tides (Mackas et al. 1980, 1988, St. John et al. 1992).

Recent multidisciplinary studies have been more concerned with how physical forcing is transmitted to zooplankton and higher trophic levels via dynamics of nutrients and phytoplankton (Mann 1993). In the classical paradigm of the relationship between phytoplankton and zooplankton, zooplankton rely on phytoplankton abundance for reproduction and their peak abundance usually lags a phytoplankton bloom because they require time to mature and lay eggs (Frost 1980). Therefore, phytoplankton production, particularly during the spring bloom is commonly thought to be lost out of the upper layer by sedimentation (Legendre 1990). The lag of zooplankton peak abundance and the sedimentation of phytoplankton raise some interesting questions: 1) how do zooplankton survive and grow during the lag and reach a peak abundance some time later if most or all phytoplankton cells are lost, and 2) what sustains phytoplankton production during the lag when nutrients are depleted after the bloom? A microbial loop is certainly a good candidate to fill in the lag and to serve as a link between phytoplankton and metazoans. However, a recent review has discussed the controversy about the function of microbial food webs as an energy link to higher trophic levels (Pomeroy and Wiebe 1988). One group, using a simulation model, demonstrated that microorganisms in aquatic food webs are potentially an energy link to metazoans (Pace et al. 1984, Fasham 1985), while another group, based on empirical data of Ducklow et al. (1986), Pomeroy and Deibel (1986) and theoretical considerations by Azam et al. (1983) argued that there was little direct transfer
of carbon to metazoans via active microbial food webs. The latter led Pomeroy and Wiebe (1988) to conclude that even a two-step microbial food chain represents an energy sink for transferring phytoplankton to metazoans. They also rejected the detritus food web as an energy link to metazoans. A recent analysis of the 'microbial loop' by Taylor and Joint (1990) does not support the hypothesis of 'microbial loop' as a food linkage. Assuming no microbial loop, possible answers to the two questions posed above, are: 1) zooplankton feed on settling phytoplankton cells since zooplankton are normally distributed deeper, and 2) nutrients are continuously supplied by physical processes. For the former, little is known although evidence indicate that phytoplankton cells can be kept viable when they sink out of the euphotic zone (Winter et al. 1975). The second possibility certainly exists, as discussed before, phytoplankton cells possess the physiological capability of responding to various physical processes, which are usually vigorous in estuaries. Thus, phytoplankton production can be maintained after a bloom. It is also known that the maximum zooplankton biomass can be found at the depth of the chl a maximum (Anderson et al. 1972, Mullin and Brooks 1972, Hobson and Lorenzen 1972, Youngbluth 1975, Gunderson et al. 1976, Haury et al. 1976, Fairbanks et al. 1980, Ortner et al. 1980, Castro et al. 1991), or at the depth of maximum phytoplankton production (Venrick et al. 1973, Longhurst 1976, Herman et al. 1981). Thus, zooplankton growth is coupled with phytoplankton production via various physical processes. However, the role of the spring bloom in zooplankton dynamics is not yet clear. Phytoplankton growth is on a time scale of hours or days (Harris 1980, Parsons et al. 1984b, Denman and Powell 1984). However, a phytoplankton bloom actually requires a time scale of days or weeks. Perhaps it is a phytoplankton bloom that triggers zooplankton reproduction. An example can be found in a study by Fortier et al. (1992) who reported that the accumulation of large diatoms triggered the reproduction of copepods in the Gaspé Current where eggs and nauplii (the main prey of first-feeding fish larvae) were 10 to 20 times more abundant than in the gyre.
In the Strait of Georgia, *Neocalanus plumchrus* is a dominant copepod during the spring bloom. An unique feature of this species is that it matures and breeds at depth during late summer and winter. The young stages migrate to and reach the surface during March and April (Fulton 1973), independent of the spring phytoplankton bloom (Harrison *et al.* 1983). However, their growth at the surface was determined by phytoplankton abundance and composition (Parsons *et al.* 1969b). It is the variations in the development of the spring bloom that determine the trophic phasing between the copepod and phytoplankton in spring if the timing of migration of this species is assumed to vary little from year to year. Thus, physical forcing by the river discharge, winds and tides results in fluctuations in zooplankton biomass through altering the course of the spring bloom development. Zooplankton fluctuations, in turn, affect juvenile fish since the linkage of fish larvae to microzooplankton has been reported (Jones 1973, Ware 1977, Wyatt 1980, Frank and Leggett 1982, Sameoto 1982).

**Juvenile Fish**

Significant effects on the biological food chains can result from physical activity on virtually all scales from seasonal circulation and stratification patterns to the localized small scale internal wave and turbulent mixing activity (Brandt *et al.* 1986). There are two current approaches concerning the variability of fish production. One is the stock-recruitment model (Ricker 1954), which is based on the assumption that the number of recruits is regulated by the density of spawners; the other concerns the early survival of fish. It was hypothesized that recruitment was determined by the success or failure of the early survival of fish larvae, which is independent of the initial number of eggs produced. The early survival of fish larvae is mainly dependent on the availability of suitable food. It is known as the match/mismatch hypothesis (Cushing 1972), which emphasizes the dependence of larvae survival on the timing between spawning and the cycle of primary and secondary production (Cushing 1982). For example, during the first feeding of herring larvae, there is a "point of no return" (a tolerance) behaviorally and
physiologically, if insufficient food is obtained (Blaxter and Hempel 1963) in a few days. Obviously, nutritious food of the right size must be present in sufficient quantity during the initial feeding of the larvae (Lasker 1985). As Tyler and Seliger (1989) suggested, there are temporal and spatial windows for species which can grow and reproduce at their maximal rates. The timing of an organism's entry into its "window" is critical to its success. When a variation in physical forcing results in a temporal change in the 'window', the success of a species will be affected. Thus, it is logical to conclude that if freshwater runoff variability has a major influence on plankton dynamics, and/or the physical oceanographic characteristics of the larval environment, that such affects should influence year-class strengths (de Lafontaine et al. 1991). In San Francisco Bay, the magnitude of the annual spring bloom (mean biomass and estimated primary production) was found to be strongly correlated with the magnitude of river flow during the wet season (Cloern 1991). The study in the Gulf of St. Lawrence indicated a significant correlation between river discharge and the annual Quebec lobster landings (by taking into account a maturity lag of the lobster) for the Magdalen Islands (Sutcliffe 1972, 1973) from the early 1970s to the mid-1980s, although the same method failed to forecast the steady increase in lobster landings since 1984 (Drinkwater et al. 1991). A similar analysis was extended for the other regions and significant coefficients were obtained (Budgen et al. 1982, Drinkwater and Myers 1987). Also, there was a significant correlation between the cod recruitment and runoff in the summer prior to spawning (de Lafontaine et al. 1991).

In the Strait of Georgia, little is known about food webs (Harrison et al. 1983) although some work has been done on feeding rate and prey size effects (Parsons et al. 1969b). Knowledge on trophodynamic phasing is definitely lacking (Parsons et al. 1988). However, it is known that many fish spend their young stage in the Strait of Georgia (Healey 1978, Ketchen 1983). These fish include the five major Pacific salmon (coho, chinook, chum, pink and sockeye); and other fish such as herring, hake, cod, etc. Their survival and growth must be dependent on food production during their residence time in
the Strait, which is eventually influenced by dynamics of nutrients and phytoplankton production coupled with physical processes.

III. The Strait of Georgia Study — Issues to Investigate

From the previous introduction, it is readily apparent that estuaries are one of the most complex and dynamic marine ecosystems to study. There are rapid and local effects of tides, winds, river discharge, currents, salinity, temperature, and nutrients. To track these changes and understand the short and long term dynamics (physical, chemical and biological) of the estuary, a large number of parameters must be measured quickly, both on the horizontal and vertical scales.

An important advance in this study was the use of a vertical profiling system which provided a detailed data set on salinity, temperature, chl a-fluorescence and nutrients. From these vertical profiles one was able to delineate layers of water with confidence that would not have been possible with point samples from water bottles. Anchoring the ship for 24-36 h with sampling every 2-3 h, allowed one to resolve the effects of tides and consequently horizontal advection on sampling and to make data interpretation with confidence. Spring/neap tidal effects were resolved by sampling daily over a fortnight. Some seasonal and interannual effects were also delineated.

Since inorganic nitrogen is frequently depleted at the surface in late spring and summer in the Strait of Georgia, a substantial effort was focused on trying to understand the influence of salt wedge breakdown, the amount of river discharge, and winds on NO3 entrainment. In the last part of the thesis, the dynamics of the physical and chemical parameters are connected to the biology of phytoplankton blooms and zooplankton grazing.
HYPOTHESES AND OBJECTIVES

Overall Objectives:

To understand the dynamics of nutrients and primary production by studying physical-biological coupling processes during the interaction of the Fraser River discharge, tides and winds:

a) over spatial scales of the riverine and the estuarine plumes;

b) over time scales:

   1. Daily tidal cycles;
   2. fortnightly tidal cycles;
   3. Seasonal changes;
   4. interannual changes.

Hypotheses:

**Entrainment**

1. In late spring and summer, the NO₃-poor estuarine plume was present between the riverine plume and the NO₃-rich deep water beyond the river mouth;

2. The NO₃-poor estuarine plume invades the river with the advance of the salt wedge, forming a barrier for entraining NO₃ from the NO₃-rich deep water by the river outflow;

3. The amount of entrained NO₃ is determined by the amount of the entrained deep water.

**Spring Bloom**

4. The onset of the spring bloom occurs early in the estuarine plume near the river mouth compared to its adjacent regions and the spring bloom progresses seaward as river discharge increases.
Specific Objectives:

**Entrainment**

1. to examine how NO$_3$ entrainment is affected by tides;
2. to examine how NO$_3$ entrainment is affected by the magnitude of river discharge;
3. to examine how NO$_3$ entrainment is affected by winds;
4. to estimate the contribution of entrained NO$_3$ relative to the river-borne NO$_3$.

**Spring Bloom**

5. to examine the effects of winds on the spring bloom;
6. to examine how the tidal cycles and the interannual variability of the Fraser River discharge, and winds are related to the spring bloom and the trophodynamic phasing between phytoplankton and zooplankton.
GENERAL MATERIALS AND METHODS

Definition of the Riverine and Estuarine Plumes

A riverine plume is formed daily during lower low water (LLW) as the river outflow spreads out into the Strait of Georgia over the estuarine plume. This released outflow forms a distinct surface layer which is referred to as the riverine plume in this study. It is often distinct visually, especially between May and August because of the large river discharge and high sediments in the water. The salinity ranges from nearly 0 at the river mouth, to < 10 at its outer edge (depending on the amount of salt water entrained as the plume moves seaward). The silicate concentration is abnormally high (60-100 \( \mu \text{M} \)). The riverine plume is several meters thick (1-5 m) and in vertical profiles of salinity, its vertical boundary is apparent as a strong halocline between the estuarine plume or the deep seawater beneath it (Figure 3). Further details on its formation and the effects of tides and river discharge are given in the GENERAL INTRODUCTION (see the section on Effects of Tides on the Formation of the Riverine and Estuarine Plumes and also Figure 3).

The estuarine plume is the remains of previous riverine plumes formed especially during wind events and during the transition from spring to neap tides. During a spring tide (and assuming no wind) the riverine plume reaches its maximum size because the LLW is the lowest it gets during the 14 day spring/neap tidal cycle. During the next 7 days as the tides move from spring to neap tides, the LLW gets progressively higher and the riverine plume formed each day gets smaller and smaller. These old riverine plumes form part of the estuarine plume. The estuarine plume has a higher salinity (~ 15-25) and lower sediment load (reduced turbidity) than the riverine plume. Its outer boundary is not visually distinct except on some occasions in the southern Strait near the Boundary Passage. The vertical extent of the estuarine plume is usually bounded by a salinity of 28. See Figures 2 and 3 in the GENERAL INTRODUCTION for further details.

Station Locations

The stations were mainly along a transect from the river mouth near Steveston (R1) to Stn 2, 8 km seaward of the Fraser River mouth (Main Arm) (Figure 1.1), from S2
(=Stn 2) northwards to S1 (=Stn 1) in the Central Strait (Figure 4.1). The exact coordinates of the stations are given in Appendix 1. The sampling strategy for the first part of the transect was to examine the dynamics of nutrients associated with the movement of the riverine plume in the Fraser River estuary, and for the second part, to examine the development of the spring bloom associated with the variation in the estuarine plume.

**Sampling and Data Processing**

At each station, a vertical profile (0 - 25 m) of temperature, salinity, current velocity (when the S4 was used), *in vivo* fluorescence and selected nutrients (nitrate+nitrite, ammonium, phosphate and silicate) was obtained. An opaque rubber hose (3.5 cm ID) was fixed to an InterOcean S4 current meter (giving depth, salinity, temperature, and current velocity) or an InterOcean CTD. As the S4 or CTD was lowered (ca. 1 m min⁻¹), water was pumped to the deck of the research vessel with a Moyno pump (flow rate ca. 20 L min⁻¹) or a larger pump (ca. 100 L min⁻¹). A Turner 111 fluorometer equipped with a flow-through cell measured *in vivo* fluorescence. A Technicon AutoAnalyzer® II was used to determine selected nutrients. Pumping time lags and machine analysis delays were carefully measured in order to coordinate sample values with the position (depth) in the water column. The water entering the AutoAnalyzer® was unfiltered. These data were logged onto a computer and plotted in real-time using a custom software program (Jones *et al.* 1991). In this way, each sampling produces a high-resolution continuous vertical profile of those 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 ship motion. Nutrient concentrations in vertical profiles were corrected for baseline drift.

Incident solar irradiance (P.A.R.) was continuously monitored with a Li-Cor (model Li-185) light meter equipped with a Lambda Instruments 190S Surface Quantum
Sensor. Total daily irradiance (0530 to 2200 h PDT) was calculated by integrating the area under the light curve (400-700 nm) and used for calculating daily primary production.

Subsurface light intensities were measured with Li-Cor Li-185B light meter equipped with a Lambda Instruments 192S Underwater Quantum Sensor. Water samples were usually collected from six depths which were selected on the basis of light penetration (usually 100, 55, 30, 10, 3 and 1 % of surface irradiance), using 5 L PVC Niskin water bottles equipped with silicon rubber springs to minimize rubber toxicity (Price et al. 1986). Samples were shielded from direct sunlight and transferred to 20 L Nalgene carboys and immediately taken into the ship's laboratory. Subsamples for nutrient analyses were removed with an acid-washed syringe and gently filtered through combusted (460°C for 4 h) Whatman GF/F filters into acid washed polyethylene bottles. Nitrate (plus nitrite), ammonium, phosphate, and silicate were analyzed immediately on board ship and samples for urea were stored frozen on board ship and analyzed ashore.

Although the deepest sample was usually from the 1% light depth, deeper samples were taken if the chl a maximum was below the 1% light depth.

**Nutrient Analysis**

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

Nitrate (plus nitrite) and ammonium were determined following the procedures of Wood et al. (1967) and Slawyk and MacIsaac (1972), respectively. Urea was determined by the diacetyl monoxime thiosemicarbazide technique described by Price and Harrison (1987), with the following modifications: 1) the temperature of the oil bath was kept at 90°C, and 2) the waste tube returned to the pump, thus forming a completely enclosed system. Silicate was determined following Armstrong et al. (1967), and phosphate according to Hager et al. (1968).
Note: phosphate concentrations of filtered water samples from bottle casts were lower than unfiltered samples, and therefore, these samples may underestimate the biologically available phosphate because phosphate is adsorbed to sediments which were present usually in large amounts in samples from the river and Stn 2 near the river mouth.

14C Uptake

NaH\textsuperscript{14}CO\textsubscript{3} (New England Nuclear; 4.5 mCi.mmol\textsuperscript{-1}) was prepared following Strickland and Parsons (1968), filter-sterilized (0.22 \(\mu\)m filters) and refrigerated before use. Disposable polypropylene pipette tips used for \textsuperscript{14}C incubations were soaked in 10\% HCl and thoroughly rinsed with distilled deionized water prior to use, in order to reduce trace metal contamination (Fitzwater \textit{et al.} 1982).

Carbon uptake rates were measured by adding 2.0 \(\mu\)Ci NaH\textsuperscript{14}CO\textsubscript{3} to duplicate 50 mL samples in transparent borosilicate glass tubes. After thorough mixing, the bottles were incubated for ca. 4 h in simulated in situ deck incubators corresponding to the light levels from which the samples were taken (achieved by placing various layers of neutral density screening around each bottle). Samples were cooled with flowing surface seawater. At the end of the incubation period, cells were collected by filtration (<100 mm Hg) onto Whatman GF/F glass-fibre filters. Filters were placed so that they laid flat on the bottom of glass scintillation vials containing 0.2 mL of 0.5 N HCl, which removed inorganic \textsuperscript{14}C (Lean and Burnison 1979). After 2 h, 10 mL Aquasol II or Ecolume scintillation fluor was added to each vial.

Zero-time blanks were used to correct for cell and bottle adsorption of \textsuperscript{14}C. Total \textsuperscript{14}C activity of the stock solution was determined by adding 20-25 \(\mu\)L H\textsuperscript{14}CO\textsubscript{3} stock solution (nominal activity 0.4-0.5 \(\mu\)Ci) to scintillation vials containing 0.2 mL phenethylamine, and then adding 10 mL of scintillation fluor (Iverson \textit{et al.} 1976). Samples were counted on Beckman LS900 liquid scintillation counter, and quench correction was by the channels-ratio method. Carbon uptake rates were calculated according to Parsons \textit{et al.} (1984a). Total carbon dioxide was determined using a
modification of Parsons et al.'s (1984a) method; sample volume was decreased from 100 to 20 mL, and the volume of 0.01 N HCl added was decreased from 25 to 5 mL.

Hourly $^{14}$C productivity rates were converted to daily productivity rates by dividing the total carbon uptake by the percentage that the incubation period represented of the total daily irradiance. For example, if the $^{14}$C uptake over a 4 h incubation was 10 mg C m$^{-3}$ (4 h)$^{-1}$ and the integrated irradiance over the 4 h incubation period was 40% of the total daily irradiance; the daily production would be $10/0.40 = 25$ mg C m$^{-3}$ d$^{-1}$.

Primary productivity per m$^2$ was calculated by averaging the measured productivity between two depths and multiplying by the depth interval (Ichimura et al. 1980). The sum of these measurements gives the daily production integrated over depth from the surface to 1% light depth, expressed as mg C m$^{-2}$ d$^{-1}$.

**Chl a, Particulate Organic Carbon and Nitrogen**

Samples for chl $a$, normally 500 mL, were filtered onto Whatman GF/F filters. Filters were placed into 10 mL of 90% acetone and sonicated for 10 min in ice-cold water (in the dark). After sonication, chl $a$ was extracted in the cold and dark for 24 h in 90% acetone, and analyzed by *in vitro* fluorometry (Parsons et al. 1984a) using a Turner Designs model 10 fluorometer. Samples for particulate organic carbon and nitrogen (generally 500 mL; POC and PON), collected on combusted (460 °C for 4 h) Whatman GF/F filters, were stored frozen in a desiccator. After the cruise, the filters were dried for 24 h at < 60 °C and analyzed with a Carlo Erba model NA 1500 CNS elemental analyzer, using the dry combustion method described by Sharp (1974).

$^3$H Uptake by Bacteria

Bacterial production assays (Fuhrman and Azam 1980, 1982) were initiated as soon as possible following sample collection. Duplicate killed (3.7% formaldehyde, final concentration) and active 10 mL samples were placed in 30 mL syringes and 15 mM $^3$H-thymidine (methyl-$^3$H-thymidine; New England Nuclear, 72 Ci mmol$^{-1}$) added. Samples were incubated in the dark for 60 min at simulated *in situ* temperatures. Incubations were
terminated by the addition of 10 mL ice cold 10% trichloroacetic acid (TCA), and samples filtered through 0.22 μm Millipore cellulose nitrate filters. Each filter was washed twice with 5 mL ice cold TCA and placed in a scintillation vial to which fluor (Scintiverse II, Fisher Scientific) had been added. Samples were counted using a Beckman LS3801 liquid scintillation counter, and the quench correction was done by the channels-ratio method (Cooper 1977). The factor used to convert rate of thymidine uptake to bacterial production (i.e. mg C m\(^{-3}\) d\(^{-1}\)) was 1.3 x 10\(^{18}\) (S. Turner, pers. comm). Integrated bacterial production (mg C m\(^{-2}\) d\(^{-1}\)) was calculated in the same way as integrated \(^{14}\)C primary production (see above).

**Microflagellate Counts**

Five mL samples (preserved as described for bacteria) were filtered (< 100 mm Hg) onto 2 μm pore size, 25 mm diameter Nuclepore filters prestained with Irgalan black, and the microflagellates stained with DAPI (Sigma Corp.). The filters were examined using an epifluorescent microscope. Microflagellates containing chl \(a\) emit orange fluorescence with longer wavelength emissions (Sherr and Sherr 1983). Therefore, cells containing chl \(a\) were identified as autotrophic eucaryotic cells less than 10 μm in diameter, with flagella that emitted blue fluorescence (Zeiss filter set 48 77 01 (BP 450-490, FT 510 and LP520) was used). Heterotrophic microflagellates were identified as those eucaryotes less than 10 μm in diameter which fluoresced blue (filter set 48 77 01 (BP 365/10, FT310 and LP395)) but had no autofluorescence due to their lack of chl \(a\). Total microflagellate numbers were calculated as the sum of autotrophic and heterotrophic microflagellates.

**Phytoplankton Counts**

Two hundred and fifty mL samples were preserved in Lugol's (Parsons et al. 1984a) and stored in the dark until analysis. Ten mL subsamples were settled (24 h) and counted on a Zeiss inverted microscope following the method of Utermöhl (1958). Typically, at least 400 cells were counted per sample. A magnification of 200X was used
for larger phytoplankton such as diatoms, while a magnification of 500X was used for nanoflagellates.

Cells were identified using the following categories: *Skeletonema costatum*, *Chaetoceros compressus*, *Chaetoceros radicans*, other *Chaetoceros* spp., *Thalassiosira* spp. other centric diatoms, pennate diatoms, photosynthetic dinoflagellates, heterotrophic dinoflagellates, cryptomonads, *Chrysochromulina* spp. and *Micromonas* spp. Biovolume \((\mu\text{m}^3 \text{ L}^{-1})\) was calculated for discrete species by multiplying the cell abundance (cells L\(^{-1}\)) by the mean cell volume \((\mu\text{m}^3)\) for that species. Cells volumes were determined by measuring the species dimensions, and then using simple geometric shapes to represent the species. At least ten cells were measured for the cell volume estimates.

**Zooplankton**

Zooplankton samples were obtained using a closing SCOR net (303 \(\mu\text{m}\) mesh, 57 cm diameter) towed vertically at ca. 1 m s\(^{-1}\). Sometimes a small mesh bongo net (54 \(\mu\text{m}\) mesh, 20 cm diameter) was used. Filtering efficiency of the nets was determined using a calibrated flow meter, which was removed during sampling in order to minimize the pressure wave in front of the net. Triplicate vertical hauls were made over two depth ranges, 10 m to the surface (the euphotic zone) and near the bottom to the surface. Samples were preserved in 5% borax buffered formalin for later identification and enumeration.

**T-S Diagrams**

T-S diagrams were frequently used to distinguish three water masses: the riverine plume, the estuarine plume and the deep seawater below the estuarine plume. When two water types A and B with different salinity and temperature are mixed in any proportion, the resulting water type C with a new salinity and temperature will be on the straight line between A and B. From the distance of C to A or B, the proportion of A and B in C can be calculated. Similarly, if three water types (A, B and C) are mixed in any proportion, the resulting water type will be within the triangle formed by A, B and C. The relative
proportions of each type can be calculated according to equations (1), (2) and (3) on the following.

A T-S diagram can be produced from each vertical profile. All the T-S diagrams from vertical profiles which were sampled during one transect, or one time series made within 24 h were plotted on one graph (e.g. Figure 4). Then the following procedures were used:

1. Plot the temperature and salinity in the river as \((S_1, T_1) = (0, T_1)\) where \(T_1\) is directly measured. \((0, T_1)\) are the characteristic S and T values for the river.

2. Obtain a maximum salinity and a minimum temperature from the graph as the characteristic S and T of the deep seawater \((S_3, T_3)\).

3. Determine the characteristic S and T of the estuarine plume \((S_2, T_2)\) by extrapolating the linear trends on the outer edge of the triangle, forming a triangular envelope as shown in Figure 4.

4. The equations for conservation of salinity, temperature and volume (Pickard & Emery, 1982):

\[
V_1*T_1 + V_2*T_2 + V_3*T_3 = T_i \quad (1)
\]

\[
V_1*S_1 + V_2*S_2 + V_3*S_3 = S_i \quad (2)
\]

\[
V_1 + V_2 + V_3 = 1 \quad (3)
\]

where \(T_i\) and \(S_i\) are the measured temperature and salinity values, respectively, at a depth \((D_i)\) in a vertical profile as shown in Figure 5, and \(V_1, V_2\) and \(V_3\) are the relative proportions per unit of water volume \((1 \text{ m}^3)\) of freshwater, the estuarine plume and the deep seawater with \((S_i, T_i)\) at \(D_i\), respectively.

5. Calculate the relative proportions \((V_{1i}, V_{2i} \text{ and } V_{3i})\) of the three water types at \(D_i\) by resolving the three equations.
Figure 4. T-S diagrams from a time series of vertical profiles taken on May 31-June 1, 1990 were plotted to determine the salinity and temperature (S2, T2).
Figure 5. A) Vertical profiles of salinity and temperature showing a depth $D_i$ with salinity and temperature ($S_i$, $T_i$); B) the vertical distribution of proportion of freshwater (FW), the estuarine plume (EP), and the deep water (DW) calculated from the equations (1), (2) and (3) in the text, showing the calculated proportion $V_{1i}$, $V_{2i}$ and $V_{3i}$ at $D_i$ for FW, EP and DW, respectively. Integrating $V_1$, $V_2$ and $V_3$ over depth to $D_0$ is the equivalent thickness of FW, the entrained estuarine plume (EEP) and the entrained deep water (EDW), respectively.
6. At the depth $D_0$ (Figure 5) at which $V_1$ (freshwater proportion) first equals 0, integrate $V_1$, $V_2$ and $V_3$ each vertically over depth to $D_0$. For example, an equivalent thickness of freshwater =

$$\frac{D_0}{D_i=0} \sum \frac{(V_{i-1} + V_{i+1})}{2} * (D_{i+1} - D_i)$$

and do the same calculation for $V_2$ and $V_3$. The integrated values are the equivalent thickness of the freshwater, the entrained estuarine plume (EEP) and the entrained deep seawater (EDW), respectively. The sum of three equivalent thicknesses is the depth of freshwater penetration ($D_0$). The equivalent thickness of the estuarine plume is obtained by integrating the proportion of it over the entire water column instead of to $D_0$.

The method for calculating the equivalent thickness of different water types in the water column is basically according to Pickard and Emery (1982). The equivalent thickness expresses a relative proportion (in meters) of each water type over a square meter of the water column. It is the same as compacting each water type into one layer.

The Practical Salinity Scale is used in the text and figures for salinity measurement. Therefore, the salinity values have no units, but they are equivalent to %o (Pond and Pickard 1978).

The amount of entrained $NO_3$ ($Ent. NO_3$) is defined as the amount of $NO_3$ in the water column minus the contribution of river-borne $NO_3$ above the freshwater penetration depth $D_0$. Thus,

$$Ent. NO_3 = \sum_{D_i=0}^{D_0} \left( \frac{C_i + C_{i+1}}{2} - Cr \frac{V_{i-1} + V_{i+1}}{2} \right) * (D_{i+1} - D_i)$$

where $C_i$ is the measured concentration at $D_i$ in a vertical profile of $NO_3$; $Cr$ is the concentration in freshwater, and $V_{1i}$ is the proportion of freshwater at $D_i$ ($Cr*V_{1i}$ = the concentration contributed by freshwater to the measured $NO_3$ concentration).
The integrated fluorescence (Int Flu) in the water column contributed by the proportion of the estuarine plume is calculated by the following integration:

\[
\text{Int Flu} = \sum_{D_i=0}^{20m} \frac{V_{2i} \cdot F_i + V_{2i+1} \cdot F_{i+1} \cdot (D_{i+1} - D_i)}{2}
\]

where \( F_i \) is fluorescence at \( D_i \). If mixing processes dominate biological processes in distributing fluorescence in the water column, a correlation between Int Flu and the equivalent thickness of the estuarine plume (EP) along a transect or over a time series should exist. Each vertical profile gives a pair of Int Flu and equivalent thickness of the estuarine plume values.

**Data on Tides, Winds and River Discharge**

Observed hourly tidal heights were provided by the Tides and Current Section, Institute of Ocean Sciences, Sidney, B.C. 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 Vancouver International Airport and provided by the Atmospheric Service, Environment Canada.
CHAPTER 1

ENTRAINMENT OF NITRATE IN THE FRASER RIVER PLUME AND ITS BIOLOGICAL IMPLICATIONS: EFFECTS OF THE SALT WEDGE

INTRODUCTION

Entrainment is one of principal physical processes which causes the transfer of salt water into the freshwater in an estuary. It usually occurs when a surface freshwater layer flows over a layer of salt water underneath and the velocity shear between the two layers is sufficiently strong. The shear instability can be observed with an echo sounder (Brandt et al. 1987, Geyer and Farmer 1989). During the process of upward entrainment in estuaries, salinity increases in the surface layer. The resulting concentration of nutrients, however, depends on concentrations of source nutrients. When the river has a lower nutrient concentration than the seawater, entrainment will result in an increase in concentration of that nutrient with salinity in the surface layer; if the river has a higher nutrient concentration, entrainment of the seawater results in a dilution. In the St. Lawrence estuary, intensive entrainment occurs at the head of the Laurentian Channel (Ingram 1979). This entrainment is suggested to play an important role in nutrient supply, by acting as a "nutrient pump" and enhancing biological production in the Gaspé Current (Steven 1974). Whether entrainment leads to dilution or enrichment of nutrients in the surface layer, it is important in understanding the dynamics of nutrients and phytoplankton production. However, there are few quantitative studies on the dynamics of nutrients associated with mixing processes caused by entrainment (Mann and Lazier 1991).

As the Fraser River discharge changes over seasons, NO₃ concentrations in the river change seasonally, with the highest values in February (ca. 14 μM) and the lowest in August (down to 2 μM) (Drinnan and Clark 1980). Because the estuarine plume is a stratified water column, nutrients (inorganic nitrogen) are often undetectable during late spring and summer (Harrison et al. 1991, Clifford et al. 1989, 1990, 1991). When the Fraser River outflow is released during ebb tides, it forms the riverine plume in the Strait
which spreads over the estuarine plume. Thus, both plumes entrain salt, with the riverine plume entraining salt from the estuarine plume and the latter entraining the deeper seawater below. In late spring and summer, no NO₃ will be entrained from the estuarine plume into the riverine plume. Horizontal mapping of salinity and vertical salinity and nutrient profiles clearly showed the two plumes in the water column based on two distinct sharp haloclines (Harrison et al. 1991). Undetectable nitrate in the estuarine plume was observed as a minimum zone at an intermediate depth in the vertical profile when the riverine plume spread over the estuarine plume (Harrison et al. 1991). The entrainment from the estuarine plume to the riverine plume results in an increase in salinity but a decrease in concentration of NO₃ in the riverine plume compared to the river.

Estimates of entrainment of salt in the Strait of Georgia due to the Fraser River runoff have been made (Cordes et al. 1980). However, such an estimate based on salt conservation without knowledge of the nutrient concentrations does not allow an estimate of the entrainment of nutrients.

The objectives of this study were: 1) to investigate if the NO₃-poor estuarine plume (summer months) invades the river with the salt wedge on the flood tides and becomes a barrier to nutrient entrainment by the surface waters since it lies between the river and the NO₃-rich deep seawater; 2) to determine if entrainment of NO₃ takes place in association with mixing processes; 3) to determine the effects of tides on entrainment; and 4) to investigate the biological significance of the entrainment. This chapter also provides some background and observational data for the subsequent two Chapters (Chapters 2 and 3).

MATERIALS AND METHODS

The study area and stations with their depths are shown in Figure 1.1. The end of the jetty extending into the Strait is called Sand Heads and is considered to be the mouth of
Figure 1.1 Map of the study area at the mouth of the Fraser River, British Columbia, Canada and the stations R1, R2, R3, R4, R5, R6, R7 and Stn 2 along the transect. Station depths: R1 = 15 m, R2 = 20 m, R3 = 12 m, R4 = 15 m, R5 = 45 m, R6 = 96 m, R7 = 146 m and Stn 2 = 200 m. The dotted line shows the edge of the shallow banks which are exposed at lower low water.
the river. Note that the depth beyond this jetty drops sharply from 15 to 200 m within 8
km. Stations along a transect at R1, R2, R3, R4, R5, R6, R7 and Stn 2 were sampled for

The methods for vertical profiles of salinity, temperature, fluorescence, and nitrate,
nutrient analyses, data processing for vertical profiles, and T-S diagrams are described in
GENERAL MATERIALS AND METHODS.

Nutrient uptake experiments were conducted by taking a water sample at the depth
of the chl $a$ maximum and incubating a subsample on deck at different irradiances ranging
from darkness and 1% to 100% surface light. The different irradiances were achieved by
placing various layers of neutral density screen over the incubated samples. The incubated
samples were cooled with flowing surface seawater. During the 9 h incubation period,
nutrient concentrations were measured at the beginning, middle and end of the incubation.
Thus, two uptake rates were obtained for each nutrient and averaged.

CONCEPTUAL MODEL

The results below clearly demonstrate the presence of the three water masses in the
Fraser River estuary: the riverine plume, the estuarine plume and the deep water. The
mixing among them and entrainment of NO$_3$ are controlled by tides and river discharge.
Based on the previous studies (Stronach 1981, Ages and Woollard 1988, Geyer and Farmer
1989) and this study, a conceptual model is put forward to describe the processes of
entrainment associated with the dynamics of the salt wedge as shown in Figure 1.2.

During a flood tide, the salt wedge invades the river at depth. The outflow of the
freshwater layer slows down (Geyer and Farmer 1989). At the same time, the freshwater
layer becomes thinner, indicating that the salt wedge entrains freshwater downwards
Figure 1.2 The conceptual model illustrating the riverine plume, the estuarine plume and the deep seawater: A) a salt wedge invades the river during a flood tide and the estuarine plume dams the river outflow at the river mouth during higher high water (HHW), and B) the riverine plume is formed as the salt wedge retreats during an ebb tide. Zone I illustrates a wall-like structure of deep seawater.
A) Flood Tide - HHW

Riverine Front

Estuarine Plume

River

Salt Wedge

Halocline

Deep Seawater

B) Ebb Tide - LLW

Riverine Plume

Wall

Halocline

Deep Seawater
(Geyer and Farmer 1989), especially during spring flood tides. This downward entrainment was observed in the Strait (Stronach 1981) and in the Duwamish River estuary in Puget Sound, Washington (Partch and Smith 1978). The maximum entrainment probably takes place at the interface between the freshwater and the salt wedge at the leading edge of the salt wedge when it is advancing upstream. By the end of the flood tide, the river outflow can be completely dammed. The position of the salt wedge head depends on tidal phase and magnitude of river discharge (Geyer and Farmer 1989, Kostaschuk and Atwood 1990). The estuarine plume is pushed up at the river mouth and can be pushed into the river at the surface. Little upward mixing takes place during the advance of the salt wedge (Geyer and Farmer 1989).

During a tidal ebb, three distinct phases of the flow can be recognized (Geyer and Farmer 1989). In the first phase, the surface flow starts to increase downstream while the salt wedge remains stagnant. There is little mixing between the freshwater layer and the lower water layer during this phase. In the second phase, the salt wedge starts to retreat as the tidal level falls. Intensive entrainment takes place between the two layers. As a result, the halocline broadens (as viewed in a vertical profile). At the same time, the freshwater layer becomes thicker and the bottom mixed layer in the salt wedge becomes thinner. This process may lead eventually to the collapse of the salt wedge in the last phase (Ages and Woollard 1988, Geyer and Farmer 1989). After the salt wedge is broken down and swept out of the Fraser River, a wall of high salinity water is formed at the river mouth (Figure 1.2B: Zone I) (Stronach 1981, Geyer and Farmer 1989, Kostaschuk and Atwood 1989). When the river outflow hits this wall, it will move over it and entrain deep water from it. The area of this wall exposed to the riverine plume depends on both tidal levels and river discharge rate. Also, the area and NO$_3$ concentration in the wall of deep seawater affect the amount of NO$_3$ entrained.
RESULTS AND DISCUSSION

The transect started at the higher high water (HHW) on August 13 and ended 1.25 h after the lower low water (LLW) on August 14 (Figure 1.3). Stations R3 and R4 were also visited during a spring and neap tide in June, 1989.

1. Transect Results

Salinity, T-S diagram, Proportion and Equivalent Thickness

Although spatial changes in vertical profiles along the transect shown in Figure 1.4 can not be separated from temporal changes due to tidal effects, they and their corresponding T-S diagrams (Figure 1.5) indicate the number of water masses present in the water column, how they are mixed relatively (Figure 1.6) and whether entrainment of NO₃ occurs.

Figure 1.4 shows the salinity profiles; surface salinity increased downstream from R1 to Stn 2. A surface mixed layer was present only at R1 and Stn 2. The major halocline became shallower and sharper as one moved just outside the river mouth (R5) from both sides (from R1 to R5 and Stn 2 to R5). These changes were probably due to the sudden shoaling which results in the formation of the high salinity wall at the river mouth as indicated in the conceptual model (Figure 1.2B). There was a mixed layer (about 2 m thick) within the halocline at R2. The mixed middle layer was eroded downstream in the river channel and was absent at the river mouth (R4). Beyond the river mouth, the water column contained the middle mixed layer and even became multi-layered (R6, R7 and Stn 2, Figure 1.4). The T-S diagrams (Figure 1.5) show that the multi-layers consisted of different water masses. There were three water masses indicated by the different slopes of three straight line segments in the T-S diagrams at R6 and R7 (Figure 1.5). The straight line segment between the lowest salinity and medium salinity (14) indicates a water mass formed from the mixing of the freshwater and the water of the estuarine plume. This water mass is referred to as the riverine plume. The second mixing line segment between the medium salinity (14) and higher salinity (25), characterizes the estuarine plume water.
Figure 1.3 Change in tidal height with time during the sampling period along the transect on August 13-14, 1991. The arrows indicate the sampling time at which the station was visited and "-2" denotes the second visit.
Figure 1.4  Vertical profiles of salinity, NO$_3$ (μM) and \textit{in vivo} fluorescence (in relative units) at R1, R2, R3, R4, R5, R6, R7, and Stn 2 (Figure 1.1) along the transect on August 13 and 14 (Figure 1.3).
Figure 1.5 Temperature-salinity (T-S) diagrams for the vertical profiles at the same stations along the transect as in Figure 1.4.
Figure 1.6  Vertical distribution of the proportions of the riverine plume, estuarine plume and deep water for the vertical profiles at the same stations along the transect as in Figure 1.4.
Proportion (%)
The higher temperature at S=14 probably resulted from solar heating of the surface of the estuarine plume in the Strait of Georgia before the riverine plume spread over it. The last water mass (the line segment for salinity > 25) was the deep seawater which was much less influenced by daily freshwater discharge. Apparently, the estuarine plume had invaded the river with the advance of the salt wedge (the middle mixed layer at R2). The T-S line becomes straighter at the river mouth as a result of intensive entrainment; there was direct contact between freshwater and the deep seawater allowing entrainment of NO₃.

Vertical profiles at R7-2, R6-2, R5-2 and R4-2 (Figure 1.4) are from a return trip to R7, R6, R5 and R4, respectively, during the late stages of the ebb tide and the beginning of the flood tide (Figure 1.3). The structure of the water column changed dramatically compared to the previous profiles a few hours earlier at the same stations. The halocline was thicker at R4 and R5 compared with the first visit. One clear piece of evidence for entrainment of the deep seawater is that at R6-2 the surface temperature (16 °C) was lower than the river temperature of 17 °C, indicating entrainment of colder water during movement of the riverine plume.

A T-S diagram can indicate how many water masses there are in the water column but it does not tell the volume of each water type. Figure 1.6 shows the vertical distribution of relative proportions of the freshwater, estuarine plume and deep seawater. The proportion of the freshwater and the depth to which the freshwater penetrated (proportion = 0) decreased downstream. The estuarine plume proportion at the river mouth at R4 was minimal among all the stations. It is worth pointing out that the proportion of the deep seawater at R6-2 (Figure 1.6) was higher at the surface (23%) than at 5 m (10%), corresponding to the colder temperature at the surface in the T-S diagram (Figure 1.5; R6-2). This is clear evidence for entrainment of deep seawater to the surface and hence, an increase in NO₃ concentration was observed to occur at the surface at R6-2.
NO$_3$

At R1, the surface NO$_3$ concentration was 3.2 $\mu$M (Figure 1.4) and it is taken to represent the NO$_3$ concentrations in the river water. The surface NO$_3$ value remained constant at 3.2 $\mu$M at R2, R3 and R4 in the river, while the deep water NO$_3$ increased from 13 $\mu$M at R1 to 25 $\mu$M at R4. Although no entrainment of NO$_3$ was seen at the surface, the decrease in NO$_3$ concentrations in the bottom and the T-S characteristics clearly show that some mixing occurred in the sub-surface. NO$_3$ concentrations were similar at the surface at R5, R6 and R7, but NO$_3$ was undetectable at the surface and only 10 $\mu$M at 15 m at Stn 2. An unique feature in the vertical profiles of NO$_3$ was a minimum concentration at an intermediate depth at each station except at Stn 2. NO$_3$ concentrations in the minimum zone increased from R7 to R5, suggesting an erosion of this minimum by more entrainment of NO$_3$-rich water into the riverine plume.

Entrainment of NO$_3$ was observed during the return trip from Stn 2 up to the river. The surface NO$_3$ concentration was 6 $\mu$M at R6-2 (Figure 1.4) which was twice as high as 3.2 $\mu$M in the river water. Surface NO$_3$ concentrations were 4.5 and 4 $\mu$M at R5-2 and R4-2, respectively. The question is: where did the increased NO$_3$ concentrations come from? Since NO$_3$ was undetectable in the surface estuarine plume (Stn 2 and R7-2), the potential sources of NO$_3$ were the river and the deep seawater. NO$_3$ concentrations were 3.2 $\mu$M in the river, and $>10$ $\mu$M in the deep seawater. Assuming no temporal changes in river NO$_3$ during such a short time, the only way to increase the surface NO$_3$ to a higher concentration than the river was from the deep seawater. However, there was a NO$_3$ minimum (lower than the river NO$_3$ concentration) between the riverine plume and the deep seawater at the stations R6 and R5, which indicated that the increased NO$_3$ concentrations could not possibly occur through local vertical mixing at R6 and R5. Therefore, the higher NO$_3$ concentration observed at R6-2 must have been entrained from the deep NO$_3$-rich seawater at sites closer to the river. However, one would expect that the surface NO$_3$ concentration at R5-2 would be higher than at R6-2, or that there would
be no minimum in NO$_3$ concentration at R5-2, because the NO$_3$ concentration at R5-2 would be decreased by dilution with the estuarine plume as the water moved from R5 to R6. The only reasonable explanation was the tidal phase change: R6-2 was sampled during the LLW, while R5-2 was sampled 1.25 h later. Current velocity in the river usually reaches a maximum shortly before LLW (Geyer and Farmer 1989). When the outflow of the freshwater reached a maximum, the estuarine plume was pushed further seaward (Figure 1.2B). At the same time, the outflow of the freshwater entrained some deep water and the amount of entrainment of NO$_3$ should be the largest at this time of the tidal cycle. When the outflow decreased, the amount of the entrained NO$_3$ decreased. The higher surface NO$_3$ concentration at R6 than at R5 could reflect this process.

From a T-S diagram, the amount of the entrained deep water expressed in equivalent thickness (m) can be calculated by the depth-integration of its vertical proportion distribution (Figure 1.6). The criteria for the entrained deep water (i.e. above which depth the deep water was considered to be "entrained") was based on the depth ($D_0$) at which the proportion of the freshwater was 0% (Figure 5). In other words, above that depth ($D_0$) the deep seawater was the entrained (entrained deep seawater) and the estuarine plume was the entrained estuarine plume. The measured NO$_3$ concentrations were contributed by the three water types. However, the estuarine plume contained undetectable NO$_3$ at Stn 2. Therefore, NO$_3$ in the estuarine plume in the river channel was originally from the deep water and the freshwater. The measured NO$_3$ concentrations minus the proportions of the river freshwater gave the amount of NO$_3$ entrained from the deep water. When integrated from the surface to the same depth as the one ($D_0$) for the entrained deep water, the integrated NO$_3$ was the amount of the entrained NO$_3$.

At R6-2 where the increased NO$_3$ concentration was seen, the calculated entrained NO$_3$ was 19.5 mmol m$^{-2}$ and the equivalent thickness of the entrained deep water was 0.65 m (Figure 1.7A). At R5-2, the entrained NO$_3$ was 9.1 mmol m$^{-2}$ with 0.46 m
Figure 1.7 Dependence of: A) depth-integrated entrained NO₃ on entrained deep seawater (EDW), and B) depth-integrated fluorescence (Int. Flu.) in the water column on the equivalent thickness of the estuarine plume (EP), for the vertical profiles at the same stations along the transect as in Figure 1.4.

**A**

Entrained NO$_3$ (mmol m$^{-2}$)

$R^2 = .894$

Equivalent Thickness of EDW (m)

**B**

Int. Flu. (m$^{-2}$)

$R^2 = .995$

Equivalent Thickness of EP (m)
equivalent thickness of the entrained deep water. However, at Stn 2 and R7-2, there was no entrained deep water and no entrained NO$_3$ either. The relationship between the entrained deep water and the entrained NO$_3$ is shown in Figure 1.7A. The regression analysis indicated a significant dependence of the entrained NO$_3$ on the entrained deep water ($R^2 = 0.894$).

**Fluorescence Maximum**

One persistent feature in fluorescence at all the stations was a fluorescence maximum present in all the vertical profiles except R1 (Figure 1.4). It was located at the bottom of the halocline or the interface between the estuarine plume and the deep water. The maximum moved up and down with the depth of the interface and its thickness also appeared to vary with the interface thickness. It is reasonable to assume that phytoplankton in the fluorescence maximum originally grew in the estuarine plume away from the river mouth. Although the mechanisms are yet to be studied, the observed fluorescence could be mainly accounted for by the volume of the estuarine plume in the water column, if mixing processes had shorter time scales than changes in chlorophyll fluorescence due to biological processes such as consumption by heterotrophic organisms and in situ growth (Harris 1980).

Regression analysis indicates that an integration of the fluorescence contributed by the estuarine plume over the water column is strongly linearly related with the equivalent thickness of the estuarine plume ($R^2 = 0.995$) (Figure 1.7B). This strong relationship indicated that the fluorescence maximum was formed in the estuarine plume away from the river mouth and advected into the river with the salt wedge. The fluorescence distribution was a result of mixing of the estuarine plume with the riverine plume and the deep seawater since mixing was much faster than biological processes.

Figure 1.8 shows uptake of nutrients incubated at different irradiances for a sample taken at the fluorescence maximum at Stn 2. The sample depth was below the 1% light
Figure 1.8 Uptake of nutrients over a range of irradiances for a sample taken at the chl maximum at 10 m at Stn 2 on June 12, 1989. The initial concentrations of nutrients were saturating (NO$_3$ = 7.9 $\mu$M, SiO$_4$ = 13.0 $\mu$M, NH$_4$ = 1.32 $\mu$M, and PO$_4$ = 1.5 $\mu$M).
depth. No nutrients were added to the samples. There was no or little uptake of nutrients in the dark. However, it is possible that those cells might have taken up nutrients rapidly when first brought to the nutrient-rich water and become internally saturated. When the samples were incubated at a range of irradiances, the uptake increased with increasing irradiance. The response clearly shows that phytoplankton at the maximum did possess the potential to increase their nutrient uptake when exposed to improved light conditions.

2. Effects of Tides (Flood vs Ebb, Spring vs Neap) on Entrainment

Observations were made at R3 and R4 during flood and ebb tides during both spring and neap tides in June 1989. In Chapter 2, the entrainment of NO$_3$ over the same tidal cycles as the time series at an anchored station (Stn 2) will be examined. Figure 1.9 shows the change in the tidal height with time and the sampling times at R3 and R4 for the spring and neap tides.

**Neap Tide**

**Flood** Although the sampling times were just after low water, the following observations indicated the status during a flood tide. At R3 inside the river, a surface mixed layer was absent (Figure 1.10: R3-A1), suggesting that a salt wedge had moved into (or remained in the river) and entrained freshwater downwards, which is consistent with the conceptual model and a previous study (Geyer and Farmer 1989). The T-S diagram shows that the estuarine plume was present, but no longer a distinct water body (Figure 1.10; R3-A2). At R4 at the river mouth, there was only a very thin riverine plume, indicating that the estuarine plume had been pushed to the river mouth (Figure 1.10; R4-A1). The estuarine plume is distinctly shown as the 'knee' at $S = 22$ in the T-S diagram (Figure 1.10; R4-A2).

**Ebb** When the tidal height approached LLW during the following ebb, the vertical profile (Figure 1.10; R3-B1) inside the river looked very similar to one during the flood (R3-A1). However, the T-S diagram is almost linear (Figure 1.10; R3-B2),
Figure 1.9  Change of the tidal height with time for the neap tide on June 11-12 and the spring tide on June 19, 1989. The arrows indicate the sampling times at which the vertical profiles were taken for Figures 1.10 and 1.11.
Tidal Height (m)

Neap
June 11–12
1989

Spring
June 19
1989

Hours
Figure 1.10. Vertical salinity profiles with their corresponding T-S diagrams at R3 and R4 during the flood and ebb of the neap tide on June 11-12, 1989.
indicating that the freshwater outflow was so strong that the estuarine plume was washed away at R3. At the same time, the freshwater outflow had started to entrain the deep water, as indicated by the colder temperature at the surface during the ebb (Figure 1.10; R3-B2) than during the flood at R3 (Figure 1.10; R3-A2). This indication became clearer at R4 (Figure 1.10; R4-B2), at which the surface temperature was colder than during the flood (R4-B1) for the same salinity. In addition, the slope of the left line segment of the T-S diagram (R4-B2) points to the deep water (the lower-right end of the T-S line), which indicates that freshwater had been mixed by entrainment with the deep water upstream initially and advected over the estuarine plume. This is the reason why the linear segment to the left of S=24 in the T-S diagram at R4 (Figure 1.10; R4-B2) is roughly parallel to the line at R3 (R3-B2). The rise of temperature at salinity of about 27 on the T-S diagram indicated the presence of the nutrient-poor estuarine plume, which could still be a barrier to nutrient entrainment as it lay between the riverine plume and the deep water at R4 during the neap tide ebb.

Spring Tide

Flood In the middle of the halocline (Figure 1.11; R3-A1), there was a layer where the salinity changed slowly; this layer was the estuarine plume being eroded between the freshwater and the deep water. This remnant of the estuarine plume can be seen in the T-S diagram (Figure 1.11; R3-A2) where there is a temperature rise at a salinity of 13 at which the eroded layer began in the vertical profile. At R4, the freshwater was completely absent and the estuarine plume was completely dominant in the top 4 m.

Ebb At R3 during the ebb, there were a 2 m thick surface mixed layer of nearly freshwater and a very broad halocline (8 m) (Figure 1.11; R3-B1). The T-S curve shows only one straight line (Figure 1.11; R3-B2), indicating no estuarine plume. At R4, 1 h later, the halocline was broadened (R4-B1) and the T-S line was also straight (Figure 1.11; R4-B2).
Figure 1.11. Vertical salinity profiles with their corresponding T-S diagrams at R3 and R4 during the flood and ebb of the spring tide on June 19, 1989.
Comparison between the Spring and Neap Tides

The vertical distribution of the proportion of freshwater, the estuarine plume and the deep water for the vertical profiles above is shown in Figure 1.12. It is apparent that the estuarine plume occupied a greater proportion in the water column at R4 than at R3 during the same tidal stages; and a greater proportion during flood tides than during ebb tides but less during the spring ebb than the neap ebb at the same station.

In general, during a flood, the freshwater outflow slows down in the river during the salt wedge invasion carrying the estuarine plume. For example, from 1900 to 1930 h at R3 the freshwater volume (equivalent thickness) was reduced (Figure 1.13; R3-A). During an ebb when the salt wedge retreats, the freshwater outflow increases and pushes the estuarine plume downstream, as seen from 0530 to 0630 h at R3 where the freshwater volume increased (Figure 1.13; R3-B). At the same time, deep seawater was entrained. When the tidal range is small during the neap tide, the estuarine plume is hardly pushed out of the river during the ebb tide (Geyer and Farmer 1989). During the spring tide, however, the estuarine plume is completely washed out of the river during the ebb. The equivalent thickness of the entrained estuarine plume averaged over 5 vertical profiles (0530-0730 h) (Figure 1.13; R3-B and R4-B) during the neap ebb approaching the LLW was 0.81 m, while during the spring ebb, the average value for two vertical profiles (0730-0830 h) was only 0.35 m (Figure 1.13; R3-D and R4-D). The decrease in the estuarine plume results in more direct contact between the two water masses: freshwater and deep seawater and more entrainment of deep water into the river outflow. The entrained deep water was 4.6 m for the spring ebb which was more than the 3.4 m for the neap ebb. The sampling times during the spring tide were only in the middle of the ebb vs at the end of neap ebb, suggesting that by the time of the LLW of the spring ebb, there would be even more entrainment of the deep water.
Figure 1.12. Vertical distribution in proportion of freshwater (FW), the estuarine plume (EP) and the deep water (DW) for the vertical profiles at R3 and R4 during the neap tide (June 11-12) shown in Figure 1.10 and during the spring tide (June 19, 1989) shown in Figure 1.11.
Figure 1.13. Equivalent thickness of the freshwater (FW), the entrained estuarine plume (EEP) and the entrained deep seawater (EDW) for vertical profiles sampled at R3 and R4 during floods and ebbs in the spring and neap tides in June, 1989. The sum of these three equivalent thicknesses is the depth at which the proportion of freshwater drops to zero. See discussion in the text.
There was a significant dependence \((p=0.05)\) of the entrained deep water on the amount of the estuarine plume present in the water column (note: the difference from the entrained estuarine plume) and it was supported by the regression analyses for the transect on August 13-14, 1991 \((R^2=0.73)\), for the neap tide \((R^2=0.84)\) and for the spring tide \((R^2=0.68)\) (Figure 1.14). Furthermore, the slope during the spring tide was steeper than the slope during the neap tide (Figure 1.14), indicating that a smaller variation in the thickness of the estuarine plume resulted in a larger change in the amount of the deep water. These results suggest that there was more entrainment of NO\(_3\) during the spring tide than during the neap tide, although NO\(_3\) concentrations were not available to estimate direct entrainment of NO\(_3\).

Also, because a neap tide is usually preceded by pre-neap tides in the similar ranges, the salt wedge may not be washed out of the river. Thus, during the neap tide, some of the estuarine plume water would remain in the river and partially mix with the deep water (Figure 1.10). In contrast, during the spring tide the estuarine plume is flushed out of the river as is shown in the T-S diagrams (Figure 1.11). As a result, the NO\(_3\) concentrations in the deep water would be more diluted by the estuarine plume water during the neap tide. This dilution was shown at R1 where the bottom mixed layer had a salinity of 22 and the NO\(_3\) concentration was 13 \(\mu\)M, lower than the expected 17 \(\mu\)M for that salinity (22) if mixing only occurred between the freshwater (3.2 \(\mu\)M) and the deep water of salinity = 30 (25 \(\mu\)M) (assuming conservative mixing). The reduced NO\(_3\) concentration will make a great difference in NO\(_3\) entrainment even when the amount of the entrained deep water is similar. The difference in entrainment of NO\(_3\) between the spring and the neap tide will be discussed in the time series at Stn 2 (Chapter 2).
Figure 1.14. The relationship between the equivalent thickness of the entrained deep water (EDW) and the equivalent thickness of the estuarine plume (EP) for the vertical profiles A) along the transect on August 13-14, 1991, B) at R3 and R4 during the neap tide on June 11-12, 1989, and C) at R3 and R4 during the spring tide on June 19 and June 22, 1989. Some vertical profiles shown in Figure 1.4 are not included in (A) because they were not deep enough for the calculation of the equivalent thickness of the estuarine plume.
Equivalent Thickness of Entrained Deep Seawater (m)

$R^2 = .725$  Transect
Aug 13-14
1991

$R^2 = .841$  Neap Tide
June 11-12
1989

$R^2 = .684$  Spring Tide
June 19
1989

Equivalent Thickness of EP (m)
3. Biological Significance

Studies of nutrient dynamics associated with entrainment are sparse. The best documented case is that of the St. Lawrence estuary. The Laurentian channel shoals in the lower estuary up to the entrance of Saguenay Fjord. The intermediate layer in the channel is cold and nutrient rich and moves upstream in the residual circulation. The intensity of upstream currents in the intermediate layer is proportional to freshwater runoff (Ingram 1979). The surface layer waters from the upper estuary and the Saguenay Fjord flow downstream. As a result, intensive upward entrainment of the intermediate layer occurs at the head of the channel. Flood tides literally lift the water column along the abrupt rise in the Laurentian Channel topography, such that intermediate cold water spills over the shallow mid-channel area (Reid 1977). During ebb tides, the upwelled cold water is mixed and flushed downstream. As a result, relatively cold water is found at the surface near the head of the lower St. Lawrence estuary, which was observed from satellite thermal image of the region (Gratton et al. 1988). Temperature and salinity distributions at the head show that isopycnals are periodically lifted towards the surface by incoming tides (Ingram 1975; Therriault and Lacroix 1976, Greisman and Ingram 1977). This entraining process has been called a "nutrient pump" (Steven 1974) and enhances biological production in the Gaspé Current downstream (see Review by de Lafontaine 1991). The nutrients originating from seawater represent 75% of the total nutrient supply to the euphotic zone in the estuary, while the freshwater origin contributes only <25% (de Lafontaine 1991).

There are similarities between the St. Lawrence estuary and the Fraser River estuary and the adjacent seawater in the Strait. For example, the riverine plume, the estuarine plume and the deep water would be similar to the surface layer, the intermediate layer and the deep layer in the St. Lawrence estuary, respectively. The bottom shoaling in the Strait beyond the river mouth would be similar to the Laurentian Channel shoaling at its head. In contrast to the St. Lawrence estuary, the estuarine plume in the Fraser River estuary is frequently nutrient poor.
Because of the presence of the estuarine plume in the middle between the freshwater layer and the deep seawater layer, the freshwater outflow first entrains the estuarine plume water seaward before it reaches the deep seawater in the Fraser River estuary. Entraining high NO₃ probably occurs later, after the estuarine plume is washed seaward. The chlorophyll maximum at the base of the estuarine plume is a common feature in this system although the formation mechanism is yet to be studied. Phytoplankton in the chl a maximum are advected towards the river and a portion of them enter the river channel with the estuarine plume as the salt wedge invades during flood tides. As the river outflow commences during ebb tides, phytoplankton are entrained upwards and advected seaward. Some marine phytoplankton may die if the salinity is below their tolerance level. The entrained phytoplankton will be in the upper layer in the Strait after they have left the river channel. By then, they must be internally nutrient saturated since these phytoplankton at the base of the estuarine plume have been exposed to nutrients in the deep water before they are advected to the river and are exposed to nutrients during the entraining process. They may serve as a seed population and grow, possibly developing a bloom further seaward as they gradually become part of the estuarine plume, utilizing the riverine nutrients and the entrained nutrients because of the improved light conditions. Part of the grown phytoplankton may sink and join the chlorophyll maximum at the base of the estuarine plume. The chlorophyll maximum might be carried back towards the river again, starting another cycle. This process occurs during tidal cycles and provides nutrients to the euphotic zone periodically. This process may be related to the maximum in primary productivity which was shown in the estuarine plume (Parsons et al. 1969, Stockner et al. 1979). It may also be a reason for zooplankton to aggregate at the riverine front (Mackas and Louittit 1988) and to be abundant in the estuarine plume (St. John et al. 1992).
CHAPTER 2
ENTRAINMENT OF NITRATE IN THE FRASER RIVER PLUME AND ITS BIOLOGICAL IMPLICATIONS: EFFECTS OF SPRING VS NEAP TIDES AND RIVER DISCHARGE

INTRODUCTION

In Chapter 1, the estuarine plume was found to invade the river with the advance of the salt wedge on flood tides and to form a barrier which hinders direct mixing between the freshwater and the deep water. Upward entrainment of high NO₃ into the riverine plume occurs during ebb tides only when the NO₃-poor estuarine plume is pushed seaward, allowing the riverine plume to come into contact with the deep NO₃-rich seawater (see Figure 1.2). Therefore, the amount of the entrained NO₃ depends on the amount of the entrained deep water, which varies with the tidal cycle. There is more direct contact between the freshwater and the deep water during a spring tide when the estuarine plume is flushed out of the river, suggesting more NO₃ entrainment during a spring tide than during a neap tide.

Entrainment of nutrients becomes very important when the nutrient concentrations of the river are lower than the receiving seawater in the estuary. This is the case for the Fraser River and the adjacent region of the Strait of Georgia. The magnitude of annual primary production has been debated for the Strait of Georgia. Stockner et al.’s (1979) estimate on annual primary production is three times higher than Parsons et al.’s (1970) estimate. Stockner et al. (1979) attributed the increase in annual primary production to eutrophication produced by the nutrients in the Fraser River runoff. However, the nutrient (nitrate) data in the Fraser River for the same period as their study (Drinnan & Clark 1980) did not support this argument. In the subsequent discussion, entrainment of nutrients (nitrate) due to the Fraser River discharge was proposed to be a major process that could supply nitrate and satisfy the nitrogen budget requirement for the increase in annual
primary production estimated by Stockner et al. (1979) (Parsons et al. 1980, Harrison et al. 1983). Entrainment of nitrate is believed to be particularly important in late spring and summer when nitrogen is undetectable in the estuarine plume in the Strait and the Fraser River carries concentrations of NO\textsubscript{3} as low as 2 µM, the minimum for the year (Drinnan and Clark 1980). In the studies of Parsons et al. (1970) and Stockner et al. (1979), the regions of higher productivity were found to occur at stations in the estuarine plume some distance away from the Fraser River. This high production cannot be explained by the nutrient input from the river outflow alone, because NO\textsubscript{3} concentrations in the river in late spring and summer are only 2-6 µM. In addition, surface nutrients are diluted when the riverine plume flows over and entrains the nutrient-depleted estuarine plume (Chapter 1). In spite of frequently undetectable concentrations of NO\textsubscript{3} in the estuarine plume, primary production remains high during the annual freshet (June and July) (Clifford et al. 1989, 1990, 1991). More recently, a phytoplankton bloom was observed during pre-neap tides in July in the estuarine plume (Harrison et al. 1991). This evidence points to the entrainment of NO\textsubscript{3} as being partially responsible for the higher productivity.

The objectives of this study were to examine the effects of tides (spring/neap) on entrainment, to estimate entrained NO\textsubscript{3} over a diurnal tidal cycle and to determine the relationship between the magnitude of the river discharge and the amount of NO\textsubscript{3} entrained into the seaward moving riverine plume.

MATERIALS AND METHODS

A map of the study area is given in the previous Chapter (see Figure 1.1 in Chapter 1). Stn 2 is 8 km seaward of Sand Heads which is assumed to be the mouth of the Fraser River (where the river leaves the edge of the banks). Vertical profiles of temperature, salinity, \textit{in vivo} fluorescence and NO\textsubscript{3} were obtained as described in GENERAL MATERIALS AND METHODS. Vertical profiles were taken every 3 or 4 h for 24 h at Stn 2 while the ship was anchored. Four time series were made under different conditions:
during a spring tide and neap tide (under similar magnitudes of river discharge) in June, 1989 and during different amounts of river discharge at the end of May (lower discharge) and early June (higher discharge), 1990.

Contour plots of salinity and NO\textsubscript{3} were made with a computer program (Surfer\textsuperscript{R}). Due to the multi-layered water column, the vertical distribution in NO\textsubscript{3} showed lower concentrations at an intermediate depth than at the surface, or a minimum, or even two minima in a profile (e.g. Figure 2.10). Such NO\textsubscript{3} distributions have made the contour plots in Figure 2.1B and 2.1D and Figure 2.5B and 2.5D look complex. The interpretation of these plots is supported by individual profiles (not shown). The time used in all the contour plots is local time (PST).

T-S diagrams were used for calculating the equivalent thickness of freshwater, the estuarine plume (EP), the entrained estuarine plume (EEP), and the entrained deep water (EDW) as well as integrated fluorescence contributed by the estuarine plume (Int. Flu.).

RESULTS

Due to the Coriolis effect, the riverine plume tends to turn to the north as it enters the Strait. Stn 2 is normally in the path of the riverine plume, but depending on winds, it is possible for the riverine plume to move north or south of Stn 2 if winds blow strongly enough to the north or south. The river outflow reaches a maximum near lower low water (LLW) at the river mouth. There is a time lag for the riverine plume to arrive at Stn 2. This time lag of a few hours was observed during the time series.

1. Effects of Tides on Entrainment (Spring vs Neap)

A. Neap Tide

Surface salinities were <10 during the two floods and >14 during the ebb tides, indicating that the riverine plume reached Stn 2 some time after ebb tide and was blocked for some time by the flood (Figure 2.1A). The salinity of 28 can be considered to
Figure 2.1 Depth contours of salinity and NO₃ (μM) for the time series at Stn 2 on June 12-13, during the neap tide (A, B) and June 19-20, 1989 during the spring tide (C, D). The arrows indicate the times when the vertical profiles were completed; it usually took about 0.5 h to complete a vertical profile.
represent the bottom of the upper stratified layer. Its depth fluctuated between 10 and 14 m, rising as higher high water (HHW) was approached (Figure 2.1A). The gradients in the isohalines were greater during tidal flooding when the surface salinity was lower (Figure 2.1A).

The time series of T-S diagrams in Figure 2.2A show that there were more than two water masses and the T-S curves changed over time. The riverine plume was identified by lower salinities (<15) and temperature; the estuarine plume was generally characterized by medium salinities (20-27) and higher temperatures than the river, and the transition to the deep seawater was represented by the steep straight line segment to the right of salinity =27. Since the temperature of freshwater changed little over a tidal cycle, it was the temperature of the estuarine plume that changed most dramatically due to mixing with the riverine plume or the deep water during a tidal cycle. For example, at T1, 2 h after the LLW, the riverine plume dominated while at T2 the estuarine plume was dominant. At other times, both the riverine and estuarine plumes were present. At T4 and T6, the temperature of the riverine plume decreased with salinity (the left part of the T-S curve) and then rose at intermediate salinities (15-20) (Figure 2.2A), indicating mixing with water which was colder than the surface estuarine plume. The mixture with the colder water in the riverine plume must have resulted from entrainment of the deep water. An interesting feature that was consistently present in each of the T-S diagrams was the little kink at about 27, which often separated the two line segments with distinctly different slopes on each side. The lines to the right of the kink represent the mixing lines between the estuarine plume and the deep seawater and the slopes were steep, indicating a rapidly increasing temperature with decreasing salinity. The curves to the left changed over the tidal cycle. The kink might be due to entrainment of the deep seawater into the estuarine plume at their interface. The kink may be expanded when entrainment increases.

The equivalent thickness in the time series (Figure 2.3A) showed that freshwater was the thickest at T1 and T5, and remained lower and similar at other times.
Figure 2.2 Time series of the T-S diagrams for A) the neap tide, and B) the spring tide.

See Figure 2.1A for the sampling times and their relation to the tidal cycles.

Successive T-S curves are offset by 5 on the salinity axis.
A

**Neap Tide**

B

**Spring Tide**

Temperature (°C)

Salinity
Figure 2.3  Time series of the equivalent thickness of freshwater, the entrained estuarine plume and the entrained deep water during A) a neap tide, and B) a spring tide.

See Figure 2.1A and B for the sampling times.
A. Neap Tide

B. Spring Tide

- Freshwater
- Entrained Estuarine plume
- Entrained Deep Seawater
The estuarine plume was thicker at T4 during HHW and thickest at T5. The equivalent thickness of the entrained deep water was the thickest (4.5 m) at T6, which indicates strong entrainment by the riverine plume, as does the T-S curve at T6 in Figure 2.2A.

The surface NO\textsubscript{3} concentrations were about 6-7 \(\mu\)M when the surface salinity was low (0900-1200 h), and very low (2 \(\mu\)M) from 1400 to 1800 h when the salinity was higher (Figure 2.1B). There was a large NO\textsubscript{3} gradient between 2200-2400 h at 10-25 m during HHW. A NO\textsubscript{3} minimum was observed at an intermediate depth (9 m) during almost the entire period (Figure 2.1B).

The amount of the entrained NO\textsubscript{3} varied greatly over the tidal cycle (Figure 2.4A) (see Chapter 1 for how the entrained NO\textsubscript{3} is defined and calculated). For example, at T1, the amount of entrained NO\textsubscript{3} was 18 mmol m\textsuperscript{-2} and at T2 there was little entrained NO\textsubscript{3} because the estuarine plume was dominant near the surface. At other times, the amount of entrained NO\textsubscript{3} was due to the combination of the riverine and estuarine plumes. Regression analysis indicated that there was no significant relationship between the entrained NO\textsubscript{3} and the entrained deep water (\(R^2=0.07\)), or between the depth-integrated fluorescence and the equivalent thickness of the estuarine plume (\(R^2=0.21\)) (Figure 2.4B).

**B. Spring Tide**

The surface salinity was <15 during the entire period and <10 at the end of time series (0200-0900 h), indicating the presence of the riverine plume (Figure 2.1C). The isohaline of 28 fluctuated between 13 m at LLW and 6 m at HHW.

Figures 2.2B and 2.3B show the time series of T-S diagrams and the equivalent thicknesses. The slopes of the estuarine plume-deep seawater mixing line segment of the T-S curves are very steep (Figure 2.2B). The rest of the T-S curves vary considerably. At T2, temperature dropped initially in the left part of the curve (Figure 2.2B), representing the entrained colder water in the riverine plume. The hollow of the kink that was seen during the neap tide became larger (T4, T5 and T6), suggesting more entrainment of
Figure 2.4  Linear regressions between the amount of the entrained NO$_3$ and the equivalent thickness of the entrained deep water (EDW) (A,C) and the depth-integrated fluorescence and the equivalent thickness of the estuarine plume (EP) (B,D) for the neap tide of June 12-13 and the spring tide: June 19-20, 1989. The slopes of A and C are indicated by b (3.1 and 15.2 $\mu$M for the neap and spring tides, respectively). T1, T2 and T5 are not included in the regression in C because NO$_3$ concentrations were not measured or not deep enough for the calculation of entrained NO$_3$. T1 and T5 are not included in the regression in D for the same reason.
CV2

Neap Tide

\[ R^2 = 0.069 \]
\[ b = 3.1 \]

Spring Tide

\[ R^2 = 0.786 \]
\[ b = 15.2 \]

Equivalent Thickness of EDW (m)

Entrained NO\textsubscript{3} (mmol m\textsuperscript{-2})

Neap Tide

\[ R^2 = 0.209 \]

Spring Tide

\[ R^2 = 0.800 \]

Integrated Flu. (m\textsuperscript{-2})

Equivalent Thickness of EP (m)
the deep water into the riverine plume. Temperature at the kink dropped by almost 1° C during the spring tide from that during the neap tide.

The surface NO₃ concentrations (Figure 2.1D) remained at about 7 μM during the larger flood and at HHW (1300-1900 h), and low higher water (LHW) (0400 h). Compared with the NO₃ concentration of 6.8 μM in the river, these values indicate some entrainment of NO₃. Because the surface salinity had increased to about 10, NO₃ in the riverine plume would be less than 6.8 μM if freshwater was mixed with the estuarine plume in which NO₃ concentrations were even lower. The surface NO₃ concentration dropped to below 2 μM during the smaller ebb (2100-0100 h). The NO₃ contour lines (8-12 μM) at the intermediate depths oscillated with tidal height, rising during the larger flood (1300-1600 h) and moving downwards during the next ebb. A depth minimum in NO₃ concentration was absent during the time series except near the end (0600-0900 h).

Several processes could cause the erosion of the NO₃ minimum. When the NO₃ concentration was 7 μM at the surface, the erosion was caused by the direct entrainment of the deep water by the riverine plume as can be seen at T3 and T7 in the T-S diagrams (Figure 2.2B) where the estuarine plume was not a distinct water mass. When the surface NO₃ concentration was below 2 μM, the absence of the minimum could be simply due to no increase in the NO₃ concentration at the surface.

The amount of the entrained NO₃ varied over time but was dependent on the amount of the entrained deep water. Regression analyses showed that the entrained deep seawater accounted for 79% of the amount of entrained NO₃ (Figure 2.4C). Similarly, the equivalent thickness of the estuarine plume explained 80% of the depth-integrated fluorescence (Figure 2.4D).
C. Comparison between the neap and the spring tides

A summary of the comparison between the spring and neap tides is shown in Table 2.1. Since the wind speed and the river discharge were similar, the differences in time-averaged parameters were apparently due to the difference in the tidal ranges, 4.0 m for the spring tide and 2.5 m for the neap tide. The equivalent thickness of the entrained estuarine plume was 1.6 m during the spring tide, whereas it was 2.8 m during the neap tide. The amount of entrained NO$_3$ was higher (24 mmol m$^{-2}$) for the spring than for the neap tide (17 mmol m$^{-2}$), although the amount of the entrained deep seawater was similar. The contribution of the entrained NO$_3$ relative to the river-borne NO$_3$ was greater for the spring (2.3) than for the neap tide (1.6), although the ratio of the entrained deep water to freshwater was almost the same (2.7). In contrast, the depth-integrated fluorescence was higher during the neap than during the spring tide.

2. Effects of River Discharge
    
    A. Lower Discharge

    The average river discharge over May 29-30 was 6720 m$^3$ s$^{-1}$. The surface salinity was $< 15$ during most of the time series (Figure 2.5A). It seems that the riverine plume frequently moved over the station, being more apparent in the beginning at LHW and the end at HLW. During these times, the gradients in the isohalines were also greater. The isohaline of 28 did not fluctuate much. The NO$_3$ concentrations in the top 3 m were low ($< 4$ µM) in the first 7 h during the large ebb and remained higher than 6 µM during the flood and the next small ebb. Particularly during HHW, the NO$_3$ concentrations were 8-9 µM (Figure 2.5B) which were higher than the river NO$_3$ concentration (7.5 µM), indicating entrainment of NO$_3$ into the riverine plume. Below these higher NO$_3$ concentrations, NO$_3$ minima were present and very low at times.
Table 2.1 Comparisons between the neap tide on June 12-13 and the spring tide on June 19-20, 1989. All the parameters are time-averaged over the time series.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Neap Tide</th>
<th>Spring Tide</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling period (h)</td>
<td>22.65</td>
<td>22.55</td>
</tr>
<tr>
<td>Tidal range (m)</td>
<td>2.5</td>
<td>4.0</td>
</tr>
<tr>
<td>Mean tidal height (m)</td>
<td>3.0</td>
<td>3.2</td>
</tr>
<tr>
<td>Wind speed (m s(^{-1}))</td>
<td>3.7(^*)</td>
<td>2.8(^**)</td>
</tr>
<tr>
<td>Discharge (m(^3) s(^{-1}))</td>
<td>6670</td>
<td>6850</td>
</tr>
<tr>
<td>Equivalent thickness (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshwater</td>
<td>1.6</td>
<td>1.4</td>
</tr>
<tr>
<td>Entrained estuarine plume (EEP)</td>
<td>2.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Entrained deep seawater (EDW)</td>
<td>3.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Freshwater-penetration depth (m)</td>
<td>7.3</td>
<td>5.8</td>
</tr>
<tr>
<td>Entrained NO(_3) (mmol m(^{-2}))</td>
<td>17.3</td>
<td>24.2</td>
</tr>
<tr>
<td>River-borne NO(_3) (mmol m(^{-2}))</td>
<td>10.6</td>
<td>9.6</td>
</tr>
<tr>
<td>Depth-integrated fluorescence (m(^{-2}))</td>
<td>3.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Ratio of sum of EEP and EDW to freshwater</td>
<td>3.7</td>
<td>3.2</td>
</tr>
<tr>
<td>Ratio of EDW to freshwater</td>
<td>1.9</td>
<td>2.0</td>
</tr>
<tr>
<td>Ratio of entrained NO(_3) to river-borne NO(_3)</td>
<td>1.6</td>
<td>2.3</td>
</tr>
</tbody>
</table>

\(^*\) East winds were dominant

\(^**\) Winds fluctuated around from the east
Figure 2.5 Depth contours of salinity and NO$_3$ ($\mu$M) for the time series at Stn 2 on May 29-30, during a day of lower river discharge (A, B) and on June 7-8, 1990 during a day of higher river discharge (C, D). The contours in A and B were plotted using more vertical profiles than the arrows indicate. The arrows indicate only the sampling times (when the vertical profiles were completed) for the time series of T-S diagrams and the equivalent thickness shown in Figures 2.6A and 2.7A. Therefore, the contours in A and B present more features than one might expect from the number of the vertical profiles indicated by the arrows (for example, around T4 when another vertical profile with a minimum of NO$_3$ at an intermediate depth is contoured close to T4 in time, two sets of circular contour lines next to each other are formed). The axis of Hour for the NO$_3$ contour D is longer than in C, because the salinity instrument for the last vertical profile was broken and not plotted in D.
(almost 0 μM, e.g. the two sets of circular contour lines between 2100 and 2300 in Figure 2.5B). The time series of the T-S curves (Figure 2.6A) and the equivalent thickness (Figure 2.7A) are consistent with the features of the NO₃ contour plot. At T1, T2 and T3, the estuarine plume was relatively dominant. The NO₃ concentrations were low. The drop in temperature at a salinity of 25 at T4 (Figure 2.6A) indicates mixing with the colder deep water by entrainment. The equivalent thickness of the entrained deep water at T4 was 4.1 m (Figure 2.7A), bringing 49 mmol m⁻² NO₃ (Figure 2.8A) into the riverine plume. At T7 (Figure 2.6A), the top part of T-S curve bent horizontally, suggesting that the estuarine plume was pushed seaward by the riverine plume, and the NO₃ concentration started to increase (Figure 2.5B). At the same time, the estuarine plume contribution was reduced (Figure 2.7A) and the NO₃ minimum disappeared (Figure 2.5B). The amount of entrained deep water was equivalent to 7.6 m in thickness (Figure 2.7A) and it entrained 122 mmol m⁻² of NO₃ (Figure 2.8A).

The time-averaged amount of the entrained NO₃ during the tidal cycle was 32 mmol m⁻² (Table 2.2). The amount of the entrained NO₃ was 89% accounted for by the amount of entrained deep water (Figure 2.8A). The slope of the regression was 16.8 μM which was actually the average concentration of source NO₃ to be entrained. The estuarine plume accounted for 68% of the depth-integrated fluorescence in the water column (Figure 2.8A).

B. Higher Discharge

The river discharge increased to 9000 m³ s⁻¹ by June 7, 1990 and the tidal cycle was similar to the May 29-30 time series (Figure 2.5C). The low surface salinities indicated that the riverine plume occupied the upper part of the water column during most of the tidal cycle. The isohaline of 28 fluctuated with the tidal height. The isohalines (10-28) were deeper (0700-0800 h) and became wider spaced during the large ebb (0800-1000 h).
Figure 2.6 Time series of the T-S diagrams for A) the smaller discharge on May 29-30, and B) the larger discharge on June 7-8, 1990. See Figure 2.5A for the sampling times. Successive T-S curves are offset by 5 on the salinity axis.
Figure 2.7 Time series of the equivalent thickness of freshwater, the entrained estuarine
plume and the entrained deep water during A) the lower discharge, and B) the
higher discharge. See Figure 2.5 for the sampling times. T5 and T6 in B are
missing because the vertical profiles at these times were not deep enough for the
calculation.
Lower Discharge

Higher Discharge

Equivalent Thickness (m)

Freshwater

Entrained estuarine plume

Entrained deep seawater
Figure 2.8 Linear regressions between the amount of the entrained NO₃ and the equivalent thickness of the entrained deep water (EDW) (A,C) and the depth-integrated fluorescence and the equivalent thickness of the estuarine plume (EP) (B,D) for the low discharge on May 29-30, and the higher discharge on June 7-8, 1990. The slopes for A and C are indicated by b (16.8 and 25.1 µM for the lower and high discharge, respectively). T5 and T6 are not included in the regression in C and D for the same reason as stated in Figure 2.7.
Equivalent Thickness of EDW (m)  

Lower Discharge  

\[ R^2 = 0.886 \]  
\[ b = 16.8 \]

Higher Discharge  

\[ R^2 = 0.816 \]  
\[ b = 25.1 \]

Equivalent Thickness of EP (m)  

Lower Discharge  

\[ R^2 = 0.683 \]

Higher Discharge  

\[ R^2 = 0.975 \]
Table 2.2 Comparisons between the low discharge on May 29-30, and the higher discharge on June 7-8, 1990. All the parameters are time-averaged over the time series.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Lower Discharge</th>
<th>Higher Discharge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling period (h)</td>
<td>23.4</td>
<td>22.6</td>
</tr>
<tr>
<td>Tidal range (m)</td>
<td>3.9</td>
<td>3.7</td>
</tr>
<tr>
<td>Mean tidal height (m)</td>
<td>3.2</td>
<td>3.2</td>
</tr>
<tr>
<td>Wind speed (m s(^{-1}))</td>
<td>3.4*</td>
<td>2.7**</td>
</tr>
<tr>
<td>Discharge (m(^3) s(^{-1}))</td>
<td>6720</td>
<td>9000</td>
</tr>
<tr>
<td>Equivalent thickness (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshwater</td>
<td>1.3</td>
<td>1.8</td>
</tr>
<tr>
<td>Entrained estuarine plume (EEP)</td>
<td>2.7</td>
<td>3.0</td>
</tr>
<tr>
<td>Entrained deep seawater (EDW)</td>
<td>3.4</td>
<td>4.8</td>
</tr>
<tr>
<td>Freshwater-penetration depth (m)</td>
<td>7.4</td>
<td>9.6</td>
</tr>
<tr>
<td>Entrained NO(_3) (mmol m(^{-2}))</td>
<td>31.7</td>
<td>72.3</td>
</tr>
<tr>
<td>River-borne NO(_3) (mmol m(^{-2}))</td>
<td>9.5</td>
<td>13.5</td>
</tr>
<tr>
<td>Depth-integrated fluorescence (m(^{-2}))</td>
<td>3.4</td>
<td>2.5</td>
</tr>
<tr>
<td>Ratio of sum of EEP and EDW to freshwater</td>
<td>4.7</td>
<td>4.3</td>
</tr>
<tr>
<td>Ratio of EDW to freshwater</td>
<td>2.7</td>
<td>2.7</td>
</tr>
<tr>
<td>Ratio of entrained NO(_3) to river-borne NO(_3)</td>
<td>3.3</td>
<td>5.4</td>
</tr>
</tbody>
</table>

* East winds were dominant

** Winds fluctuated between the east and south
During the following flood (1000-1600 h), however, the isohalines became shallower and the gradient increased (Figure 2.5C).

Surface NO₃ concentrations remained nearly constant at 6-8 μM (Figure 2.5D). The most pronounced feature in the contour plot is the absence of the NO₃ minimum. The estuarine plume was no longer a distinct water mass in the water column, as indicated in the T-S diagrams (Figure 2.6B). The left segments of the T-S lines were bent more horizontally than ones on May 29-30 and generally, temperatures on the bent line segments were lower than ones for the same salinities on the T-S diagrams of the May 29-30 series. The kinks are nearly absent. The equivalent thickness of the freshwater appeared to vary over time, but the equivalent thickness of the entrained deep seawater remained unchanged (Figure 2.7B). The regression analysis indicated that the amount of the entrained deep seawater accounted for 82% of the amount of entrained NO₃ and the slope was 25 μM (Figure 2.8C). Similarly, the depth-integrated fluorescence was strongly determined by the equivalent thickness of the estuarine plume (R²=0.975, Figure 2.8D).

The most remarkable difference in the NO₃ contours between low and high discharges was that the NO₃ minimum was absent during the larger discharge. Table 2.2 shows a summary comparison between the two time series. The equivalent thickness of the freshwater was thicker for the larger discharge than for the smaller one, indicating that the riverine plume occupied the station more frequently and/or was more pronounced. The amount of the entrained NO₃ during the higher discharge was (73 mmol m⁻²), twice as much as during lower discharge. The contribution of the entrained NO₃ relative to the river-borne NO₃ increased to 5.4 from 3.3 for the lower discharge. The fluorescence in the water column decreased during the larger discharge.
DISCUSSION

Spring vs Neap tides

In the Strait of Georgia, the differences in tidal range depend on the change in LLW during spring and neap tides. More of the river discharge entered the Strait during the spring ebb of June 19 than during the neap ebb of June 12 because the water level in the Strait was 2 m lower at LLW during the spring tide, even though over the two tidal cycles, the amount of river discharge and the wind speeds were almost the same between the two tidal cycles. Furthermore, during the subsequent spring flood on June 19, the river outflow and the rising water levels squeezed the estuarine plume in the middle. As a result, the salinity gradients were greater and the estuarine plume was thinner during the spring tide. A similar process has been demonstrated in a lab experiment by Nof (1979) who showed that the middle layer decreased in its thickness when a surface layer flowed from one end and a bottom layer invaded on the other end of the water tank. Because of stronger bottom stirring during the spring tide, NO3 concentrations in the deep water were higher, as indicated by the steeper slope of the regression between the amount of the entrained NO3 and the entrained deep water. Particularly in the region at the river mouth (Zone I in Figure 2.9) where the bottom depth rapidly decreases toward the river mouth, the bottom stirring induced during the spring flood is stronger and could mix higher concentrations of NO3 upward into the salt wedge or in the salinity wall near the mouth and expose them to the riverine plume. In fact, NO3 concentrations in the lower part (below 12 m) of the water column were higher during the spring tide than during the neap tide (Figure 2.1B and 1D). There was more entrained NO3 during the spring tide, although the amount of the entrained deep seawater during the spring tide was not greater. The ratio of the contribution of the entrained NO3 to the surface layer relative to the river-borne NO3 during the spring tide was greater than during the neap tide although the ratios of the entrained deep seawater to the freshwater were very similar (Table 2.1).
Figure 2.9 The conceptual model illustrating how Zone I (the area of the deep seawater exposed to the riverine plume seaward of the river mouth) changes with the riverine plume, the estuarine plume and the deep water at different stages of tidal cycles and river discharge. The dashed line indicates a condition during a neap ebb or smaller discharge and the solid line indicates a spring ebb or larger discharge condition.
Consequently, due to stronger mixing during the spring tide, the amount of entrained NO₃ was more dependent on the amount of entrained deep seawater and the depth-integrated fluorescence decreased, as was more closely related to the estuarine plume than during the neap tide. Lack of a relationship between the entrained NO₃ and the entrained deep seawater during the neap tide might be due to two reasons. One is that the deep seawater contained different NO₃ concentrations, which was seen in the NO₃ contour plot (Figure 2.1B) where NO₃ contour lines below 12 m had lower values during the later part of the time series during the neap tide. The other reason is that mixing was slow and the mixture of the water masses during the neap tide had been there for a sufficiently long time for NO₃ to be consumed. This idea is supported by higher chlorophyll in the water column indicated by the greater depth-integrated fluorescence and no significant relationship between the equivalent thickness of the estuarine plume and the integrated fluorescence, compared with a significant relationship for the spring tide.

It appears that there can be fortnightly tidal cycles in nutrient mixing and the phytoplankton biomass in the water column. During a spring tide, phytoplankton biomass could be reduced (by dilution) and nutrient mixing be increased. After the spring tide, the tide-induced mixing processes would slow down and the estuarine plume would increase in thickness possibly by wind mixing of the remnants of the discharged freshwater. Supplied nutrients could be taken up with a subsequent increase in phytoplankton biomass. During an approaching neap tide, a bloom might develop, resulting in a higher fluorescence (e.g. Table 2.1) and lower NO₃ concentrations in the source water which could be entrained during the neap tide. A pre-neap tide bloom has been observed by Harrison et al. (1991) for the same region in July.

**Higher vs Lower River Discharge**

The time series on May 29-30 and June 7-8, 1990 were during similar tidal ranges, close to the spring tide, with similar low average wind speeds. Thus, comparison between the two time series to examine the effects of the discharge is possible. Furthermore, the
discharge of 9000 m$^3$ s$^{-1}$ on June 7 had been preceded by four days of higher discharge which were near the annual maximum (10,100 m$^3$ s$^{-1}$). Therefore, the results of this study also represent the interaction between the maximum river discharge and the biggest spring tide of the year and its effects on entrainment as well as water column structure. It appears that the discharge on June 7-8 was so strong that a large area of deep water beyond the river mouth was exposed to the riverine plume. As shown in Figure 2.9, Zone I would extend much farther into the Strait beyond the river mouth (solid line) than during the small discharge condition (dashed line). As a result, the riverine plume will have more direct contact with the deep seawater during high discharge. This is probably why there was no NO$_3$ minimum in the contour plot (Figure 2.5D). Also, the freshwater penetrated deeper into the water column, 9.6 m compared to 7.4 m for the smaller discharge on May 29-30 (Table 2.2). This deeper penetration of the riverine plume allowed it to contact the higher NO$_3$ concentrations indicated by the higher slope (25 $\mu$M). As a result, more NO$_3$ (72 mmol m$^{-2}$) was entrained during higher discharge, about twice as much (32 mmol m$^{-2}$) as during lower discharge. The entrained NO$_3$ contribution to the surface layer was 5 times the river NO$_3$ contribution, compared to 3 times for the smaller discharge on May 29-30 (Table 2.2). It is interesting to note that the ratios of the entrained deep water to the freshwater were the same between the two discharges. This was also the case between the spring and neap tides. It appears that any physical and biological processes which affect the source NO$_3$ concentration would affect the amount of the entrained NO$_3$ as well.

**Entrainment and Its Biological Significance**

In previous studies and this one, the fluorescence maximum was located at the interface between the estuarine plume and the deep water and coincided with the NO$_3$ minimum. The maximum is advected with the interface toward or into the river and phytoplankton are entrained into the riverine plume above the interface. Figure 2.10
Figure 2.10 Vertical profiles of salinity (S), nitrate (N) and fluorescence (F) with their corresponding temperature-salinity diagram and NO$_3$-salinity and fluorescence-salinity diagrams, at T2 (A, B) and T3 (C, D) (see Figure 2.1 for sampling times) during the neap tide of June 12, 1989. These graphs demonstrate the entrainment of NO$_3$ accompanied by a second shallower fluorescence maximum entrained from the deeper fluorescence maximum.
shows two vertical profiles and their corresponding T-S diagrams with NO3 and fluorescence. There are double fluorescence maxima. The deeper fluorescence maximum coincides with the NO3 minimum just above the nutricline (Figure 2.10A and C). In Figure 2.10A, the shallower fluorescence maximum is seen to coincide with a NO3 maximum. In Figure 2.10C, the shallower fluorescence maximum is accompanied by the riverine plume with higher NO3 concentrations at the surface. When fluorescence and NO3 were plotted against salinity, it became clear that the entrainment of both into the surface and above the interface took place. In Figure 2.10B and 10D, the temperature drop at the kink in the T-S line, which indicates the entrainment of the colder deep water, coincides with the maximum in NO3 and fluorescence, and the temperature rise at the kink is accompanied by the minimum of NO3 and fluorescence. These results indicate that the shallower fluorescence maximum was entrained from the deeper maximum. Figure 2.11 demonstrates the process of the formation of such a double fluorescence maxima. One vertical profile (indicated by the dotted lines) was taken in the estuarine plume (i.e. seaward side of the riverine plume) 50 m away from the riverine front (see Figure 2.9). The other vertical profile (indicated by the solid lines) was taken 15 min after the riverine front crossed the anchored ship. While the deep layer remained very similar, the salinity in the surface layer decreased by 7 and the temperature decreased by more than 1° C. The increase in the silicate concentration was another indicator of the presence of the riverine plume. NO3 entrainment was evident from this cross-front vertical profile. More interesting is the formation of double fluorescence maxima when the riverine front crossed the station. The shallower one was located at the sharp halocline. Apparently it was entrained from the deep maximum and dragged along as the front advanced. The feature of the double chlorophyll maxima coinciding with the NO3 concentration minima in the water column has been reported for the same area (Cochlan et al. 1989).
Figure 2.11 A riverine front (shown in Figure 2.9) crossed a station, 35 km away from the river mouth on June 14, 1989. Two vertical profiles were taken within 30 min, one (dotted line) was 50 m away from the riverine front (seaward of the riverine plume) and the other (solid line) after the riverine front passed the station 20 m away (within the riverine plume). The movement of the riverine front induced entrainment of NO3 and produced double chl a maxima.
Salinity $T \, ^{\circ}C$  NO$_3$ ($\mu$M)  SiO$_4$ ($\mu$M)  Flu.

Outside the riverine plume
--- Inside the riverine plume
The double chlorophyll maxima feature associated with the water flow was also reported for Chesapeake Bay where a deep maximum of dinoflagellates moved via the bottom, up into the Chester River, emerged upstream at the surface, and then flowed downstream, forming a surface maximum (Tyler 1984). When it entered the bay proper, it moved underneath the surface of the lighter water, forming a near-surface maximum. In the lower St. Lawrence estuary, the seeding of the fresher surface layer by entrainment of seed cells from the saline deeper layer is suggested to be of great importance in initiating the spring phytoplankton bloom (Therriault and Levasseur 1986). A recent study in the Gulf of Maine applying temperature-salinity diagrams in the analysis of water masses, indicated that the colder nutrient-rich deeper waters of the slope origin contribute a significant fraction of the high nutrient concentrations (Townsend et al. 1987). The entrained phytoplankton would be very important in seeding downstream in the estuary. In the estuarine plume in the Strait of Georgia, the entrained phytoplankton would take up the entrained nutrients and grow faster because of the improved light conditions due to settling of suspended sediments as they move away from the river. A bloom should develop, forming a regional maximum of primary production in the estuarine plume. Previous studies in the Strait found a productivity maximum in the estuarine plume (Parsons et al. 1969, Stockner et al. 1979, Harrison et al. 1991). Zooplankton appear to form a regional abundance maximum around this region (Parsons et al. 1969, Mackas and Louttit 1988, St. John et al. 1992).

Parsons et al. (1980) suggested that nutrient-poor water could be drawn under the plume and entrained. The previous study (Chapter 1) supports this suggestion. Salt entrainment does not necessarily mean NO₃ entrainment. The amount of entrained NO₃ was accounted for by the entrained deep seawater (EDW) rather than the sum of EDW plus the entrained estuarine plume (EEP). Most upward entrainment occurred during tidal ebbs, especially during spring tides. An increase in river discharge results in an increase in the amount of NO₃ entrained. The process starts in the salt wedge and extends beyond the
river mouth. Winds will also play an important role in regulating entrainment processes (Chapter 3, St. John et al. 1993). The fluorescence maximum at the bottom of the estuarine plume is advected towards the river underneath the riverine plume or into the river with the advance of the salt wedge. Then, phytoplankton in the maximum are entrained upward into the riverine plume and become seed populations for future blooms in the estuarine plume. Tidal cycles and changes in river discharge should produce temporal phytoplankton blooms and a regional maximum in primary production. This will be examined in future studies (Yin et al., in prep.).
CHAPTER 3
ENTRAINMENT OF NITRATE IN THE FRASER RIVER PLUME AND ITS BIOLOGICAL IMPLICATIONS: EFFECTS OF WINDS

INTRODUCTION

Winds act on the surface of a water column and cause vertical mixing, resulting in deepening of the mixed upper layer in the water column (Farmer 1972, Denman and Powell 1984, Mann and Lazier 1991). Nutrient distribution can be controlled by wind mixing (Foster et al. 1985). Winds, along with tides and river discharge, determine the stratification and mixing of the water column in the Strait of Georgia estuary (LeBlond 1983). The plume characteristics (surface average salinity, horizontal maximum salinity gradient) on the southern section was found to be correlated with the along-strait component of the wind (Royer and Emery 1982).

The previous studies have shown that entrainment of NO$_3$ in the river and in the area beyond the river mouth (a few kilometers away) is influenced by tides and the magnitude of the river discharge: a spring tide and higher river discharge result in more NO$_3$ entrainment than a neap tide and lower river discharge (Chapters 1 and 2). The river outflow is stronger at lower LLW during a spring tide than during a neap tide, or during higher river discharge. Thus the velocity shear between the outflow and the layer below is greater during the spring tide or higher river discharge. The stronger shear results in more entrainment. It is expected that shears between the surface layer (the riverine plume or the estuarine plume) and the water below would be increased when sufficiently strong winds blow over it. If the surface layer velocity is great enough under strong winds, shear between the two layers will be sufficient to overcome the stratification and mixing across the pycnocline will take place.

In this study, a wind event during a time series at the same anchored station (Stn 2) as in Chapter 2, 8 km away from the river mouth, is reported and the mixing effects on the water column and subsequent NO$_3$ entrainment are described.
MATERIALS AND METHODS

Two time series on August 23-24, 1990 and on August 7-8, 1991 were conducted at Stn 2 (see Figure 1.1 for its position). A continuous vertical profile of salinity, temperature, fluorescence, velocity and nutrients was taken every 3-4 h over a 24 h period when the ship was anchored. The details of the vertical profiling and the methods for nutrient analyses, chl a and primary production, the data processing for vertical profiles and the equivalent thickness are described in GENERAL MATERIALS AND METHODS. The wind speeds were recorded at Vancouver International Airport (close to the river mouth) for the time series of August 23-24, 1990 and at Sand Heads (right at the river mouth) for August 7-8, 1991.

A gradient Richardson number was calculated according to the following equation:

\[ \text{Richardson number} = \left( \frac{g}{\rho} \right) \frac{dp/dz}{(du/dz)^2} \]

where \( g \) is gravity acceleration, \( \rho \) is density, \( dp/dz \) is the vertical density gradient and \( du/dz \) is the velocity shear in the vertical. The \( u \) direction is taken to be parallel to the surface flow; the perpendicular component is generally small. Thus, our calculation is an upper bound for the value.

RESULTS AND DISCUSSION

Figure 3.1 shows the winds and tides for the two time series at Stn 2. The winds were much stronger during August 7-8, 1991 than during August 23-24, 1990. The strong winds on August 7-8 were greatly reduced after the time series. The direction of the stronger winds was persistently from the north. The time series of weak winds on August 23-24, 1990 is presented as a control for the windy time series.
Figure 3.1  Tidal height (A) and wind speed (B) for the two time series at Stn 2, 8 km seaward of the mouth of the Fraser River. The solid line represents the time series on August 7-8, 1991 with 8 solid filled triangles indicating the sampling times. The dotted line represents the time series on August 23-24, 1990 with 6 open inverted triangles indicating the sampling times.
Weak Winds

The time series of vertical profiles of salinity, NO₃ and fluorescence for August 23-24, 1990 are shown in Figure 3.2. At T1 and T2, there was a shallow mixed surface layer (about 2 m). At T3 during the tidal flood, the riverine plume was weakly present. When the riverine plume flowed to Stn 2 in the top 1-2 m at T4, T5 and T6, the mixed layer became deeper (6-8 m) (Figure 3.2). The T-S diagrams (Figure 3.3) basically show that there are three water masses and that all the lines (indicating water masses) are smooth. Although the invasion of the riverine plume was observed during T4 to T6 (Figure 3.3), the estuarine plume size (proportion) appeared to be larger in the upper 10 m during the same time than during T1-T3 (Figure 3.4). Also, during T4-T6, the deep water proportion in the same upper 10 m was reduced (Figure 3.4). A NO₃ minimum was located near the bottom of the intermediate salinity layer which is dominated by the estuarine plume water and an increase in NO₃ concentration at the surface was accompanied by the invasion of the riverine plume (Figure 3.2). Fluorescence vertical profiles were almost mirror images of the NO₃ distribution: the fluorescence maximum coincided with the NO₃ minimum (Figure 3.2).

Strong Winds

Since the wind blew towards the south and the riverine plume usually turns to the north due to the Coriolis force, these forces would tend to balance out and allow the riverine plume to pass Stn 2. In addition, the wind component towards Stn 2 would increase the outflow. Figure 3.5 shows the time series of vertical profiles of salinity, NO₃ and fluorescence during the strong wind event on August 7-8, 1991. At T1, 1 h after LLW, the riverine plume was already observed at Stn 2. During the middle of the flood (T2), the riverine plume became distinct. In the T-S diagram in Figure 3.6, the T2 curve at salinity < 23 representing the mixture of the riverine and estuarine plumes is not straight as at T1, suggesting entrainment of water colder than that of the estuarine plume.
Figure 3.2 Time series of six vertical profiles of salinity, NO$_3$ and fluorescence under weak winds for August 23-24, 1990 (see Figure 3.1 for the sampling times).
Figure 3.3 Time series of T-S diagrams under weak winds on August 23-24, 1990 (see Figure 3.1 for the sampling times).
Figure 3.4 Time series of vertical distribution in proportion of freshwater (FW), the estuarine plume (EP) and the deep water (DW) under weak winds on August 23-24, 1990 (see Figure 3.1 for the sampling times).
Figure 3.5 Time series of eight vertical profiles of salinity, NO$_3$ and fluorescence under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times).
Figure 3.6  Time series of T-S diagrams under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times).
By T3 during the higher high water (HHW), the riverine plume was mixed in the top 2 m. The corresponding T-S diagram reveals that much colder seawater had been entrained (Figure 3.6). During the rest of the time series, the riverine plume appeared to be present but gradually mixed with other water masses. The water column was basically multi-layered and the halocline became broadened and gradual, indicating entraining and vertical mixing processes (Figures 3.5 and 3.6). The halocline extended to the deeper layer below 12 m during T6 to T8, a result of gaining a water volume due to wind-assisting entrainment by the riverine plume. The vertical mixing becomes clearer in the T-S diagrams (Figure 3.6). During T1 to T4, the riverine plume and the estuarine plume were readily apparent. During T5 to T8, however, they were almost mixed into one line as shown on the T-S diagrams, indicating that the water column became almost one water mass. The slopes for salinities > 25 were also a bit lower for T5 to T8 than the ones for T1 to T4, indicating fresher water penetrating deeper by wind mixing. The tidal stage might also play a role in this mixing process. As the tide approached high water levels at T5, T6, and T7 (Figure 3.1), the river outflow would slow down and even be dammed. While the wind continued to blow and exert a force on the surface, the remaining riverine plume water was mixed deeper. Although our observation at a fixed station could not separate horizontal advection from vertical mixing, it is reasonable to assume that the water masses advected to Stn 2 from other areas were subjected to the same wind force. It also should be mentioned that mixing among the three water types into one water mass (one slope in a T-S diagram) does not mean homogeneous mixing since there are still salinity gradients throughout the upper part of the water column (Figure 3.5).

The vertical NO₃ distribution demonstrated a clear response to wind mixing (Figure 3.5). A NO₃ minimum was present during T1 to T5 and disappeared during T6 to T8. The disappearance of the NO₃ minimum in the water column was eventually due to entrainment of NO₃-rich deep water into this 4-8 m layer because the riverine plume water mixing with the estuarine plume would reduce NO₃ to levels lower than the river water.
NO$_3$ or the initial surface NO$_3$ of the time series. As shown in Figure 3.5, the surface NO$_3$ concentrations remained similar throughout the time series, or were slightly higher at the end. Since the NO$_3$ minimum occupied a relatively thick layer of the water column, the vertical mixing of the riverine plume, the estuarine plume and the deep seawater resulted in a decrease in NO$_3$ concentrations in the lower layer during T6 to T8, compared to earlier times.

Fluorescence responded to wind mixing and its change reflected closely the change in NO$_3$ distribution (Figure 3.5). The fluorescence maximum coincided with the NO$_3$ minimum initially and then it became mixed in the upper layer when the NO$_3$ minimum was eroded. Note that phytoplankton cells did not appear to be lost during mixing from the upper stratified layer, as shown by the distribution of fluorescence (Figure 3.5). These phytoplankton cells could rapidly respond to the increase in nutrients.

The change in the distribution of salinity, NO$_3$ and fluorescence during the time series indicated vertical mixing among the three water types. Figure 3.7 shows vertical profiles of velocity and Richardson numbers as well as salinity. Currents were strong at the surface and were reduced in the lower layer. Most of the time, there was two-layer flow in the water column (T2, T3, T5, T6 and T7). The surface layer flowed in one direction and the water below flowed in the opposite direction. There was a depth at which the two flows moved opposite each other and hence the current speed was zero. This depth will be referred to as the null depth. A halocline was also located at the null depth. A strong shear often occurred near the null depth because of the two flows moving opposite each other. Mixing most likely took place near this depth. Richardson numbers (Figure 3.7) indicted that parts of the water column were turbulent because Richardson numbers were often less than 0.25. A Richardson number of 0.25 is a critical value below which velocity shear is considered to be strong enough to overcome density stability and allow turbulence and turbulent mixing to occur (Dyer and News 1986, Geyer and Farmer 1989, Partch and Smith 1978). As shown in Figure 3.7,
Figure 3.7 Time series of vertical profiles of velocity (solid line) and Richardson number (circles) under windy conditions on August 7-8, 1991. The velocity shown is the component in the direction of the surface flow, which changes somewhat between the vertical profiles. The component perpendicular to the surface component is generally small. The vertical dotted line delineates zero in velocity. The filled circles indicate Richardson numbers that are < 0.25. Salinity (dotted line) is also plotted for comparison.
Richardson numbers <0.25 (filled circles) frequently occurred near the null depth. As entrainment and mixing took place, the upper layer became thicker. Another indication of entrainment was that the null zone moved noticeably deeper near the end of the time series (T5, T6 and T7). The water of the surface layer was also getting heavier as the denser deep water was entrained upward and mixed as the wind continued blowing. This deepening slowed down the surface layer flow near the end of the time series even before the wind speeds were reduced. Interestingly, the rapid changes in velocities and salinities frequently coincided with each other (Figure 3.7), indicating a close coupling between water flows and salinity structure. Particularly, the null depth was sometimes located right at a major halocline (T2, T3 and T5, Figure 3.7).

The result of wind-induced entrainment and mixing is clearly shown in Figure 3.8: over the time series, freshwater penetrates deeper, the estuarine plume volume shrinks in the top 10 m and the deep water proportion increases in the same layer and at the surface as well.

**Strong vs Weak Winds**

The equivalent thickness of entrained deep seawater was thicker during the strong wind time series (Figure 3.9B) than during the weak wind time series (Figure 3.9A) (see the text in Chapter 1 for the definition and calculation of equivalent thickness and the amount of entrained NO3). Also shown in Figure 3.9B are tidal effects. Entrainment of the deep seawater and the freshwater penetration depth (bottom depth of the sum of the three equivalent thicknesses) appeared to decrease during the flood (T2) and high waters (T3 and T4), and then to increase (T5, T6 and T8). Entrainment of the deep seawater affected entrainment of NO3. A regression analysis (data not shown) indicated that 97% of the amount of entrained NO3 was accounted for by the equivalent thickness of the entrained deep seawater during the strong wind event and 72% during the weak wind time series. Regression analyses (data not shown) also indicated that depth-integrated
Figure 3.8  Time series of vertical distribution in proportion of freshwater, the estuarine plume and the deep seawater under windy conditions on August 7-8, 1991 (see Figure 3.1 for the sampling times).
Figure 3.9 Time series of equivalent thickness of freshwater, the entrained estuarine plume and the entrained deep seawater under: A) a weak wind condition on August 23-24, 1990, and B) a strong wind condition on August 7-8, 1991 (see Figure 3.1 for the sampling times).
Wind 2.3 m s$^{-1}$
August 23–24, 1990

A

Wind 7.3 m s$^{-1}$
August 7–8, 1991

B

- Freshwater
- Entrained estuarine plume
- Entrained deep seawater
fluorescence was explained by the volume (equivalent thickness) of the estuarine plume during both time series ($R^2 > 0.9$). The amount of entrained NO$_3$ under strong wind conditions was increased compared to weak wind conditions, as shown in Table 3.1 which summarizes a comparison between the two time series. The ratio of entrained deep seawater to freshwater during the windy time series was highest among all the time series although river discharge was the lowest (this study and Chapter 2). A possible explanation is that for the same amount of freshwater released from the river, speeds of the riverine plume must have been increased when constant winds blew in the right direction. In other words, the momentum and kinetic energy of the riverine plume was increased by winds. Therefore, more deep seawater was mixed with freshwater. At the same time, freshwater penetrated deeper (3 m deeper for the windy condition than for weak winds in Table 3.1). The contribution of entrained NO$_3$ was 12 times the river-borne NO$_3$ for the strong wind event and 5.6 times for the weak wind time series. Although low NO$_3$ concentrations in the river ($< 4 \mu M$) are mainly responsible for these high ratios, the high contribution of entrained NO$_3$ indicates that entrainment of NO$_3$ in summer is particularly important in supplying NO$_3$ and supporting new primary production for the region when NO$_3$ concentrations are low in the river.

During the time series of August 23-24, 1990, the tidal conditions were close to a neap tide and river discharge was lower, whereas the time series of August 7-8, 1991 was conducted during a pre-spring tide and under higher river discharge. Certainly, as shown in the previous study (Chapter 2), higher tidal range and river discharge contributed to entrainment of NO$_3$ during the strong wind event. However, the amount of entrained NO$_3$ (44 mmol m$^{-2}$) during the wind event of August 7-8, 1991 was even more than the amount (32 mmol m$^{-2}$) during the time series of May 29-30, 1990, which was conducted during higher tidal range and higher river discharge but low winds (3.6 m s$^{-1}$) (see Table 2.2, Chapter 2). The winds were mainly responsible for the higher entrainment of NO$_3$
Table 3.1 Comparisons between the weak wind condition on August 23-24, 1990 and the strong wind condition on August 7-8, 1991. All the parameters are time-averaged over the time series.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Weak Winds</th>
<th>Strong Winds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling period (h)</td>
<td>20.5</td>
<td>21.7</td>
</tr>
<tr>
<td>Tidal range (m)</td>
<td>2.6</td>
<td>3.8</td>
</tr>
<tr>
<td>Mean tidal height (m)</td>
<td>3.0</td>
<td>3.1</td>
</tr>
<tr>
<td>Wind speed (m s(^{-1}))</td>
<td>2.3(^*)</td>
<td>7.3(**)</td>
</tr>
<tr>
<td>Discharge (m(^3) s(^{-1}))</td>
<td>2890</td>
<td>4200</td>
</tr>
<tr>
<td>Equivalent thickness (m)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshwater</td>
<td>0.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Entrained estuarine plume (EEP)</td>
<td>4.1</td>
<td>4.9</td>
</tr>
<tr>
<td>Entrained deep seawater (EDW)</td>
<td>1.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Freshwater-penetration depth (m)</td>
<td>6.4</td>
<td>9.5</td>
</tr>
<tr>
<td>Entrained (\text{NO}_3) (mmol m(^{-2}))</td>
<td>15.9</td>
<td>43.7</td>
</tr>
<tr>
<td>River-borne (\text{NO}_3) (mmol m(^{-2}))</td>
<td>2.8</td>
<td>3.7</td>
</tr>
<tr>
<td>Depth-integrated fluorescence (m(^2))</td>
<td>7.7</td>
<td>3.1</td>
</tr>
<tr>
<td>Ratio of sum of EEP and EDW to freshwater</td>
<td>8.0</td>
<td>8.8</td>
</tr>
<tr>
<td>Ratio of EDW to freshwater</td>
<td>2.1</td>
<td>3.0</td>
</tr>
<tr>
<td>Ratio of entrained (\text{NO}_3) to river-borne (\text{NO}_3)</td>
<td>5.6</td>
<td>12.0</td>
</tr>
</tbody>
</table>

* There were no dominant directions

** Winds from the north were dominant
during the August 7-8 time series. Other strong evidence for the wind effect is that the NO₃ minimum layer was broken down by winds. This wind effect is comparable to the time series near the maximum river discharge which swept the NO₃ minimum away (Chapter 2).

When the water column is more stratified, more energy will be required to break down stratification. If a pycnocline is strong, the surface flow can be decoupled from the water below (Buckley and Pond 1976). Therefore, the degree of vertical mixing in the water column depends on stratification and the depth of stratification. The degree will increase with the distance away from the river mouth since the riverine plume produces a greater salinity gradient close to the river mouth. The increase in vertical mixing with distance was shown in the vertical profiles along a transect of stations from Stn 2 to 110 km north in the Strait of Georgia (Yin et al., in prep.). Those vertical profiles were conducted on the same day after the end of the time series on August 8, 1991. The water column further seaward was more mixed and NO₃ concentrations were increased in the surface layer compared to the profile at T8 in Figure 3.5. A recent model for the same region also suggests that the water column will be more mixed by a constant wind speed at a zone farther away than one near the river mouth (St. John et al. 1993).

Phytoplankton cells during the wind event remained in the surface mixing layer (which was still stratified within itself and relative to the layer below), as shown in vertical profiles of fluorescence in Figure 3.5. They should be capable of taking up the entrained nutrients quickly and growing rapidly. In Figure 3.10, vertical profiles of chlorophyll and primary production at the beginning and end of the windy time series show that both chlorophyll and primary production were increased at the end (T8) compared to the beginning (T1). The difference in primary production between the profiles was not due to differences in surface irradiances since daily solar radiation on August 8 was even lower than on August 7. In fact, a summer wind-induced bloom was observed in the estuarine plume immediately after this wind event (Yin et al., in prep.). Such a rapid response is
Figure 3.10  Vertical profiles of chl \( a \) and primary production at the beginning (T1) and the end (T8) of time series of August 7-8, 1991 (see Figure 3.1 for the sampling times).
August 7  T1 = 1000 h  (○)
August 8  T8 = 0745 h  (●)
different from wind effects producing upwelling in coastal oceans, where it usually takes
days to weeks for upwelled phytoplankton to respond to the upwelled nutrients and
improved light conditions (MacIsaac et al. 1985, Zimmerman et al. 1987).

In conclusion, under windy conditions, entrainment of NO₃ was increased
compared to weak winds. High winds enhanced the effects of tidal conditions and the
magnitude of river discharge. Winds transferred horizontal momentum to the surface layer
and induced a strong shear between the different layers, which could be sufficient for
across-pycnocline mixing. As a result of wind-induced entrainment, phytoplankton cells
remained in the euphotic zone and could take up the entrained nutrients rapidly, enabling
the development of a summer phytoplankton bloom.
CHAPTER 4
SPRING BLOOM IN THE VICINITY OF THE FRASER RIVER PLUME:
INTERACTIONS OF RIVER DISCHARGE, WINDS AND GRAZING

INTRODUCTION

The Fraser River discharge plays a key role as a physical driving force for productivity in the Strait (LeBlond 1983, Harrison et al. 1983). Early work by Parsons et al. (1969a, 1970) and Stockner et al. (1979) mainly focused on the seasonal change in nutrients and plankton production in the entire Strait, including some inlets, and their sampling frequency was on bi-weekly or monthly time scales. Their findings show that phytoplankton production starts to increase slowly in early March and the spring bloom occurs in April during the beginning of the Fraser River freshet. In particular, the region near the Fraser River shows an earlier onset of the spring bloom compared to the adjacent regions due to stratification caused by river discharge (Parsons et al. 1969a, Stockner et al. 1979). This observation has been reported in many other estuaries (Smayda 1983, Legendre 1990, and Mann and Lazier 1991). However, not all estuaries show the early inception of the spring bloom (Legendre 1990).

Recently, increased numbers of studies over short time scales or scales of an episodic event show that biological processes are closely coupled with physical processes (Legendre and Demers 1984, Mann and Lazier 1991). Such short time scale studies have increased the understanding of the effects of tidal mixing and circulation in estuaries on biological processes. Examples can be found in the York River (Haas et al. 1977, Webb and D'Elia 1980), Chesapeake Bay (Tyler 1984, Brandt et al. 1986). In the vicinity of the Fraser River, a high resolution continuous zooplankton counting system equipped with a salinity and temperature sensor revealed a high aggregation of copepods (mainly Neocalanus plumchrus) at the riverine front (Mackas et al. 1988). The aggregation was believed to be caused by a physical driving mechanism or the behavior of copepods.
responding to some physical processes at the front (Mackas et al. 1988). Studies in short
time scales (hourly, daily and weekly scales) for the Strait of Georgia are still lacking,
particularly for nutrient dynamics associated with phytoplankton production. A wind event
can delay the spring bloom and hence, change trophodynamic relationships. An example
of wind effects on pelagic food chains was shown in New York Bight (Walsh et al. 1978).

The objective of this study was to investigate how temporal (day-to-day) and
mesoscale spatial variations in the spring bloom were influenced by the Fraser River
discharge, winds and grazing.

MATERIALS AND METHODS

The study area and the stations are shown in Figure 4.1 (solid circles). The cruise
was conducted during April 2-19, 1991. The transect was designed to cover zones from
the riverine plume (Stn 2) to an area (Stn 1) in the Strait of Georgia not influenced by
recent river discharge. By sampling the transect daily during the cruise, I was able to
observe how a wind event and an increase in river discharge influenced hydrodynamics and
biological processes in the region.

The methods for vertical profiles of salinity, temperature, fluorescence, and nitrate,
for the nutrient analyses, for measurements of chl $a$ and primary production, and for the
data processing for vertical profiles are described in GENERAL MATERIALS AND
METHODS.

RESULTS

Winds, Tides and River Discharge

Figure 4.2 shows river discharge, winds and tidal ranges during the cruise between
April 2-19, 1991. The river discharge started to increase gradually from April 2 (1000 m$^3$
s$^{-1}$) to April 14 (1500 m$^3$ s$^{-1}$) and then rapidly climbed to 2750 m$^3$ s$^{-1}$ on April 19,
indicating the beginning of the spring freshet of 1991 (Figure 4.2A). A wind event
occurred during April 3-10, with speeds $>$ 6 m s$^{-1}$ on April 3 and remained above 4 m s$^{-1}$
Figure 4.1 Map of the stations in the Strait of Georgia for the cruise conducted during April 2-19, 1991.
Figure 4.2  A) Fraser River discharge for 1991 at Hope; B) Fraser River discharge and daily averaged wind speed, and C) tidal ranges during April 1-19, 1991.
Julian Days 1991

Discharge (m$^3$ s$^{-1}$)

0 60 120 180 240 300 360

- 8000

- 6000

- 4000

- 2000

0

Discharge

Wind (m s$^{-1}$)

April 1–19

A

B

C

Tidal Range (m)

0 1 2 3 4 5

April 1991

April 1991
until April 10 (except for April 7) (Figure 4.2B). Wind direction was mainly from the south and east during April 3-9 and then during April 15-18, it shifted to mostly westerly, varying between northwesterly and southwesterly. Tidal ranges indicate that there was a neap tide on April 11 and spring tides on April 2 and 17 (Figure 4.2C).

Winds are certainly crucial to the water column stability before the freshet and a phytoplankton bloom is only possible under low winds at this time of the year. The results below show that an underway spring bloom was interrupted by the wind event and this delay allowed zooplankton grazing to catch up with or exceed phytoplankton production.

**Areal Phytoplankton Biomass and Production**

High chl \(a\) concentrations and primary production on April 4-5 indicated that a spring bloom had been underway in the Strait of Georgia before the beginning of the cruise (Figure 4.3). However, as the winds continued to blow during April 7-10, chl \(a\) concentrations and primary production dramatically decreased except at Stn 2. Chl \(a\) concentrations and primary production on April 15-16 were even lower, suggesting a continuing decrease after the winds had decreased (ca. 2 m s\(^{-1}\)) on April 11. During April 15-18, phytoplankton biomass and production increased gradually, but the magnitude did not reach that at the beginning of the wind event. Both chl \(a\) concentrations and primary production were highest at Stn 3 on April 4-5 and higher near the river mouth (Stns 2 and 3) than Stn 1 during April 7-10. After the wind storm, the region of maximal chl \(a\) and production moved to P3, further seaward of the river. These changes are attributed to coupling with the hydrodynamics of the water column.

**Salinity**

Vertical profiles of salinity along the transect during April 2-9 are shown in Figure 4.4. On April 2, before the wind event, the water column was stratified near the river mouth (Stn 2 and P1A) and the halocline almost occupied the entire stratified upper layer extending down to 12 m. In other words, the top of the lower deep layer was at 12 m.
Figure 4.3 Temporal and spatial changes in chl \( a \) (mg m\(^{-2}\)) and primary production (mg C m\(^{-2} d^{-1}\)) along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 4-18, 1991. Note that the Y axis scale for April 4-5 differs from those of the other periods.
Figure 4.4  Vertical profiles of salinity along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9.
In this system, due to the nature of the pulsed river outflow, the water column is frequently multi-layered. Therefore, a surface mixed layer in a conventional sense rarely exists. Often there is a lower mixed layer. More practically, the layer above the top boundary of this lower mixed layer is stratified and can be considered to be a stable zone for phytoplankton growth. On April 4-5, the stratification was stronger near the river mouth due to the influence of the riverine plume. The water column at Stn 1 had not been influenced by recent river discharge since the water column was almost homogeneously mixed. Near the end of the wind event on April 8-9, the water column was still strongly stratified near the river mouth (Stn 2 and P1), but the stratified layer was shallower (ca. 5 m) and the salinity at depth increased. Stn 3 was almost completely mixed in the upper 22 m with salinity >29. Although there was a surface mixed layer at stations P2 and P4 (35 and 45 km away), the differences in salinity between the upper and lower layers were reduced compared to those on April 4-5 because of an increase in salinity in the upper mixed layer. Stn 1 was more stratified, suggesting advection of lower salinity water from the south due to the southerly winds during this period.

Figure 4.5 shows vertical profiles of salinity during April 15-18. The surface salinity increased seaward of Stn 2. The riverine plume was observed at Stn 2 and slightly at P1. The surface layer salinities did not decrease with time until April 18 although the freshwater discharge rapidly increased during the same period, indicating there was a time lag for the freshwater outflow of the Fraser River to be reflected in changes of salinity structure in regions further from the river. If a difference in salinity between the surface and the bottom (20 m) of a vertical profile is used to indicate the strength of the stratification of the water column, it is clear that the water column had been stratified during this period and that the stratification became stronger near the river mouth. Note that the halocline was gradual and occupied most of the upper 20 m water column at all the stations. The outflowing freshwater could not remain as a distinct water mass due to continuous vertical mixing as it moved away from the river mouth.
Figure 4.5  Vertical profiles of salinity along the transect from Stn 2 to Stn 1 during April 15-19.
These hydrodynamic features of the spatial change in the surface salinity and the gradual and broader halocline indicate a stratified water column.

**Nutrients**

On April 2, only two stations were sampled and they were the two nearest the river (Figure 4.6). NO$_3$ concentrations in the water column were only ca. 7 $\mu$M at the surface and ca. 10 $\mu$M at 15 m (Figure 4.6). The major nutricline appeared to be located below 20 m. On April 4-5, the surface NO$_3$ concentrations remained similar near the river mouth (Stns 2 & 3) and were even lower at P4 and P5. NO$_3$ concentrations increased considerably at P7 and Stn 1. By April 8-9, NO$_3$ concentrations increased at all the stations except Stn 1 where they were somewhat lower. The water at Stn 1 appeared to be advected from the southern region due to dominant southerly winds, as indicated by the salinity distribution shown in Figure 4.4.

Five days after the wind event, NO$_3$ concentrations at almost all stations were less on April 15 than on April 8-9 (Figure 4.7). During the period of April 15-18, the most striking feature is that NO$_3$ concentrations in the water column decreased gradually and slightly (P1, Stn 3, P2, and P3) over time.

**DISCUSSION**

**River Discharge and Winds**

As shown in Figure 4.4, the water column stratification was well developed before and at the beginning of the wind event from near the river mouth to P5 (55 km away from the river mouth). The freshwater accumulated and contributed to the stratification of the water column, suggesting that the gradual increase in the Fraser River discharge in late March had been sufficient to outweigh tidal turbulent mixing and wind mixing. The freshwater influenced region had not yet expanded into the entire central Strait of Georgia region. The stratified layer must have been stable enough to allow phytoplankton to bloom. However, the water column at this stage was still vulnerable to wind mixing.
Figure 4.6 Vertical profiles of \( \text{NO}_3 \) along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9.
\[ \text{NO}_3 (\mu M) \]

- April 2
- April 4-5
- April 8-9

Depth (m)

- S2
- P1
- S3
- P2
- P4
- P5
- P7
- S8
Figure 4.7  Vertical profiles of NO₃ along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 15-19.
Winds about 5 m s\(^{-1}\) on average during the wind event were destructive during the early establishment of the stratification in spring. A decrease in stratification from March to April has been shown for this region (Crean and Ages 1971, see their Figures 14 and 18). Since density differences (salinity differences in the Strait of Georgia) determine the degree of vertical mixing caused by winds, vertical mixing is more vigorous at stations further away from the river mouth than near it during a wind event. This spatial variation in wind mixing has also been demonstrated in a model for this region (St. John et al. 1993). After the wind event, the stratification was re-established quickly at the start of the annual freshet. Horizontal advection might have occurred during the wind event. However, water from other regions must have been subjected to the same wind mixing effect. In addition, spatial coverage in my sampling was over 100 km and similar trends in data occurred over this large area. It was unlikely that the water in this region could be advected out to other regions. Therefore, the temporal changes in the vertical structure of the water column during the wind event could be identified.

Set by these physical processes, the spring bloom in 1991 was underway in late March and early April and its magnitude was greater near the river mouth, indicating that the freshwater discharge resulted in an early onset of the spring bloom near the river. These results agree with earlier work by Parsons et al. (1969a). They reported that biomass and primary production at their Stn 7 (equivalent to Stn 2 in this study) started to increase in February and peaked in late March and early April. In contrast, no appreciable primary production occurred at their Stn 1 (further west than P5) until the end of March. A similar observation was made by Stockner et al. (1979) who sampled more stations and found that the peak bloom started in April in the vicinity of the Fraser River and occurred in May further away. This spatial pattern in the spring bloom certainly results from the freshwater influence of river discharge and cannot be attributed to temperature because vertical profiles of temperature displayed little stratification during April 2-9 (Figure 4.8).
Figure 4.8 Vertical profiles of temperature along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9.
Slow Recovery of the Spring Bloom

Nitrate concentrations were coupled with the chl $a$ and primary production distributions. Before the wind event, a spring bloom was developing and NO$_3$ had been reduced to low concentrations (Figure 4.6). In the early part of the wind event, the wind effect on vertical NO$_3$ distribution was not clearly shown. It could be due to a time lag for the winds to exert effects on vertical mixing, particularly where the freshwater influence on the water column stratification was strong enough to reduce vertical mixing (Figure 4.4: Stn 2, Stn 3, P2, P3 and P5). But since the vertical profiles on April 2 did not cover all the regions, the ones on April 4-5 could not be compared. As the winds continued to blow and vigorous mixing took place, the spring bloom was halted and NO$_3$ was mixed to the surface at the end of the wind event. Once the winds decreased, NO$_3$ consumption resumed (lower NO$_3$ concentrations on April 15 than on April 8-9). As shown in Figure 4.3, the gradual increase in chl $a$ and production, accompanied by a slow decrease in NO$_3$ concentrations, indicated a slow recovery of the spring bloom after the wind event.

A few possibilities which could be responsible for the slow recovery of the spring bloom are a time lag, sedimentation and grazing. These are discussed below.

**Time Lag**

During this cruise, the water column was still weakly stratified at the end of the wind event. However, stratification should not be a requirement for phytoplankton bloom to occur if there was no mixing. In a microcosm containing a sample of diatoms from the Strait of Georgia, a bloom usually can take place within a week (Spies and Parsons 1985). NO$_3$ vertical profiles displayed lower concentrations on April 15 than on April 8-9, indicating a utilization of nutrients during April 10-15. The decreased NO$_3$ did not appear to increase chl $a$ concentrations in the water column. Therefore, a time lag was the least likely to be responsible for low biomass and the slow recovery of the spring bloom.
**Sedimentation**

Sedimentation of phytoplankton cells is often reported to be the fate of the spring bloom in various regions (Smetacek *et al.* 1978, Skjoldal and Lannergren 1978, Conover and Mayzaud 1984, Riebesell 1991a, 1991b). Usually, sedimentation takes place particularly near the end of the spring bloom when a nutrient is depleted. During the bloom, however, daily sedimentation loss is relatively small, <10% of primary production (Riley 1970, Taguchi and Hargrave 1978, Parsons *et al.* 1984b). Sinking rates of phytoplankton cells under nutrient replete conditions usually are around 1-2 m d⁻¹ (Bienfang 1980, 1981, Bienfang and Harrison 1984). This rate only represents a 10-20% loss from a 10 m euphotic zone. Turbulent mixing decreases sinking and sedimentation rates of phytoplankton cells (Walsby and Reynolds 1980). Sinking rates of phytoplankton cells were also reported to decrease during a wind event (Malone 1983). Thus, during the April 4-9 wind event, probably little sedimentation occurred. Rather, phytoplankton cells could be mixed to a deeper depth. With the restratification of the water column, it was possible that phytoplankton cells in the lower layer might be lost, whereas a bloom could start in the upper stratified layer. An example of the re-establishment of a bloom after a wind storm interruption can be found in a lake study (Jewson *et al.* 1981). In this study, however, phytoplankton biomass and production increased very slowly during April 15-18, with a slow decrease in NO₃ concentrations. It appears that sedimentation was not responsible for the slow recovery of the spring bloom because nutrients should have been utilized at faster rates during April 15-18 if sinking loss had balanced production. Thus, grazing appears most likely to be in control of the recovery of the spring bloom.

**Grazing**

Total zooplankton consisted mostly (more than 95%) of copepods in the upper 25 m of the water column during the cruise (Goldblatt in prep.). The copepods *Neocalanus plumchris* and *Pseudocalanus minutus* were abundant (Figure 4.9A and B). However, the total biomass of *N. plumchris* was probably the largest (due to their larger body size),
Figure 4.9  Zooplankton abundance in the top 25 m at some stations along the transect during April 4-18.  A) *Neocalanus plumchrus*, showing the portion of copepodite stages C1 through C5, B) *Peudocalanus minutus*, and C) other zooplankton including *Calanus* sp., *Acartia longiremis*, *Eucalanus* sp. and *Centropages* sp.
During the Wind  After the wind

**N. plumchrus**

- C1
- C2
- C3
- C4
- C5

**P. minutus**

- S2
- S2
- S3

**Other copepods**
as indicated by an apparent increase in the number of their copepodite stage V (which are approximately 3 times stage IV and 10 times *P. minutus* in dry weight) after the wind event (Figure 4.9A). The abundance of other zooplankton also increased after the wind event (Figure 4.9C). The presence of these zooplankton in large numbers certainly exerted a large grazing pressure on phytoplankton. As a result, there are three features indicative of this grazing control mechanism.

1) **NO₃ concentrations** Only a small amount of NO₃ in the water column was consumed over 4 days (April 15-18, Figure 4.7). Zooplankton growth is known to lag phytoplankton growth during the spring bloom (Frost 1980). When the former suppresses the latter, nutrient concentrations will remain constant over time and no burst in phytoplankton biomass will occur. This theory has been used to offer one explanation of no spring bloom and non-depleting nutrients in the Pacific Ocean compared to the Atlantic Ocean where a pronounced spring bloom occurs and nutrients are depleted at the end of spring bloom because of the lag of zooplankton growth and grazing (Parsons *et al.* 1988).

2) **NH₄ concentrations** NH₄ is generated by zooplankton during grazing. Figures 4.10 and 11 show vertical profiles of NH₄ during April 2-9 and 15-19, respectively. NH₄ concentrations were around 0.5 µM at most stations during April 2-9. During April 15-18, NH₄ concentrations increased to 1.5 to 2 µM at almost all the stations. The question is: where did the increased NH₄ come from? NH₄ in the Fraser River was about 5 µM during the cruise. This concentration was not high enough to maintain 1.5-2 µM in the water column after the freshwater had been mixed with seawater of low concentrations of ca. 0.5 µM on April 8-9. Although the river discharge increased during April 15-18, salinity at the surface (Figure 4.5) was >25, representing about 16.7% freshwater, if a salinity of 30 was taken as the receiving seawater. This amount of freshwater would only produce 0.84 µM NH₄ in the surface under a condition of conservative mixing. Bacterial activity was not measured during this cruise. But bacterial activity is not important in this region when salinity exceeds 20 (Albright 1983a and
Figure 4.10 Vertical profiles of NH$_4$ concentrations along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 2-9.
Figure 4.11 Vertical profiles of NH$_4$ concentrations along the transect from Stn 2 to Stn 1 (Figure 4.1) during April 15-18.
A similar example was observed in the St. Lawrence estuary where bacterial importance was reduced in the seaward regions (Painchaud and Therriault 1989). In addition, NH₄ is a preferred nitrogen form over NO₃ by phytoplankton and its uptake is often enhanced (Dortch 1990). In a natural system without a large input of anthropogenic NH₄, NH₄ is frequently undetectable or very low (McCarthy and Goldman 1979). The Strait of Georgia does not receive appreciably higher NH₄ except from the Fraser River. The increase in NH₄ concentrations after the wind event had to come from zooplankton excretion and the higher remaining NH₄ concentrations during April 15-19 indicated that NH₄ generated by zooplankton exceeded phytoplankton utilization.

3) Total Nitrogen

Even more direct evidence to demonstrate the impact of grazing on phytoplankton biomass is the mass balance of total nitrogen (TN) including inorganic (DIN: NO₃+NO₂, NH₄, and urea) and particulate organic nitrogen (PON). When DIN starts to decrease due to phytoplankton utilization, PON will increase at the same rate. In other words, the decrease in the concentration of DIN is the same as the increase in the concentration of PON, but TN remains unchanged unless there are losses by grazing or sedimentation of phytoplankton out of the defined layer. In this mass balance, dissolved organic nitrogen (DON) is not included. As long as dissolved organic nitrogen is not substantially different between depths, this approach is valid. Figure 4.12 shows vertical profiles of TN during the wind event on April 4-9. TN was above 20 μM at the surface at all the stations and as high as 32 μM at depth. The maximum vertical difference in TN was about 6 μM. Unfortunately, particulate nitrogen data were not collected after the wind event. However, particulate nitrogen was significantly (p<0.0005) related with chl a during April 4-9 (Figure 4.13). The equation derived from the regression was used to calculate PON during April 15-18. Vertical profiles of TN during April 15-18 were shown in Figure 4.14. TN was reduced (to as low as 16 μM) at both the surface and the deeper depths. Also, the vertical differences in TN between the surface and the lower layer (<28 μM at most stations) were increased. It is clear that there was greater loss of
Figure 4.12 Vertical profiles of total nitrogen (TN) during April 4-9, 1991. Triangle symbols indicate the sampling next day at the same station (Stn 2 and Stn 3).
Figure 4.13  Regression of particulate nitrogen (PN) over chl a a during April 4-9, 1991.

\[ PN = 0.859 \times \text{Chla} + 3.396 \] (\( R^2 = 0.835 \), \( p < 0.0005 \)). The two dotted lines are 95% confidence intervals.
April 4–10, 1991

\[ PN = 0.859 \times \text{Chl a} + 3.396 \]

\[ R^2 = 0.835 \]
Figure 4.14  Vertical profiles of total nitrogen (TN) along the transect from Stn 2 to Stn 1 (Figure 4.1) on April 15-18. PON is calculated using the regression in Figure 4.13.
TN after the wind event than during the wind event, which resulted from higher grazing pressure by more abundant zooplankton during April 15-18.

Thus, all the evidence presented above, indicates that zooplankton grazing appeared to be responsible for the slow recovery of the spring bloom after the wind event.

**Significance of the Wind Event**

Where did the increased amount of zooplankton come from after the wind event when phytoplankton biomass and production was low at the end of the wind event? As described in the GENERAL INTRODUCTION, the young stages (copepodites) of *Neocalanus plumchrus* migrate in large numbers to the surface during April (Fulton 1973), independent of the spring phytoplankton bloom (Harrison *et al.* 1983), which is supported by zooplankton abundance shown in Figure 4.9. They are herbivorous. Therefore, the wind event had altered the phasing between the stage of the spring bloom and the appearance of zooplankton. Such alterations have been discussed (Parsons 1988) and demonstrated in the computer model analysis of pelagic ecosystems in estuarine waters (Parsons and Kessler 1986). In the model, a change in light extinction coefficient shifted zooplankton growth and abundance. For example, when the extinction coefficient was 0.2 m\(^{-1}\), phytoplankton grew so fast that zooplankton missed the bloom. When the extinction coefficient was increased to 0.3 m\(^{-1}\), phytoplankton growth was slowed down by the lack of light and zooplankton grazed the slower growing phytoplankton more efficiently and attained a higher maximum standing stock, indicating closer coupling (Parsons and Kessler 1986). This simulation is comparable to this wind mixing event. When the winds mixed the water column, the average light that phytoplankton experienced in the mixing layer was reduced, similar to an increase in the extinction coefficient. The reduction in the average light halted the spring bloom in addition to dispersing phytoplankton cells by wind-driven vertical mixing. When the bloom started to recover, large numbers of copepods had independently migrated to the surface layer due to their ontogenic migration. Thus, the phytoplankton biomass was suppressed to lower levels by heavy zooplankton grazing and
NO₃ concentrations decreased slowly. The slow decrease in NO₃ over time might also be due to an inhibition of NO₃ uptake by the increase in NH₄ produced from grazing. Mediating algal growth by nutrients and zooplankton was observed in studies by Elser et al. (1987) and Lampert et al. (1986). The latter study had a similar sequence to this study: NO₃ decreased with an increase in chl a during the spring bloom. When zooplankton grazing pressure increased, chl a decreased. As a result, NO₃ levels remained high and decreased little during the peak in abundance of zooplankton. At the same time, NH₄ concentrations greatly increased. Wind events have also been reported to affect food chain dynamics within the New York Bight, where the interaction between storms and stratification affects the structure and frequency of chl a distributions across the shelf which may influence both the survival strategies of herbivores and the loci of energy transfer to the rest of the food chain (Walsh et al. 1978).

In summary, the spring bloom was underway in late March and early April, 1991 in the Strait of Georgia in the vicinity of the Fraser River plume. The magnitude of the bloom was greater near the river mouth, indicating an earlier onset of the spring bloom there. A week-long wind event (wind speed >4 m⁻¹) occurred on April 3-10. At this time of the year, prior to and during the beginning of the annual freshet, the stratification was still vulnerable to wind mixing. The winds during the wind event were strong enough to cause considerable mixing. Coupled with the hydrodynamic change, phytoplankton biomass and production were reduced and NO₃ was increased at the end of the wind event. The spring bloom was interrupted by physical processes due to the winds. Five days after the wind event (on April 15), phytoplankton biomass and production were lower than at the end (April 9) of the wind event and remained even lower in spite of greater stratification and sufficient nutrients. NO₃ had been utilized to levels lower than at the end of the wind event. During the next four days, April 15-18, phytoplankton biomass and production gradually increased, NO₃ concentrations in the water column decreased slowly, indicating a slow recovery of the spring bloom. NH₄ concentrations remained at levels higher than
during the wind event and total nitrogen in the water column decreased. This evidence suggests that zooplankton grazing exceeded phytoplankton production. By June, NO$_3$ concentrations decreased to undetectable levels at the surface (Clifford et al. 1992). One might speculate that higher trophic predators such as juvenile salmonids and other juvenile fish grazed on the herbivorous copepods during May and thus allowed NO$_3$ utilization and phytoplankton growth. It is also possible that juvenile salmon survival and growth could be related to these trophodynamic changes as a result of wind events.
CHAPTER 5
INTERANNUAL VARIABILITY IN THE TIMING OF THE SPRING BLOOM IN
THE STRAIT OF GEORGIA ESTUARY

INTRODUCTION

The development of the spring bloom is usually shown as a rapid burst in biomass over a short time (Parsons et al. 1984b). In fact, phytoplankton biomass often increases in steps as a succession of peaks and troughs (e.g. Sverdrup 1953, Erga and Heimdal 1984, Klein and Sournia 1987, Sournia et al. 1987). How the spring bloom develops is certainly important in determining trophodynamic matching between phytoplankton and zooplankton and subsequently juvenile fish.

Interannual variability in nutrient loading and plankton production has been commonly observed in various regions (Cloern et al. 1983, 1985, Malone et al. 1984, 1988, Tyler 1986, Pennock and Sharp 1986, Thordardottir 1986, Sancetta 1989, Cloern 1991). Few studies have provided data of major physical conditions such as river discharge, tidal cycles and winds during the time of the spring bloom investigation.

In this chapter, I will present day-to-day changes in salinity, temperature, nutrients and phytoplankton production and some zooplankton data for 1988, 1992 and 1993. The two objectives were: 1) to examine if the spring bloom in the Central Strait develops as a steady continuation or as a series of steps, and 2) to examine if there is interannual variability in the development of the spring bloom. Based on the observed responses of the spring bloom to winds, river discharge and tidal cycles, I will present data on river discharge, tidal range and winds for 1988-1993 and examine how interannual variability in river discharge and winds affect the onset of the spring bloom and the course of its development.

In this chapter, I will focus on temporal changes. Since the sampling transects covered over 100 km in the open region of the Central Strait, horizontal advection would
not likely affect the identification of the temporal changes in my observations described below, unless the water was advected out of the sampled region very rapidly.

MATERIALS AND METHODS

The cruises were conducted during May 31-June 9, 1988; April 6-15, 1992; April 19-22, 1993. The sampling stations are shown in Figure 5.1.

The methods for vertical profiles of salinity, temperature, fluorescence, and nitrate, for the nutrient analyses, for measurements of chl a and primary production, and for the data processing for vertical profiles are described in GENERAL MATERIALS AND METHODS.

RESULTS

1988 June Cruise

River Discharge, Winds and Tidal Cycles  As shown in Figure 5.2, a spring tide occurred on June 2 and the neap tide occurred on June 8, 1988. Winds were weak during the cruise period and river discharge declined rapidly after the annual maximum during the same period. However, the river was still in a stage of high flow (Figure 5.2).

Salinity  Salinity profiles (Figure 5.3) revealed strong vertical gradients near the river mouth. The salinity gradient decreased with the distance away from the river mouth. The gradient penetrated to a depth of about 10 m, indicating a larger freshwater influence by the annual maximum river discharge (Figure 5.2).

Fluorescence  Fluorescence started to increase at the surface on June 1, forming a fluorescence maximum at the surface. Fluorescence gradually increased downwards and developed into a subsurface maximum during June 6-7 (Figure 5.4). The increase in fluorescence was coupled with a decrease in nitrate.

Nitrate  On May 31 and June 1, NO3 was undetectable at the surface of the station closest to the river mouth and increased with distance away from the river (> 10 \( \mu \text{M} \) at a few stations Figure 5.5). On June 4 and 6, at the stations further away from the
Figure 5.1  Map of the study area indicating stations for 1988 (X), 1992 (●), and 1993 (△). The stations in 1992 were the same as in 1991, but some stations in 1991 were not visited in 1992.
Figure 5.2 A) and B) The Fraser River discharge, C) wind speed and tidal ranges for the cruise period: May 31-June 9, 1988.
Figure 5.3. Vertical profiles of salinity along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988.
Figure 5.4. Vertical profiles of fluorescence along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988.
Figure 5.5 Vertical profiles of NO₃ along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988.
river mouth, nitrate was undetectable at the surface. By June 7, a subsurface minimum in NO₃ at an intermediate depth (7 m) at Stn 2 (near the river mouth) was observed.

**Silicate** Silicate concentrations decreased over time, especially at Stn 3 and Sf. A minimum in the silicate concentration occurred at an intermediate depth (around 6 m) (Figure 5.6). The position of the silicate minimum coincided with the fluorescence maximum. In general, the spatial distribution of silicate showed higher concentrations near the river mouth (Sa and Stn 2) than away from it (Sf) (Figure 5.6).

**NH₄** NH₄ concentrations during the entire cruise were generally lower than 1 μM and 0.5 μM at the end of the cruise (Table 5.1). There were some higher concentrations (> 1 μM) at Sf on June 2 and Stn 2 on June 3.

**Chl a, Primary Production and Bacterial Production** Phytoplankton biomass and production were high during this cruise (Table 5.2). Chl a ranged from 43.5 to 67.1 mg m⁻² at Stns 2, 3, 4, and Sf. Daily primary production ranged from 1190 to 2990 mg C m⁻² d⁻¹. Bacterial production was extremely low, only 8.97-28.1 mg C m⁻² d⁻¹ on average.

**Phytoplankton Populations and Total Microflagellates** The phytoplankton assemblage was made up almost entirely of three genera of diatoms: *Thalassiosira* spp., *Skeletonema costatum* and *Chaetoceros* spp. (Table 5.3). *Thalassiosira* spp. accounted for 70% or more (range from 26-87%) of the total phytoplankton volume at four stations during the entire cruise. Abundance of total microflagellates on average was low, on the order of 100 cells mL⁻¹ for all stations during the cruise (Table 5.2).

**Zooplankton** The zooplankton assemblage was mostly copepods with the most abundant genera being *Microcalanus* and *Pseudocalanus* at different times (Table 5.4). The number of *Neocalanus plumchrus* was small within the euphotic zone throughout the time series at Stn 4. Larvacea were the most abundant group among other zooplankton and *Euphausia* sp. became dominant one time and they were mostly juvenile (Appendix 5).
Figure 5.6 Vertical profiles of SiO$_4$ along the transect from the river mouth (Sa) to the other side of the Strait (Se and Sf) (see Figure 5.1) during May 31-June 7, 1988.
Table 5.1 Average (Avg) NH₄ concentrations (μM) over the sampling depth (m) at four stations along the transect (see Figure 5.1) in the Strait of Georgia during May 31-June 9, 1988. n = the number of concentrations at different depths being averaged. min = the minimum concentration. max = the maximum concentration. ud = undetectable. See Appendix 2 for the actual concentrations.

<table>
<thead>
<tr>
<th>Date</th>
<th>Time (hour)</th>
<th>0-8 m</th>
<th>0-12 m</th>
<th>0-16 m</th>
<th>0-22 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stn 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun 1</td>
<td>0900</td>
<td>0.47</td>
<td>0.48</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>1400</td>
<td>1.55</td>
<td>0.24</td>
<td>0.37</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>0900</td>
<td>0.55</td>
<td>0.60</td>
<td>0.37</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>1230</td>
<td>0.54</td>
<td>0.13</td>
<td>0.14</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>1700</td>
<td>0.59</td>
<td>ud</td>
<td>ud</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>2100</td>
<td>0.35</td>
<td>ud</td>
<td>ud</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>0100</td>
<td>0.33</td>
<td>0.25</td>
<td>0.50</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>0500</td>
<td>0.04</td>
<td>0.16</td>
<td>0.41</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>0900</td>
<td>0.51</td>
<td>0.04</td>
<td>0.29</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>0900</td>
<td>0.21</td>
<td>0.33</td>
<td>0.19</td>
<td>0.05</td>
</tr>
<tr>
<td>Stn 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun 8</td>
<td>1400 h</td>
<td>0.48</td>
<td>0.48</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>1800 h</td>
<td>0.24</td>
<td>0.24</td>
<td>0.37</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>2200 h</td>
<td>0.60</td>
<td>0.60</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>0200 h</td>
<td>0.13</td>
<td>0.13</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>0600 h</td>
<td>ud</td>
<td>ud</td>
<td>ud</td>
<td>ud</td>
</tr>
<tr>
<td></td>
<td>1000 h</td>
<td>0.25</td>
<td>0.25</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>1400 h</td>
<td>0.16</td>
<td>0.16</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>Stn 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun 1</td>
<td>1300 h</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>0800 h</td>
<td>0.37</td>
<td>0.37</td>
<td>0.37</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>1200 h</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.51</td>
<td>0.51</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sf</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 31</td>
<td>1300 h</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>0830 h</td>
<td>1.07</td>
<td>1.07</td>
<td>1.07</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1230 h</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>1630 h</td>
<td>0.78</td>
<td>0.78</td>
<td>0.78</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>2030 h</td>
<td>0.47</td>
<td>0.47</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>0030 h</td>
<td>0.55</td>
<td>0.55</td>
<td>0.55</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>0430 h</td>
<td>1.08</td>
<td>1.08</td>
<td>1.08</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>0830 h</td>
<td>0.52</td>
<td>0.52</td>
<td>0.52</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>1300 h</td>
<td>0.18</td>
<td>0.18</td>
<td>0.18</td>
<td>0.18</td>
</tr>
<tr>
<td>Jun 2</td>
<td>1300 h</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>0830 h</td>
<td>1.07</td>
<td>1.07</td>
<td>1.07</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1230 h</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>1630 h</td>
<td>0.78</td>
<td>0.78</td>
<td>0.78</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>2030 h</td>
<td>0.47</td>
<td>0.47</td>
<td>0.47</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>0030 h</td>
<td>0.55</td>
<td>0.55</td>
<td>0.55</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>0430 h</td>
<td>1.08</td>
<td>1.08</td>
<td>1.08</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>0830 h</td>
<td>0.52</td>
<td>0.52</td>
<td>0.52</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>1300 h</td>
<td>0.18</td>
<td>0.18</td>
<td>0.18</td>
<td>0.18</td>
</tr>
</tbody>
</table>
Table 5.2 Average chl \( a \) (mg m\(^{-2}\)), primary production (P.P.), and bacterial production (Bact. P.) at 4 stations during May 31 to June 9, 1988. Averaged total microflagellates during the same period are included (the values are depth-weighted averages first, and then averaged over a few days). \( n \) = the number of days which were averaged. The values in the bracket are the minimum and maximum. See Appendices 3 and 6 for the actual data.

<table>
<thead>
<tr>
<th>Average</th>
<th>Stn 2</th>
<th>Stn 3</th>
<th>Stn 4</th>
<th>Sf</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chl ( a )</td>
<td>43.5 (30.4-56.1)</td>
<td>58.7 (12.6-101)</td>
<td>67.1</td>
<td>47.7 (26.2-72.8)</td>
</tr>
<tr>
<td>(mg m(^{-2}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>1190 (150-2770)</td>
<td>1830 (843-2540)</td>
<td>2540</td>
<td>2990 (1240-5000)</td>
</tr>
<tr>
<td>(mg C m(^{-2}) d(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>8.97 (2.7-18)</td>
<td>14.4 (9.3-18)</td>
<td>9.4</td>
<td>28.1 (11-40)</td>
</tr>
<tr>
<td>(mg C m(^{-2}) d(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microflagellates</td>
<td>162 n=5</td>
<td>169 n=4</td>
<td>840 n=1</td>
<td>446 n=4</td>
</tr>
<tr>
<td>(cells mL(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5.3 Average abundance (10^3 cells mL\(^{-1}\)) and relative biovolume (% of total phytoplankton biovolume) of major phytoplankton genera: *Skeletonema costatum*, *Thalassiosira* spp. and *Chaetoceros* spp. at the surface or at a depth of 1-2 m at 4 stations during May 31 to June 9, 1988. \(n\) = number of days which were averaged. See Appendix 4 for the actual data.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. spp.</em></td>
<td>33</td>
<td>74%</td>
<td>224</td>
<td>78%</td>
<td>219</td>
<td>81%</td>
<td>265</td>
<td>72%</td>
</tr>
<tr>
<td><em>C. spp.</em></td>
<td>126</td>
<td>9%</td>
<td>534</td>
<td>15%</td>
<td>742</td>
<td>9%</td>
<td>601</td>
<td>9%</td>
</tr>
<tr>
<td><em>S. costatum</em></td>
<td>165</td>
<td>7%</td>
<td>67</td>
<td>1%</td>
<td>314</td>
<td>3%</td>
<td>751</td>
<td>7%</td>
</tr>
<tr>
<td>(n=5)</td>
<td>(n=2)</td>
<td>(n=2)</td>
<td>(n=4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5.4 Total number (per m$^3$) of calanoid copepods, *Neocalanus plumchrus*, and the most dominant genera of copepod during a time series at Stn 4 on June 8-9, 1988. Relative abundance is given as % of total number of copepods. See Appendix 5 for more data.

<table>
<thead>
<tr>
<th>Date</th>
<th>Stn 4</th>
<th>Abundance</th>
<th>% of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 8</td>
<td>8 m</td>
<td>4580</td>
<td>2.0%</td>
</tr>
<tr>
<td>T=1910 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>90</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>1530 33.4%</td>
</tr>
<tr>
<td>June 8</td>
<td>8 m</td>
<td>6450</td>
<td>33.4%</td>
</tr>
<tr>
<td>T=1925 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>2190 33.9%</td>
</tr>
<tr>
<td>June 8</td>
<td>10 m</td>
<td>7530</td>
<td>5.0%</td>
</tr>
<tr>
<td>T=2211 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>379</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>1920 25.4%</td>
</tr>
<tr>
<td>June 9</td>
<td>8 m</td>
<td>12900</td>
<td>1.1%</td>
</tr>
<tr>
<td>T=0230 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>139</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>3580 27.7%</td>
</tr>
<tr>
<td>June 9</td>
<td>8 m</td>
<td>7580</td>
<td>0%</td>
</tr>
<tr>
<td>T=0607 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>4920 64.9%</td>
</tr>
<tr>
<td>June 9</td>
<td>8 m</td>
<td>9100</td>
<td>0%</td>
</tr>
<tr>
<td>T=1135 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>3090 33.9%</td>
</tr>
<tr>
<td>June 9</td>
<td>8 m</td>
<td>8040</td>
<td>0%</td>
</tr>
<tr>
<td>T=1415 h</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Calanoids</td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Paracalanus</em></td>
<td>2780 34.6%</td>
</tr>
</tbody>
</table>
1992 April Cruise

River Discharge, Winds and Tidal Cycles A rapid increase in river discharge occurred just prior to the cruise and was followed by a rapid decrease during the cruise period (Figure 5.7A). Winds were calm (<3 m s⁻¹) during the cruise (Figure 5.7B). The cruise began during a spring tide and ended during a neap tide (Figure 5.7C).

Salinity and Temperature Freshwater influence was seen at stations near the river (S2-P3) and it penetrated below 10 m at these stations on April 7 (Figure 5.8). A recent freshwater influence had not yet reached stations further away (e.g., P6) on April 7 since the salinity at the surface was only slightly lower than at depth. The estuarine plume expanded to P6 after a few days (on April 13-15) (Figure 5.8), reflecting the rapid increase in river discharge (Figure 5.7A). However, it is not clear that the estuarine plume reached Stn 1 during the cruise period since the salinity gradient was small.

Temperature at the surface appeared to increase with time at each station during April 6-15 and the difference between the surface and 20 m became larger (Figure 5.9). The temperature increase at the surface progressed downwards during the same period (Figure 5.9). As a result, the base of the thermocline penetrated deeper (below 15 m) than the base of the halocline, particularly at the stations further away from the river mouth (P6 and Stn 1, Figure 5.9). This evidence indicates that the water column had stabilized during April 6-15.

Silicate Due to much higher concentrations of silicate in the Fraser River than in the surface of the Strait, silicate can be used as a tracer for the freshwater influence, along with salinity. For example, higher silicate at the surface than at a depth, definitely indicates a freshwater influence.

As shown in Figure 5.10, surface silicate was higher near the river mouth (Stn 2 and Stn 3) than at Stn 1 (further away from the river) on April 6 and 7. The higher silicate surface water appeared to move to Stn 1 on April 8 and was also there on April 13, indicating an expansion of the freshwater influence to Stn 1. This influence was probably
Figure 5.7  A) The Fraser River discharge, B) wind speed and C) tidal ranges for the period: January 1- April 30. Circles indicate the period of the cruise during April 6-15, 1992 and triangles represent April 19-22, 1993.
Figure 5.8  Vertical profiles of salinity along the transect (see Figure 5.1) during April 6-15, 1992. A dotted line indicates a profile sampled at a different time of the day.
Figure 5.9 Vertical profiles of temperature along the transect (see Figure 5.1) during April 6-15, 1992. A dotted line indicates a profile sampled at a different time of the day.
a lagged response to a peak in the river discharge that occurred just prior to the cruise on April 6. The lower concentrations near the surface or at the silicate minimum compared with silicate in the deep water, indicated a large consumption of silicate by the abundant diatoms.

**Nitrate and Phosphate** Both nutrients showed a similar distribution (Figures 5.11 and 12). On April 7, nitrate concentrations were higher at Stn 2 to P3 than at P6 to Stn 1, reflecting a response to the sharp increase in river discharge prior to April 6 and possibly the spring tide that resulted in an enhanced entrainment (Chapter 2). The nutrients at the surface were not high at all the stations during the cruise. However, profiles of nitrate and phosphate showed a slow decrease and no depletion of the two nutrients in the surface layer during the entire 10 day cruise. Nitrate concentrations at 20 m were mostly below 20 \( \mu M \) and phosphate concentrations were below 2 \( \mu M \). As shown for silicate, the difference in concentrations between the surface and the deep water indicated that a large amount of nutrients had been utilized.

**Ammonium and Urea** \( \text{NH}_4 \) concentrations were usually higher than 1 \( \mu M \) and sometimes exceeded 4 \( \mu M \) at intermediate depths on April 12-14 (Figure 5.13). Urea concentrations were frequently high (> 5 \( \mu M \)) at some depths (Figure 5.14). For example, at Stn 2, urea concentrations were 10 \( \mu M \) (0 m) on April 8, > 6 \( \mu M \) (3-15 m) on April 12 and 7.4 \( \mu M \) (0 m) on April 13; at P3 urea was 9 \( \mu M \) (6 m) on April 12; and at Stn 1, it was 6.7 \( \mu M \) (18 m) on April 7 (Figure 5.14).

**Chl a and Primary Production** Both chl \( a \) and primary production were low during this period (Figures 5.15 & 5.16), but they increased during April 13-15, particularly chl \( a \). The increase coincided with the sharp drop in river discharge and the neap tides during this period. Chl \( a \) appeared to be higher at Stn 2 than other stations during April 8-15.
Figure 5.10  Vertical profiles of silicate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Silicate (μM)

Apr 6 1992

Apr 7

Apr 8

Apr 12

Apr 13

Apr 14-15

S2 S3 P3 P6 S1
Figure 5.11  Vertical profiles of nitrate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Nitrate (μM)

Depth (m)

1992

Apr 6

Apr 7

Apr 8

Apr 12

Apr 13

Apr 14-15

S2

S3

P3

P6

S1
Figure 5.12  Vertical profiles of phosphate along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Phosphate (µM)

Depth (m)

Apr 6 1992

Apr 7

Apr 8

Apr 12

Apr 13

Apr 14-15

S2 S3 P3 P6 S1
Figure 5.13 Vertical profiles of ammonium along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Ammonium (μM)

Depth (m)

Apr 6 1992

Apr 7

Apr 8

Apr 12

Apr 13

Apr 14-15

S2 S3 P3 P6 S1
Figure 5.14 Vertical profiles of urea along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Figure 5.15. Vertical profiles of chl a along the transect (see Figure 5.1) during April 6-15, 1992. The triangles in the same graph indicate a profile sampled at a different time of the day.
Chl a (mg m$^{-3}$)

April 6

April 7

April 8

April 12

April 13

April 14–15
Figure 5.16. Vertical profiles of primary production along the transect (see Figure 5.1) during April 6-15, 1992.
Production (mg C m$^{-3}$ d$^{-1}$)

1992

Apr 7

Apr 8

Apr 12

Apr 13

Depth (m)

S2  S3  P3  P6  S1
1993 April Cruise

River Discharge, Winds and Tidal Ranges  Figure 5.7 shows daily river discharge, winds and tidal ranges during January-April, 1993. River discharge was very low during March, 1993 (approximately half that of 1992). A rapid increase at the beginning of April marked the beginning of the annual freshet. Winds exceeded 4 m s⁻¹ during early March and March 17-23. Tidal ranges during the cruise were in a transition period from a neap to spring tide.

Nutrients and Chl a  Table 5.5 shows concentrations of chl a and nutrients during April 19-22, 1993. NO₃ concentrations ranged from 2 - 10 μM at the surface and lower than 17 μM at 20 m except at one station. The vertical difference in NO₃ between the minimum and the maximum (usually corresponding to the surface and 20 m) in the water column was around 10 μM. Changes in PO₄ and SiO₄ concentrations were similar. The exception was at some stations where SiO₄ was higher at the surface accompanied by lower PO₄, (indicating the presence of the riverine plume which brought higher SiO₄). NH₄ concentrations were above 1 μM at almost all the stations and sometimes above 2 μM. Chl a was highest at the surface and ranged between 13.3 - 60.1 μg L⁻¹.

Zooplankton  Table 5.6 shows total zooplankton abundance and relative abundance of species during April 19-22, 1993. Copepods were the most abundant (more than 60% of total zooplankton except for P1) followed by euphausiids. Among copepods, the most abundant species was Pseudocalanus minutus. However, Neocalanus plumchrus is larger in size and its biomass was probably the greatest. Most of N. plumchrus was stages C4 and C5 (C4 is 3-6 times and C5 is 10-20 times higher than P. minutus in dry weight, respectively) and the euphausiids were also juveniles. Other numerous copepods were Acartia spp. and Oithona spp. Calanus spp. were appreciably abundant but only dominant at one station (M2).
Table 5.5 Chl $a$ and nutrients at 9 stations (see Figure 5.1) in the Strait of Georgia during April 19-22, 1993. The unit for integrated chl $a$ is mg m$^{-2}$.

<table>
<thead>
<tr>
<th>Date Time</th>
<th>Station</th>
<th>Depth (m)</th>
<th>Chl $a$ (mg/m$^3$)</th>
<th>NO$_3$ (µM)</th>
<th>NH$_4$ (µM)</th>
<th>SiO$_4$ (µM)</th>
<th>PO$_4$ (µM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr. 19 T=1830 h</td>
<td>P1</td>
<td>0</td>
<td>2.59</td>
<td>5.76</td>
<td>1.60</td>
<td>20.0</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1.30</td>
<td>7.21</td>
<td>2.04</td>
<td>19.0</td>
<td>1.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>1.07</td>
<td>8.98</td>
<td>3.06</td>
<td>23.2</td>
<td>1.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>1.19</td>
<td>10.0</td>
<td>2.10</td>
<td>22.1</td>
<td>1.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>0.79</td>
<td>15.7</td>
<td>1.40</td>
<td>32.3</td>
<td>2.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.70</td>
<td>17.8</td>
<td>1.36</td>
<td>31.1</td>
<td>2.40</td>
</tr>
<tr>
<td></td>
<td>Integrated</td>
<td></td>
<td>20.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr. 19 T=2000 h</td>
<td>T3</td>
<td>0</td>
<td>1.96</td>
<td>4.35</td>
<td>1.09</td>
<td>34.0</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1.79</td>
<td>9.97</td>
<td>2.22</td>
<td>22.2</td>
<td>1.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.84</td>
<td>11.7</td>
<td>2.32</td>
<td>26.4</td>
<td>1.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>0.75</td>
<td>11.8</td>
<td>2.19</td>
<td>25.7</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>0.55</td>
<td>13.5</td>
<td>1.93</td>
<td>29.0</td>
<td>2.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.45</td>
<td>14.6</td>
<td>1.66</td>
<td>26.9</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td>Integrated</td>
<td></td>
<td>15.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr. 20 T=1100 h</td>
<td>T5</td>
<td>0</td>
<td>0.71</td>
<td>10.0</td>
<td>2.38</td>
<td>31.8</td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.83</td>
<td>9.11</td>
<td>1.99</td>
<td>22.3</td>
<td>1.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.96</td>
<td>9.68</td>
<td>2.37</td>
<td>24.2</td>
<td>1.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>0.74</td>
<td>10.3</td>
<td>2.42</td>
<td>25.4</td>
<td>1.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>0.32</td>
<td>8.57</td>
<td>2.04</td>
<td>22.8</td>
<td>1.63</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>14.1</td>
<td>1.88</td>
<td>37.4</td>
<td>2.16</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Integrated</td>
<td></td>
<td>8.70</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr. 20 T=1530 h</td>
<td>T7</td>
<td>0</td>
<td>3.14</td>
<td>7.12</td>
<td>2.08</td>
<td>33.6</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>6.83</td>
<td>5.16</td>
<td>0.74</td>
<td>15.4</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>6.19</td>
<td>9.89</td>
<td>1.39</td>
<td>21.1</td>
<td>1.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>2.01</td>
<td>11.1</td>
<td>2.25</td>
<td>23.8</td>
<td>1.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>0.45</td>
<td>13.4</td>
<td>2.30</td>
<td>28.0</td>
<td>1.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.43</td>
<td>15.1</td>
<td>2.60</td>
<td>31.6</td>
<td>1.98</td>
</tr>
<tr>
<td></td>
<td>Integrated</td>
<td></td>
<td>40.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date Time</td>
<td>Station</td>
<td>Depth</td>
<td>Chl $a$</td>
<td>NO$_3$</td>
<td>NH$_4$</td>
<td>SiO$_4$</td>
<td>PO$_4$</td>
</tr>
<tr>
<td>-----------</td>
<td>---------</td>
<td>-------</td>
<td>---------</td>
<td>--------</td>
<td>--------</td>
<td>---------</td>
<td>--------</td>
</tr>
<tr>
<td>Apr. 20 T=1815 h</td>
<td>T9</td>
<td>0</td>
<td>5.08</td>
<td>2.02</td>
<td>0.42</td>
<td>22.5</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>3.51</td>
<td>3.42</td>
<td>1.17</td>
<td>17.1</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.78</td>
<td>6.64</td>
<td>2.12</td>
<td>16.3</td>
<td>1.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>0.81</td>
<td>8.40</td>
<td>1.89</td>
<td>19.0</td>
<td>1.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>0.96</td>
<td>12.7</td>
<td>1.46</td>
<td>29.7</td>
<td>1.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.72</td>
<td>11.0</td>
<td>1.01</td>
<td>25.2</td>
<td>1.85</td>
</tr>
<tr>
<td>Integrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>26.4</td>
</tr>
<tr>
<td>Apr. 21 T=1130 h</td>
<td>S4</td>
<td>0</td>
<td>9.49</td>
<td>2.46</td>
<td>0.66</td>
<td>9.93</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>6.46</td>
<td>2.01</td>
<td>0.51</td>
<td>8.45</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>4.59</td>
<td>2.50</td>
<td>0.57</td>
<td>9.73</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>6.85</td>
<td>2.09</td>
<td>0.45</td>
<td>8.90</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>1.14</td>
<td>10.6</td>
<td>1.16</td>
<td>25.7</td>
<td>1.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.17</td>
<td>16.6</td>
<td>0.93</td>
<td>37.8</td>
<td>2.22</td>
</tr>
<tr>
<td>Integrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>61.0</td>
</tr>
<tr>
<td>Apr. 21 T=1800 h</td>
<td>Stn 2</td>
<td>0</td>
<td>3.09</td>
<td>8.72</td>
<td>1.81</td>
<td>41.7</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>6.72</td>
<td>3.26</td>
<td>1.12</td>
<td>10.0</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>3.50</td>
<td>9.03</td>
<td>2.01</td>
<td>22.7</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>0.50</td>
<td>11.2</td>
<td>2.01</td>
<td>27.2</td>
<td>1.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>1.58</td>
<td>12.7</td>
<td>1.57</td>
<td>31.2</td>
<td>1.97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.25</td>
<td>16.2</td>
<td>1.34</td>
<td>35.3</td>
<td>2.23</td>
</tr>
<tr>
<td>Integrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>37.3</td>
</tr>
<tr>
<td>Apr. 22 T=1050 h</td>
<td>M1</td>
<td>0</td>
<td>0.55</td>
<td>3.38</td>
<td>3.02</td>
<td>11.5</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.48</td>
<td>3.52</td>
<td>3.07</td>
<td>12.0</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.32</td>
<td>2.93</td>
<td>2.54</td>
<td>10.0</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>0.82</td>
<td>3.65</td>
<td>2.53</td>
<td>11.9</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>1.10</td>
<td>7.33</td>
<td>2.85</td>
<td>18.7</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.20</td>
<td>13.7</td>
<td>2.40</td>
<td>31.0</td>
<td>1.86</td>
</tr>
<tr>
<td>Integrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13.4</td>
</tr>
<tr>
<td>Apr. 22 T=1645 h</td>
<td>M2</td>
<td>0</td>
<td>2.80</td>
<td>2.11</td>
<td>0.96</td>
<td>9.71</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>2.10</td>
<td>5.83</td>
<td>0.88</td>
<td>15.5</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>2.14</td>
<td>7.00</td>
<td>1.20</td>
<td>18.7</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6</td>
<td>1.55</td>
<td>10.3</td>
<td>1.23</td>
<td>25.2</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>1.01</td>
<td>15.2</td>
<td>1.09</td>
<td>32.9</td>
<td>2.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>0.54</td>
<td>20.8</td>
<td>1.16</td>
<td>44.1</td>
<td>2.46</td>
</tr>
<tr>
<td>Integrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>25.7</td>
</tr>
</tbody>
</table>
Table 5.6 Total zooplankton abundance and relative abundance of major zooplankton species (% of total zooplankton abundance) at 8 stations in the Strait of Georgia during April 19-22, 1993. See Appendix 7 for more data.

<table>
<thead>
<tr>
<th>Station</th>
<th>P1</th>
<th>T5</th>
<th>T7</th>
<th>Stn 4</th>
<th>T9</th>
<th>Stn 2</th>
<th>M1</th>
<th>M2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Zooplankton (m$^{-3}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>140</td>
<td>1215</td>
<td>1312</td>
<td>1107</td>
<td>787</td>
<td>641</td>
<td>1027</td>
<td>1350</td>
<td></td>
</tr>
<tr>
<td>Total Copepods</td>
<td>57%</td>
<td>80%</td>
<td>89%</td>
<td>64%</td>
<td>69%</td>
<td>87%</td>
<td>85%</td>
<td>64%</td>
</tr>
<tr>
<td>Neocalanus plumchrus</td>
<td>19%</td>
<td>21%</td>
<td>7%</td>
<td>13%</td>
<td>14%</td>
<td>15%</td>
<td>44%</td>
<td>8%</td>
</tr>
<tr>
<td>C1-C3</td>
<td>0.7%</td>
<td>7.1%</td>
<td>3.1%</td>
<td>2.0%</td>
<td>0.7%</td>
<td>5.5%</td>
<td>9.5%</td>
<td>0.8%</td>
</tr>
<tr>
<td>C4</td>
<td>4.1%</td>
<td>7.6%</td>
<td>1.4%</td>
<td>3.6%</td>
<td>2.8%</td>
<td>3.9%</td>
<td>23%</td>
<td>1.3%</td>
</tr>
<tr>
<td>C5</td>
<td>14%</td>
<td>5.9%</td>
<td>2.4%</td>
<td>7.0%</td>
<td>11%</td>
<td>5.5%</td>
<td>11%</td>
<td>5.6%</td>
</tr>
<tr>
<td>Pseudocalanus minutus</td>
<td>14%</td>
<td>39%</td>
<td>60%</td>
<td>17%</td>
<td>22%</td>
<td>40%</td>
<td>45%</td>
<td>9.8%</td>
</tr>
<tr>
<td>Acartia sp.</td>
<td>13%</td>
<td>9.5%</td>
<td>1.8%</td>
<td>12%</td>
<td>8.8%</td>
<td>1.6%</td>
<td>16%</td>
<td>4.5%</td>
</tr>
<tr>
<td>Calanus sp.</td>
<td>3.3%</td>
<td>0.7%</td>
<td>1.2%</td>
<td>4.0%</td>
<td>3.9%</td>
<td>1.0%</td>
<td>2.2%</td>
<td>12%</td>
</tr>
<tr>
<td>Metridia pacifica</td>
<td>6.6%</td>
<td>3.8%</td>
<td>2.5%</td>
<td>5.8%</td>
<td>12%</td>
<td>12%</td>
<td>2.9%</td>
<td>2.1%</td>
</tr>
<tr>
<td>Oithona spp.</td>
<td>2.6%</td>
<td>4.6%</td>
<td>2.5%</td>
<td>7.2%</td>
<td>4.9%</td>
<td>10%</td>
<td>1.7%</td>
<td>9.0%</td>
</tr>
<tr>
<td>Copepod stages</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>0%</td>
<td>12.7%</td>
<td>14.5%</td>
<td>4.8%</td>
<td>0%</td>
<td>4.1%</td>
<td>0%</td>
<td>3.7%</td>
</tr>
<tr>
<td>Nauplii</td>
<td>0%</td>
<td>0%</td>
<td>3.5%</td>
<td>0%</td>
<td>1.8%</td>
<td>2.7%</td>
<td>0.7%</td>
<td>2.4%</td>
</tr>
<tr>
<td>Copepodite</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>4.7%</td>
<td>0%</td>
<td>6.4%</td>
</tr>
<tr>
<td>Euphausia pacifica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zoa</td>
<td>2.2%</td>
<td>2.3%</td>
<td>1.5%</td>
<td>4.8%</td>
<td>1.8%</td>
<td>0%</td>
<td>1.2%</td>
<td>1.4%</td>
</tr>
<tr>
<td>Protozoea</td>
<td>14.0%</td>
<td>5.5%</td>
<td>1.4%</td>
<td>9.6%</td>
<td>10.9%</td>
<td>0%</td>
<td>0.7%</td>
<td>0.6%</td>
</tr>
<tr>
<td>Larva</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>5.4%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Adult</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0.1%</td>
<td>0%</td>
<td>4.1%</td>
</tr>
</tbody>
</table>
DISCUSSION

Interannual Variability

River Discharge, Winds and Tidal Cycles

The hydrodynamics in the Strait of Georgia is largely determined by runoff, winds and tides (LeBlond 1983). In general, tidal ranges were minimal during March in all the years (Figure 5.17). The beginning of the Fraser River spring freshet occurred in the beginning of April (1989, 1990, and 1991) (Figure 5.18). These years can be viewed as normal years. Winds appeared to be variable from year to year (Figure 5.19). Therefore, in spring when tidal mixing is reduced and river discharge remains constant before the spring freshet, winds become a critical force to determine the stability of the water column in the Strait of Georgia. The estuarine plume can be formed and be stable during March under weak winds. However, the stratification may not last long enough to allow a bloom to develop if strong winds occur. Thus, the spring bloom will not fully develop until an increase in river discharge offsets wind and tidal mixing and increases the stratification for a sufficiently long time. As a result, the decrease in nutrients and the increase in phytoplankton biomass will be in successive steps with peaks and troughs during the spring bloom. In 1991, winds were reduced in March (only on three days did the wind speed exceed 4 m s\(^{-1}\)), and the spring bloom developed in late March and early April. This bloom was interrupted during a wind event (Chapter 4). Therefore, it is an interaction between freshwater discharge and winds that controls the course of development of the spring bloom which may occur in a sequence of bursts or steps.

The Delayed Spring Bloom in 1988

The temporal increase in fluorescence, the decrease in NO\(_3\) and high phytoplankton biomass and production indicated the development of a bloom during the cruise period. The question is whether this bloom is the spring bloom or a secondary one (referring to a bloom that occurs due to resupply of nutrients after winter nutrients are depleted during the spring bloom).
Figure 5.17 Tidal ranges (m) at Point Atkinson in the Strait of Georgia for 1988, 1989, 1990, and 1991. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study.
Figure 5.18 Daily discharge (m$^3$ s$^{-1}$) of the Fraser River at Hope for 1988, 1989, 1990, and 1991. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study.
Figure 5.19 Daily average wind speed (m s\(^{-1}\)) at the Vancouver International Airport (VIA) for 1988, 1989, 1990, and 1991. VIA is very close to the Fraser River mouth. The wind direction was not taken into account. The circles framed by squares represent the periods during which the cruises were conducted. Not all the cruise data are presented in this study.
In the Strait of Georgia, it has been observed that the spring bloom occurs earlier in the estuarine plume near the river mouth than in adjacent waters and progresses seaward (Parsons et al. 1969a, Stockner et al. 1979, Chapter 4). Correspondingly, NO₃ concentrations at the surface are lower near the river mouth than adjacent waters, showing an increase seaward. With the seaward progression of the spring bloom, NO₃ in the estuarine plume will be utilized, resulting in a low or undetectable level during this time of the year (June) (Parsons et al. 1970, Harrison et al. 1991, Clifford et al. 1989, 1990, 1991a, 1991b, 1992). In this situation, a subsurface NO₃ minimum at an intermediate depth will be formed when the riverine plume (carrying NO₃) spreads over the estuarine plume (with lower or undetectable NO₃), particularly near the river mouth. Thus, NO₃ concentration decreases seaward at the surface (Chapter 1). However, the observations during May 31-June 7, 1988 showed that NO₃ increased seaward along the transect at the beginning of the cruise. The distribution of an increase in NO₃ concentration seaward of the river mouth at the beginning of the cruise and the appearance of a subsurface NO₃ minimum in the water column at the end of the cruise indicated that the spring bloom was developing during this period. In addition, NO₃ concentrations were high (close to 15 μM) at stations Sd, Se and Sf away from the river mouth at the beginning of the cruise. Phytoplankton biomass and production during this cruise were comparable to the early spring bloom of 1991 (Chapter 4). The decrease in SiO₄ concentrations over time indicates that the developing spring bloom mainly consisted of diatoms. A common feature in species succession during the spring bloom in the Strait is that the dominant phytoplankton species usually start with *Thalassiosira* spp. and is closely followed by *Skeletonema costatum*, (Shim 1977, Hasle 1978, Harrison et al. 1983). Although the 1988 cruise was at the end of May and early June, the most dominant phytoplankton species during the cruise were *Thalassiosira* spp. (Table 5.3). Therefore, the combined evidence above indicated that this bloom was probably the spring bloom. The question is why the spring bloom was delayed rather than whether this bloom was a secondary one.
An examination of the river discharge and wind levels in 1988 (Figure 5.18 and 5.19) reveals that winds were strong in March until the middle of April and the annual freshet did not start until the same time. The spring bloom could then start in late April and early May. However, it is known that the massive recruitment of nauplii and early copepodite stages of *Neocalanus plumchrus* from the deep water to the surface occurs during April and May (Table 5.6, Figure 4.9, Fulton 1973, Mackas and Louttit 1988). It was likely that grazing by this abundant copepod had suppressed the early development of the spring bloom during this period, which further delayed the spring bloom. The full development of the spring bloom could not occur until the grazing pressure to phytoplankton was relieved. The low abundance of *Neocalanus plumchrus* in the 10 m water layer during the time series at Stn 4 (Table 5.4) suggests that this species had descended to deeper waters. Low ammonium concentrations (compared to the other cruises) also supported the suggestion that grazer abundance was not great enough to suppress the spring bloom during this cruise. In addition, winds (mostly below 4 m s\(^{-1}\)) from mid-April to the end of May, 1988 were not strong enough to increase nitrate to those high concentrations at Sf on May 31 shown in Figure 5.4. Therefore, this high nitrate rules out the possibility of a secondary bloom during May 31-June 7, 1988. A missing spring bloom (which might be delayed) was noted for the same region in the late 1960s by Parsons (pers. comm.). In a recent study, the spring diatom bloom was not observed in the Northern Strait of Georgia (Haigh and Taylor 1991), and the authors suggested that its absence was due to strong winds. High NO\(_3\) concentrations in mid-May in 1970s were also observed at stations in the estuarine plume by Stockner *et al.* (unpubl.), suggesting that the spring bloom had not ended.

**The Early Spring Bloom in 1992**

Great differences in the concentrations of nutrients (silicate, nitrate and phosphate) between the surface and the deep water (Figures 5.10, 5.11 and 5.12) indicated a large consumption of nutrients and that the spring bloom had occurred prior to the cruise in
April, 1992. However, low biomass and production of phytoplankton indicated that the utilized nutrients did not end up in phytoplankton biomass. The loss of phytoplankton out of the sampled upper layer must have been due to sinking or export to organisms of higher trophic levels via grazing. A striking feature is that the remaining nutrients decreased slowly over time although they were not high. This phenomenon indicated that biomass and production were not limited by these nutrients. The questions are, what caused nutrients to remain in the beginning of the cruise and what suppressed their utilization during the cruise?. To answer these questions, it is necessary to examine the major driving force such as river discharge, winds and tidal cycles. The Fraser River discharge started its annual freshet at the beginning of March, 1992 (the El Niño year), one month earlier than in the previous four years (Figure 5.18). Winds in March were weak. These conditions must have favored an earlier onset of the spring bloom. However, there were three days in March in which wind speeds were 5.2 m s\(^{-1}\) on March 7, 5.0 m s\(^{-1}\) on March 15 and 12.6 m s\(^{-1}\) on March 27. Relative to the stability of the water column during their respective times, mixing energy generated by winds on these three days could have been destructive to the stratification, particularly the magnitude of winds on March 27. It was likely that the spring bloom started in late February or early March and was interrupted by the March 7 event. The spring bloom was possibly halted further by the March 15 wind event and again by the wind event on March 27. During the March 27 event, there must have been much NO\(_3\) mixed up into the surface layer. This wind effect is supported by a model run for the same region, which showed that deep water nitrate was almost completely mixed up under a constant wind speed of 10 m s\(^{-1}\) for 48 h (St. John et al. 1993). Extremely calm weather and a rapid increase in river discharge followed this wind event. These conditions had favored a fast recovery of the spring bloom. However, why were chl \(a\) concentrations low 10 days (April 6) after this wind event? One obvious possibility was zooplankton grazing. During this period, the high abundance of \textit{Neocalanus plumchrus} at the surface layer due to its ontogenic migration (Table 5.6 for
1993, Chapter 4 for 1991) could be mainly responsible. The grazing mechanism was also supported by evidence such as a slow decrease in nitrate and phosphate (Figures 5.11 and 5.12) and high ammonium concentrations in the water column (Figure 5.13) during the entire period of April 6-15. In addition, urea was abnormally high (Figure 5.14). The grazing resulted in low biomass, remaining nutrients and subsequent slow utilization during the cruise (April 6-15). These features are very similar to the observations during April, 1991. A major difference is that nitrate concentrations in the upper layer in 1992 were lower (<5 μM) than those (ca. 10 μM) in 1991. This difference was due to the earlier inception of the spring bloom in 1992, which had allowed greater consumption of nutrients.

The spring bloom in 1993

The Fraser River discharge was lower during the spring of 1993 than in 1992 (Figure 5.7), possibly due to warm weather in the winter of 1992, the El Niño year, which reduced snow packs. Winds were not particularly strong during March and April prior to the cruise although winds (exceeding 4 m s^{-1}) during March 17-23 might have been destructive (Figure 5.19). The spring bloom could develop during March and particularly during April when the annual freshet started. Chl a and nutrients indicate that the spring bloom had occurred before the cruise.

NO₃ concentrations at a depth of 20 m in the Strait are usually higher than 20 μM (Clifford et al. 1989, 1990, 1991a, 1991b, 1992). NO₃ concentrations in winter are usually around 25 μM (Stephens 1969). Lower levels of NO₃ at 20 m (< 17 μM) and the vertical difference in NO₃ levels between the surface and 20 m in April, 1993 indicated consumption of NO₃ in the water column (assuming that the water column was homogeneously mixed and NO₃ concentrations were 20 μM at the beginning of the spring bloom). However, chl a values were not particularly high to account for this consumption of NO₃, as can be judged from Table 5.5 itself. For example, at P1 the vertical difference in NO₃ was 12 μM (17.78-5.76 μM) and chl a was 20 mg m^{-2}. In comparison, at Stn 2
the difference was 7.5 μM and chl \( a \) was 37.3 mg m\(^{-2} \). In addition, NH\(_4\) concentrations were relatively high. This evidence points to zooplankton grazing which was responsible for the remaining NO\(_3\) and high NH\(_4\). This mechanism of zooplankton generated NH\(_4\) was supported by high copepod abundance during the same time: high biomass of \textit{Neocalanus plumchrus} and high abundance of \textit{Pseudocalanus minutus}.

\textbf{Interannual Variability}

The interannual variability of biological production is common in estuaries. In the upper reach of the northern San Francisco Bay estuary, the summer diatom bloom was absent during two successive years of very low river discharge (the drought of 1976-77) (Cloern \textit{et al.} 1983, Peterson \textit{et al.} 1985). The annual cycles of dissolved inorganic nutrients were modified accordingly (Peterson \textit{et al.} 1985). In South San Francisco Bay, the magnitude of the annual spring bloom (mean biomass and estimated primary production) was strongly correlated with the magnitude of river flow during wet seasons in the past decade of climatic and hydrologic extremes (Cloern 1991). A recent study in two fjords of British Columbia over a three year period showed that the El Niño event of 1986-1987 had an opposite effect in the fjords (Sancetta 1989). In Sannich Inlet the unusually high degree of sunshine during fall resulted in the largest bloom of the entire year, but not in Jervis Inlet. Whereas the normal late-spring stabilization of the water column from snow melt did not occur and the spring bloom was eliminated as a result of unusually warm air temperatures which prevented the build-up of winter snow around Jervis Inlet (Sancetta 1989). In the Chesapeake Bay, a six-year time series of measurements of algal production and chl \( a \) at stations in the middle bay exhibited considerable year-to-year variability (Boynton \textit{et al.} 1982). In particular, the drought year 1981 produced an increase in the dominance of a diatom, shortening of the typical episodes of anoxia throughout the summer period, and up-estuary penetration of phytoplankton species normally confined to the southern bay. Whereas the wet year 1983 resulted in the early onset and persistence of anoxia in mid-May (Tyler 1986). These biological variations were attributed to a change
in mixing between the two years. The interannual variability in the spring bloom (magnitude and timing) was also reported to respond to the peak in the annual freshet for 1984 and 1985 in the Chesapeake Bay (Malone et al. 1988). In the Delaware estuary, annual phytoplankton production for 1981-1985 displayed marked interannual variability (Pennock and Sharp 1986).

**Implications for Trophodynamic Phasing**

Recently, Mann (1993) reviewed the interactions among physical oceanography, food chains and fish stocks and pointed out that not only the magnitude but also the timing of the spring bloom affects a fish stock by altering its food chains. One example is the delayed spring bloom in the waters of western Europe in 1970s due to much stronger northerly winds in the springtime in the 1970s than the 1950s (Dickson et al. 1988). The delayed spring bloom resulted in a decline in phytoplankton biomass and zooplankton biomass.

In the Strait of Georgia, existing evidence indicates that bacterial abundance and production are a small proportion of total phytoplankton biomass and production (Valdes and Albright 1981, Albright 1983a, 1983b, Bell and Albright 1981, Clifford et al. 1989, 1990, Harrison et al. 1991). Microflagellates and ciliates were not abundant during the study period (Clifford et al. 1989, 1990). Thus, the microbial loop is not an important linkage between phytoplankton and zooplankton along food chains.

**Zooplankton** In the Strait of Georgia, the zooplankton community is dominated by copepods in the spring. They include *Neocalanus plumchrus* (Fulton 1973), *Pseudocalanus minutus*, *Calanus marshallae*, *C. pacificus*, and *Metridia pacifica* (LeBrasseur et al. 1969). Among them, *N. plumchrus* is probably the most abundant in terms of biomass (Harrison et al. 1983), which is supported by the 1991 and 1993 data (Figure 4.9 in Chapter 4, Table 5.6). Reproduction of this species takes place only in deep waters, and the nauplii and copepodites then migrate to the surface (no reproduction at the surface until descending in late May and June). However, the survival and growth of the
copepods after surfacing depend on the phytoplankton biomass and production. The massive biomass of *Neocalanus plumchrus* can suppress the spring bloom when they start to graze on phytoplankton. Therefore, matching or mismatching between phytoplankton and zooplankton will depend on the timing of the spring bloom, if timing in the annual ontogenic migration of zooplankton is assumed to vary little. Here the bloom timing is arbitrarily defined by the difference in NO₃ between the surface and the deep water (20 m). A small difference in NO₃ indicates an early part of the spring bloom and a large difference indicates the late part. When the spring bloom is at an early part, grazing pressure from migrating zooplankton will prevent the development of the spring bloom. The consequences of the delayed spring bloom in 1988 might have resulted in mismatching by zooplankton. The mismatch could be cascaded to juvenile fish including juvenile salmon entering the Strait during this period, and affect the return of adults in later years.

In comparison, the spring bloom in 1992 (the El Nino year) started earlier and was well developed when the copepods started their migration. The spring bloom in 1991 (a normal year) was at the usual time when it was interrupted by a week-long wind event. The subsequent recovery was slow due to zooplankton grazing. Sampling in April, 1993 showed that NO₃ concentrations were not depleted yet in the water column in the Strait. Winds and zooplankton migration appear to play an important role in governing the course development of the spring bloom and trophodynamic phasing between phytoplankton and zooplankton in the Strait of Georgia. The effect of winds on pelagic food chains was reported for coastal regions of New York Bight (Walsh *et al.* 1978). In Suisan Bay (part of the San Francisco Bay), reduced river discharge resulted in a summer maximum in phytoplankton biomass but the maximum disappeared due to an introduction of a clam (Alpine and Cloern 1992).

**Juvenile Fish** In the Gulf of St. Lawrence, most fish species have a relatively fixed spawning period (Qazim 1956, Cushing 1970 and Ware 1975). Larval fish of most species in the Strait start feeding from spring to early summer. Each species is supposed to
have its own entry time "window" for food. For example, herring starts spawning in the Strait during March and the juvenile herring remains in the Strait of Georgia until autumn (Ketchen et al. 1983). Newly hatched larvae of lingcod are pelagic and appear by early March (Philips and Barraclough 1977). Juveniles of all five species of Pacific salmon were found to reside from spring to summer throughout the Strait before they migrate to the Pacific Ocean and all except for sockeye appeared to grow significantly during their residence time in the Strait (Healey 1978). Their diet was found to include copepods in the early stage of larval fish (Parsons et al. 1969b) and small crabs, shrimp and small fish in the later stage (Healey 1978). In the Gulf of St. Lawrence, larval fish abundance was shown to be positively correlated to zooplankton biomass (>202 μm) in Baie-des-Chaleurs (de Lafontaine et al. 1984 cf. de Lafontaine 1991). The relationship between zooplankton as food and juvenile fish in the Strait has been little studied. However, the coincidence of the period of these feeding "windows" with the spring bloom and the annual Fraser River freshet (June-July) suggests the significance of the spring bloom development in trophodynamic phasing among trophic levels. Consequently, changes in river discharge and winds would greatly influence the survival and growth of the juvenile fish via the coupling with nutrients and phytoplankton production.

It is the interannual variability in physical forcing that results in a change in the annual production cycle which is subsequently cascaded to fish. The transfer of the signal in climatic change and physical forcing is complex because it will vary in relation to the different food web interactions (e.g. Runge 1988) and will not generate the same effect among the various food webs. This complexity may explain why a recent study on the effects of Fraser River discharge on interannual production of Pacific salmon and herring in the Strait of Georgia found that variations in river discharge were associated with some species and not with others (Beamish et al., in prep.).
SUMMARY

The most important feature in this study is the presentation of data over a few days on both physical and biological parameters including salinity, temperature, fluorescence or chl a, primary production, and nutrients (nitrate, phosphate, silicate, ammonium and urea). Spatial variability in these parameters was apparent but the spatial scale of sampling was great enough to ensure that temporal variability was not due to horizontal advection.

In some years, dominant species of phytoplankton and zooplankton, bacterial production and total number of microflagellates are included. Such data sets provide convincing evidence for what was happening in the water column during the investigation.

The observations in this study show that both nitrate and phosphate remained undepleted and their utilization in the water column was slow in April (1991, 1992 and 1993). Silicate concentrations suggested a large consumption by diatoms. Ammonium concentrations remained high during April. Chl a did not appear to account for the changes in nutrients during the same period. This evidence led to the suggestion that zooplankton grazing controlled the development of the spring bloom.

The examination of data on river discharge, winds and tidal cycles for 1988-1993 showed that the beginning of the annual freshet of the Fraser River occurred at the beginning of April in a normal year (1989, 1990, 1991, and 1993); tidal ranges are smallest in March; and winds appear to be variable. These data and the observations in this study in addition to Chapter 4, indicate that tidal cycles and the river discharge determined the inception of the spring bloom and winds controlled the course of its development. Thus, it appeared that the spring bloom in the Central Strait developed in sequence of successive steps in biomass increase and troughs depending on the frequency and strength of wind events. Great numbers of zooplankton due to the ontogenic migration from deep waters to the surface in April further affected the development of the spring bloom. For example, the start of the freshet one month earlier in the El Niño year of 1992 resulted in an earlier onset of the spring bloom, but was possibly interrupted by a few wind
events and further halted by zooplankton. In addition to strong winds, the late start of the freshet in 1988 delayed the spring bloom and it was further delayed by zooplankton. Therefore, it is the interannual variability in river discharge, winds and tidal cycles that controls the timing of spring bloom and its development in the Central Strait. This timing, in turn, determines the matching or mismatching between phytoplankton and zooplankton in spring due to ontogenic migration of large numbers of zooplankton during this period. The matching or mismatching bears significant implications for juvenile fish in the Strait of Georgia.
GENERAL CONCLUSIONS

The dynamics of nutrients and phytoplankton production are coupled with physical processes driven by river discharge, winds and tidal cycles over various spatial and temporal scales in the Strait of Georgia estuary. In the estuarine plume, the dynamics are more influenced by the variations in river discharge. In the Fraser River estuary and its vicinity, the tidal cycle is dominant in the movement of the riverine plume. Winds are the most variable parameter and influence the dynamics of both the riverine and estuarine plumes.

Hypotheses:

Entrainment

All three hypotheses were found to be true. In late spring and summer, the seasonal NO₃-poor estuarine plume is present between the riverine plume and the NO₃-rich deep water beyond the river mouth (Hypothesis 1). The estuarine plume invades the river channel with the advancing of the salt wedge (Hypothesis 2). The entrainment of NO₃ from deep NO₃-rich water will not occur until the estuarine plume is washed out by the river flow during ebb tides. Therefore, the amount of entrainment of NO₃ is determined by the amount of entrained deep water (Hypothesis 3).

Spring Bloom

The evidence (1991 and 1988) in this study appears to indicate that the onset of the spring bloom occurs earlier near the river mouth in the estuarine plume (Hypothesis 4). However, the seaward progression of the spring bloom is not conclusive due to insufficient data.

Specific Conclusions

Entrainment

1. There is more entrained NO₃ during spring tides than during neap tides;
2. The amount of entrained NO₃ increases as river discharge increases;
3. The amount of entrained NO$_3$ increases when winds are strong.

4. The contribution of entrained NO$_3$ is more than river-borne NO$_3$ under all conditions; the ratio of entrained NO$_3$ to river-borne NO$_3$ is 1.6-5.4 during June and 5.6-12 during summer.

**Spring Bloom**

5. Wind events interrupted the development of the spring bloom by mixing the water column (1991).

6. The interannual variability in tidal cycles, and the timing of the spring freshet and winds determine the interannual variability in the timing (initiation and duration) of the spring bloom. Tidal mixing energy is the lowest in March and in a normal year, the annual freshet normally starts in the beginning of April. Therefore, the reduced tidal mixing would allow the initiation of the spring bloom in March. In 1992 (an El Niño year), the earlier initiation of the annual Fraser River freshet resulted in the earlier onset of the spring bloom. Wind events appear to interrupt the development of the spring bloom. Depending on the frequency and strength of the wind events, the spring bloom develops in a sequence of steps. In 1988, the later start of the freshet and strong winds between March and mid-April led to a delayed spring bloom. Due to the ontogenic nature of the dominant zooplankter *Neocalanus plumchrus* in the Strait of Georgia, its migration to the surface layer from deep waters in spring interacts with wind events and causes dramatically different effects on the development of the spring bloom depending on the degree of wind effects. Therefore, it is the timing of the spring bloom resulting from the interannual variability of the physical driving forces that determines the trophodynamic phasing between phytoplankton and zooplankton.
REFERENCES


Gunderson, K.R., J.S. Corbin, C.L. Hanson, M.L. Hanson, R.B. Hanson, D.J. Russel, A. Stollar and O. Yamada. 1976. Structure and biological dynamics of the oligotrophic ocean photic zone off the Hawaiian Island. Pac. Sci. 30: 45-68.


Sutcliffe Jr., W.H. 1973. Correlations between seasonal river discharge and local landings of American lobster (Homarus americanus) and Atlantic halibut


APPENDICES


<table>
<thead>
<tr>
<th>Stations</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>49° 06.45' N</td>
<td>123°10.04' W</td>
</tr>
<tr>
<td>R2</td>
<td>49° 07.52' N</td>
<td>123°13.58' W</td>
</tr>
<tr>
<td>R3</td>
<td>49° 07.52' N</td>
<td>123°16.0' W</td>
</tr>
<tr>
<td>R4</td>
<td>49° 06.25' N</td>
<td>123°18.05' W</td>
</tr>
<tr>
<td>R5</td>
<td>49° 06.0' N</td>
<td>123°18.6' W</td>
</tr>
<tr>
<td>R6</td>
<td>49° 05.75' N</td>
<td>123°19.4' W</td>
</tr>
<tr>
<td>R7</td>
<td>49° 05.40' N</td>
<td>123°20.8' W</td>
</tr>
<tr>
<td>Sa</td>
<td>49° 06.42' N</td>
<td>123°20.7' W</td>
</tr>
<tr>
<td>Stn 2 = S2</td>
<td>49° 05.10' N</td>
<td>123°22.5' W</td>
</tr>
<tr>
<td>P1</td>
<td>49° 33.35' N</td>
<td>123°28.0' W</td>
</tr>
<tr>
<td>P1A</td>
<td>49° 02.3' N</td>
<td>123°36.6' W</td>
</tr>
<tr>
<td>P1B</td>
<td>49°03.15' N</td>
<td>123°27.9' W</td>
</tr>
<tr>
<td>Stn 4 = S4</td>
<td>49° 07.8' N</td>
<td>123°28.6' W</td>
</tr>
<tr>
<td>Stn 3 = S3</td>
<td>49° 07.25' N</td>
<td>123°34.10' W</td>
</tr>
<tr>
<td>P2</td>
<td>49° 09.9' N</td>
<td>123°36.10' W</td>
</tr>
<tr>
<td>P2A</td>
<td>49° 09.9' N</td>
<td>123°36.0' W</td>
</tr>
<tr>
<td>P3</td>
<td>49° 12.4' N</td>
<td>123°38.20' W</td>
</tr>
<tr>
<td>P4</td>
<td>49° 15.9' N</td>
<td>123°41.8' W</td>
</tr>
<tr>
<td>P4A</td>
<td>49° 17.42' N</td>
<td>123°38.05' W</td>
</tr>
<tr>
<td>P4B</td>
<td>49° 15.1' N</td>
<td>123°48.2' W</td>
</tr>
<tr>
<td>P5</td>
<td>49° 19.7' N</td>
<td>123°44.2' W</td>
</tr>
<tr>
<td>P6</td>
<td>49° 21.4' N</td>
<td>123°52.5' W</td>
</tr>
<tr>
<td>P7</td>
<td>49° 21.5' N</td>
<td>124°01.8' W</td>
</tr>
<tr>
<td>Stn 1 = S1</td>
<td>49° 21.4&quot; N</td>
<td>124°11.0' W</td>
</tr>
<tr>
<td>Sb</td>
<td>49° 07.3' N</td>
<td>123°26.0' W</td>
</tr>
<tr>
<td>Sd</td>
<td>49° 09.53' N</td>
<td>123°36.0' W</td>
</tr>
<tr>
<td>Se</td>
<td>49° 10.68' N</td>
<td>123°39.43' W</td>
</tr>
<tr>
<td>Sf</td>
<td>49° 14.14' N</td>
<td>123°54.0' W</td>
</tr>
</tbody>
</table>
Appendix 2  Vertical distribution in NH$_4$ concentrations (μM) at four stations along the transect in the Strait of Georgia during May 31-June 9, 1988. The blank spaces indicate no sampling at these depths. ud = undetectable.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Jun 1</th>
<th>Jun 3</th>
<th>Jun 5</th>
<th>Jun 6</th>
<th>Jun 7</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.18</td>
<td>1.61</td>
<td>0.55</td>
<td>0.67</td>
<td>0.65</td>
</tr>
<tr>
<td>1</td>
<td>0.06</td>
<td>1.61</td>
<td>0.72</td>
<td>0.44</td>
<td>0.85</td>
</tr>
<tr>
<td>2</td>
<td>0.33</td>
<td>1.59</td>
<td>0.53</td>
<td>1.04</td>
<td>0.62</td>
</tr>
<tr>
<td>3</td>
<td>0.44</td>
<td>1.49</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
<td>0.65</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>0.87</td>
<td>1.45</td>
<td>0.16</td>
<td></td>
<td>0.70</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>0.39</td>
<td>0.37</td>
<td>0.25</td>
<td>0.13</td>
<td>0.04</td>
</tr>
<tr>
<td>9</td>
<td>1.39</td>
<td>0.38</td>
<td>0.18</td>
<td></td>
<td>0.65</td>
</tr>
<tr>
<td>10</td>
<td>0.64</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.65</td>
</tr>
</tbody>
</table>
Appendix 2. Continued.

### Stn 3

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Jun 1 1300 h</th>
<th>Jun 4 0800 h</th>
<th>Jun 4 1200 h</th>
<th>Jun 8 0830 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.11</td>
<td>0.24</td>
<td>ud</td>
<td>0.04</td>
</tr>
<tr>
<td>1</td>
<td>0.10</td>
<td>0.27</td>
<td>ud</td>
<td>0.22</td>
</tr>
<tr>
<td>2</td>
<td>0.16</td>
<td>0.16</td>
<td>0.10</td>
<td>0.08</td>
</tr>
<tr>
<td>3</td>
<td>0.08</td>
<td>0.24</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>ud</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.10</td>
<td>0.42</td>
<td></td>
<td>0.27</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td></td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>0.15</td>
<td>0.92</td>
<td>0.18</td>
<td>1.39</td>
</tr>
<tr>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td>1.05</td>
</tr>
</tbody>
</table>

### Sf

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>May 31 1300 h</th>
<th>Jun 2 0830 h</th>
<th>Jun 2 1230 h</th>
<th>Jun 2 1630 h</th>
<th>Jun 2 2030 h</th>
<th>Jun 3 0030 h</th>
<th>Jun 3 0430 h</th>
<th>Jun 6 0830 h</th>
<th>Jun 6 1300 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.39</td>
<td>0.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.06</td>
</tr>
<tr>
<td>2</td>
<td>0.39</td>
<td>0.71</td>
<td>0.33</td>
<td>0.50</td>
<td>0.41</td>
<td>0.69</td>
<td>1.18</td>
<td>0.23</td>
<td>0.05</td>
</tr>
<tr>
<td>3</td>
<td>0.41</td>
<td>1.42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.24</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.67</td>
<td>0.06</td>
</tr>
<tr>
<td>7</td>
<td>1.51</td>
<td>1.36</td>
<td>0.62</td>
<td>0.45</td>
<td>0.67</td>
<td>1.45</td>
<td></td>
<td></td>
<td>0.06</td>
</tr>
<tr>
<td>8</td>
<td>0.89</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.96</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.83</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.36</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.50</td>
</tr>
<tr>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.83</td>
</tr>
<tr>
<td>22</td>
<td>0.34</td>
<td>0.74</td>
<td>0.58</td>
<td>1.21</td>
<td>0.55</td>
<td>0.29</td>
<td>0.61</td>
<td>0.19</td>
<td></td>
</tr>
</tbody>
</table>
Appendix 3  Chl a (mg m$^{-2}$) and primary production (PP.; mg C m$^{-2}$d$^{-1}$), and bacterial production (Bact. P.; mg C m$^{-2}$d$^{-1}$) during May 31 to June 9, 1988. The values in the bottom row represent the averages at one station at different dates.

<table>
<thead>
<tr>
<th>Date</th>
<th>Stn 1</th>
<th>Stn 2</th>
<th>Stn 3</th>
<th>Stn 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td>49.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2650</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 1</td>
<td></td>
<td>56.1</td>
<td>52.9</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2770</td>
<td>1700</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>7</td>
<td>17.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 2</td>
<td></td>
<td>72.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2440</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>20.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 3</td>
<td></td>
<td>46.2</td>
<td>34.8</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>3610</td>
<td>293</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>36.3</td>
<td>9.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 4</td>
<td></td>
<td>26.2</td>
<td>67.7</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>5000</td>
<td>2540</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>40.2</td>
<td>15.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 5</td>
<td></td>
<td></td>
<td>43.6</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>150</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>7.87</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 6</td>
<td></td>
<td>43.6</td>
<td>30.4</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>1240</td>
<td>670</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>10.7</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 7</td>
<td></td>
<td>52.7</td>
<td>12.6</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2060</td>
<td>843</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>18.2</td>
<td>15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 8</td>
<td></td>
<td></td>
<td>101.4</td>
<td></td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2260</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>9.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 9</td>
<td></td>
<td></td>
<td></td>
<td>67.1</td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>2540</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bact. P.</td>
<td>9.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Averaged</td>
<td></td>
<td>43.5</td>
<td>58.7</td>
<td>67.1</td>
</tr>
<tr>
<td>Chl a</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.P.</td>
<td>1190</td>
<td>1830</td>
<td>2540</td>
<td>2990</td>
</tr>
<tr>
<td>Bact. P.</td>
<td>8.97</td>
<td>14.4</td>
<td>9.4</td>
<td>28.1</td>
</tr>
</tbody>
</table>
Appendix 4 Abundance ($10^3$ cells ml$^{-1}$) and relative biovolume (% of total phytoplankton biovolume) of major species: *Skeletonema costatum*, *Thalassiosira* spp. and *Chaetoceros* spp. at the surface or depth of 1-2 m during May 31 to June 7, 1988.

<table>
<thead>
<tr>
<th>Date</th>
<th>Stn 1</th>
<th></th>
<th>Stn 2</th>
<th></th>
<th>Stn 3</th>
<th></th>
<th>Stn 4</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>May 31</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td>7.7</td>
<td>45.3</td>
<td>48.6</td>
<td>66.6</td>
<td>36.0</td>
<td>81.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>53.8</td>
<td>12.1</td>
<td>146</td>
<td>9.2</td>
<td>70.0</td>
<td>6.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>96</td>
<td>12.1</td>
<td>336</td>
<td>10.3</td>
<td>80.6</td>
<td>4.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>146</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>955</td>
<td>7.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 2</td>
<td>161</td>
<td>76.9</td>
<td>336</td>
<td>10.3</td>
<td>80.6</td>
<td>4.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>23.8</td>
<td>7.8</td>
<td>3.86</td>
<td></td>
<td>26.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>661</td>
<td>6.7</td>
<td>3.86</td>
<td></td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 3</td>
<td>408</td>
<td>81.8</td>
<td>111</td>
<td>78.9</td>
<td>7.4</td>
<td></td>
<td>1640</td>
<td>7</td>
</tr>
<tr>
<td>T. spp.</td>
<td>955</td>
<td>7.4</td>
<td>111</td>
<td>78.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.86</td>
<td></td>
<td>201</td>
<td>32</td>
</tr>
<tr>
<td>S. costatum</td>
<td>1640</td>
<td>7</td>
<td></td>
<td></td>
<td>3.86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 5</td>
<td>161</td>
<td>76.9</td>
<td>336</td>
<td>10.3</td>
<td>80.6</td>
<td>4.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td>485</td>
<td>82.5</td>
<td></td>
<td></td>
<td>2.44</td>
<td>77.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>1370</td>
<td>9.9</td>
<td></td>
<td></td>
<td>12.2</td>
<td>1.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>605</td>
<td>2.2</td>
<td></td>
<td></td>
<td>39.0</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 6</td>
<td>485</td>
<td>82.5</td>
<td>2.44</td>
<td>77.9</td>
<td>109</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>336</td>
<td>19.1</td>
<td>1410</td>
<td>11.7</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>263</td>
<td>5.8</td>
<td>548</td>
<td>2.4</td>
<td>109</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 7</td>
<td>70.2</td>
<td>71.2</td>
<td>402</td>
<td>80.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td>336</td>
<td>19.1</td>
<td>1410</td>
<td>11.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>23.5</td>
<td>67.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>220</td>
<td>23.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 8</td>
<td>24.6</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. spp.</td>
<td>424</td>
<td>87.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. spp.</td>
<td>848</td>
<td>5.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. costatum</td>
<td>109</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix 5  Total number (m⁻³) of calanoid copepods, *Neocalanus plumchrus* and the most dominant copepod (Abund.); and total others (m⁻³) including the most dominant genera during a time series at Stn 4 on June 8-9, 1988. Relative abundance is presented as % of total zooplankton.

<table>
<thead>
<tr>
<th>Date</th>
<th>Stn 4</th>
<th>Abundance</th>
<th>% of total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>June 8</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T=1910 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>4576</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>90</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>1527</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>1515</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>929</td>
</tr>
<tr>
<td>T=1925 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>6445</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>2186</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>2546</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>2000</td>
</tr>
<tr>
<td>T=2211 h</td>
<td>10 m</td>
<td>Total Calanoids</td>
<td>7531</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>379</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>1915</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>3859</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>2000</td>
</tr>
<tr>
<td>T=0230 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>12898</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>139</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>3575</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>3374</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>1374</td>
</tr>
<tr>
<td>T=0607 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>7578</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Microcalanus</em></td>
<td>4919</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>1172</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>566</td>
</tr>
<tr>
<td>T=1135 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>9099</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Pseudocalanus</em></td>
<td>3089</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>2344</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- Larvacea</td>
<td>566</td>
</tr>
<tr>
<td>T=1415 h</td>
<td>8 m</td>
<td>Total Calanoids</td>
<td>8041</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>N. plumchrus</em></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Paracalanus</em></td>
<td>2779</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total others</td>
<td>1859</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dominant genera -- <em>Euphausia</em> (juvenile)</td>
<td>566</td>
</tr>
</tbody>
</table>
Appendix 6  Total microflagellates during May 31-June 9, 1988. The values are depth-weighted averages (i.e. the integrated value of microflagellates over a depth (20 m) divided by the depth). The minimum count is zero and the maximum is 2120 cells mL$^{-1}$.

<table>
<thead>
<tr>
<th>Date</th>
<th>Stn 1</th>
<th>Stn 2</th>
<th>Stn 3</th>
<th>Stn 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 31</td>
<td>707</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 1</td>
<td></td>
<td>225</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td>June 2</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 3</td>
<td></td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 4</td>
<td>676</td>
<td></td>
<td>88</td>
<td></td>
</tr>
<tr>
<td>June 5</td>
<td></td>
<td>106</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 6</td>
<td>302</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 7</td>
<td>276</td>
<td>370</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 8</td>
<td></td>
<td></td>
<td>137</td>
<td></td>
</tr>
<tr>
<td>June 8</td>
<td></td>
<td></td>
<td></td>
<td>840</td>
</tr>
</tbody>
</table>
Appendix 7 Total zooplankton abundance and relative abundance as % of major zooplankton species at 8 stations in the Strait of Georgia during April 19-22, 1993.

<table>
<thead>
<tr>
<th>Station</th>
<th>P1</th>
<th>T5</th>
<th>T7</th>
<th>Stn 4</th>
<th>T9</th>
<th>Stn 2</th>
<th>M1</th>
<th>M2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Zooplankton (m⁻³)</td>
<td>140</td>
<td>1215</td>
<td>1312</td>
<td>1107</td>
<td>787</td>
<td>641</td>
<td>1027</td>
<td>1350</td>
</tr>
<tr>
<td>Total Copepods</td>
<td>56.9%</td>
<td>80.3%</td>
<td>89.4%</td>
<td>63.7%</td>
<td>69.3%</td>
<td>86.8%</td>
<td>85.1%</td>
<td>63.7%</td>
</tr>
<tr>
<td>Neocalanus plumchrus</td>
<td>19.1%</td>
<td>20.6%</td>
<td>6.9%</td>
<td>12.6%</td>
<td>14.1%</td>
<td>14.9%</td>
<td>44.1%</td>
<td>7.7%</td>
</tr>
<tr>
<td>C1-C3</td>
<td>0.7%</td>
<td>7.1%</td>
<td>3.1%</td>
<td>2.0%</td>
<td>0.7%</td>
<td>5.5%</td>
<td>9.5%</td>
<td>0.8%</td>
</tr>
<tr>
<td>C4</td>
<td>4.1%</td>
<td>7.6%</td>
<td>1.4%</td>
<td>3.6%</td>
<td>2.8%</td>
<td>3.9%</td>
<td>23.4%</td>
<td>1.3%</td>
</tr>
<tr>
<td>C5</td>
<td>14.4%</td>
<td>5.9%</td>
<td>2.4%</td>
<td>7.0%</td>
<td>10.6%</td>
<td>5.5%</td>
<td>11.2%</td>
<td>5.6%</td>
</tr>
<tr>
<td>Pseudocalanus minutus</td>
<td>13.6%</td>
<td>39.2%</td>
<td>60.4%</td>
<td>17.0%</td>
<td>22.2%</td>
<td>40.3%</td>
<td>45.4%</td>
<td>9.8%</td>
</tr>
<tr>
<td>Acartia sp.</td>
<td>13.3%</td>
<td>9.5%</td>
<td>1.8%</td>
<td>11.8%</td>
<td>8.8%</td>
<td>1.6%</td>
<td>16.1%</td>
<td>4.5%</td>
</tr>
<tr>
<td>Calanus sp.</td>
<td>3.3%</td>
<td>0.7%</td>
<td>1.2%</td>
<td>4.0%</td>
<td>3.9%</td>
<td>1.0%</td>
<td>2.2%</td>
<td>11.6%</td>
</tr>
<tr>
<td>Metridia pacifica</td>
<td>6.6%</td>
<td>3.8%</td>
<td>2.5%</td>
<td>5.8%</td>
<td>12.0%</td>
<td>12.2%</td>
<td>2.9%</td>
<td>2.1%</td>
</tr>
<tr>
<td>Oithona similis</td>
<td>2.6%</td>
<td>3.9%</td>
<td>2.5%</td>
<td>7.2%</td>
<td>4.9%</td>
<td>10.2%</td>
<td>1.7%</td>
<td>3.9%</td>
</tr>
<tr>
<td>Oithona spinirostris</td>
<td>0.7%</td>
<td>5.1%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oncaea sp.</td>
<td>1.1%</td>
<td>0.4%</td>
<td>3.2%</td>
<td>2.8%</td>
<td>1.6%</td>
<td>4.2%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepod stages</td>
<td>Eggs</td>
<td>12.7%</td>
<td>14.5%</td>
<td>4.8%</td>
<td>4.1%</td>
<td>3.7%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nauplii</td>
<td>3.5%</td>
<td>1.8%</td>
<td>2.7%</td>
<td>0.7%</td>
<td>2.4%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepodid</td>
<td>4.7%</td>
<td>6.4%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphausia pacifica</td>
<td>Zoea</td>
<td>2.2%</td>
<td>2.3%</td>
<td>1.5%</td>
<td>4.8%</td>
<td>1.8%</td>
<td>1.2%</td>
<td>1.4%</td>
</tr>
<tr>
<td>Protozoa</td>
<td>14.0%</td>
<td>5.5%</td>
<td>1.4%</td>
<td>9.6%</td>
<td>10.9%</td>
<td>0.7%</td>
<td>0.6%</td>
<td></td>
</tr>
<tr>
<td>Larva</td>
<td>5.4%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.1%</td>
<td>4.1%</td>
<td></td>
</tr>
<tr>
<td>Cyphonautes sp.</td>
<td>5.2%</td>
<td>2.7%</td>
<td>1.5%</td>
<td>14.8%</td>
<td>11.3%</td>
<td>10.5%</td>
<td>7.7%</td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td>21.7%</td>
<td>9.1%</td>
<td>6.0%</td>
<td>7.2%</td>
<td>6.7%</td>
<td>7.7%</td>
<td>2.4%</td>
<td>22.5%</td>
</tr>
</tbody>
</table>