

Factors controlling the timing of the spring bloom in the Strait of Georgia estuary, British Columbia, Canada

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Abstract: We present a conceptual model to illustrate how wind events and the annual migration and grazing of the dominant copepod *Neocalanus plumchrus* interact and affect the development of the spring bloom. The model was supported by observations made during 1988, 1992, and 1993. For example, in 1992, an El Niño year, the annual freshet of the Fraser River and probably the spring bloom started 1 month earlier. The bloom was interrupted by a wind event in late March. A few days later, its full recovery was interrupted by the peak in zooplankton grazing, and ambient ammonium concentrations increased. In contrast, in 1988, the annual freshet started later (mid-April), and winds remained strong throughout the same period, hindering the development of the spring bloom. The spring bloom was further suppressed by large numbers of zooplankton during April, resulting in a prolonged spring bloom. These observations indicate that interannual variations in winds and the timing of the annual freshet determine the timing and duration of the spring bloom, which in turn, determine the matching of phytoplankton to zooplankton in the Strait of Georgia. The matching or mismatching bears significant implications for food availability for juvenile fish.

Résumé : Nous présentons un modèle conceptuel pour illustrer comment les événements liés au vent ainsi que la migration et le broutage annuels du copépode dominant *Neocalanus plumchrus* interagissent ensemble et influent sur le développement de la prolifération printanière. Le modèle était appuyé par des observations réalisées en 1988, 1992 et 1993. Par exemple, en 1992, qui était une année de El Niño, la crue nivale annuelle du fleuve Fraser et probablement la prolifération printanière ont commencé 1 mois plus tôt. La prolifération a été interrompue par les vents à la fin mars. Quelques jours plus tard, son rétablissement complet a été interrompu par le maximum dans le broutage zooplanctonique et les concentrations d'ions ammonium ambiantes ont augmenté. Par opposition, en 1988, la crue nivale annuelle a débuté tard (mi-avril) et les vents sont demeurés forts pendant cette période, gênant le développement de la prolifération printanière. Cette dernière a été réduite encore davantage par la forte abondance de zooplancton en avril, ce qui a entraîné une prolifération printanière prolongée. Ces observations ont indiqué que les variations interannuelles dans les vents et le moment de la crue nivale annuelle déterminent le moment et la durée de la prolifération printanière qui, à son tour, détermine la synchronisation du phytoplancton au zooplancton dans le détroit de Géorgie. La synchronisation ou la non-synchronisation comportent des implications importantes du point de vue de la disponibilité des aliments pour le poisson juvénile.

[Traduit par la Rédaction]

Introduction

The interaction of freshwater discharge, winds, and tides in an estuary cause spatial and temporal variation in nutrients, phytoplankton biomass, and production. Freshwater input into an estuary increases the stability of the water column, whereas mixing produced by tides and winds decreases the stability. It is these changes in water column stability that control the dynamics of nutrients and biological production (Legendre et al. 1988). The variability in the timing and magnitude of the annual freshet in river discharge and winds often results in inter-

annual variability in the timing and magnitude of the spring bloom (Malone et al. 1988; Cloern 1991). Two previous studies (Parsons et al. 1969a; Stockner et al. 1979) sampled nutrients and phytoplankton in the Strait of Georgia on a monthly basis. However, the dynamics of bloom formulation occurs on much shorter time scales. Therefore, there is a need to study the spring bloom dynamics in the Strait of Georgia estuary on a time scale of days to weeks.

Phytoplankton biomass has been observed to increase as a succession of peaks and troughs (Erga and Heimdal 1984; Sournia et al. 1987), probably because of wind events, tidal cycles, or zooplankton grazing. Our study of the spring bloom in 1991 (Yin et al. 1996), which resolved day-to-day variations in the distribution of nutrients and phytoplankton biomass, found that the spring bloom in the Strait of Georgia estuary was underway and was interrupted when a wind event occurred. The copepod *Neocalanus plumchrus* is the predominant mesozooplankton in the Strait of Georgia during the spring because of its ontogenetic migration of newly hatched larvae from deep waters to the surface where it develops into a copepodite stage V before descending to deep waters in May–June

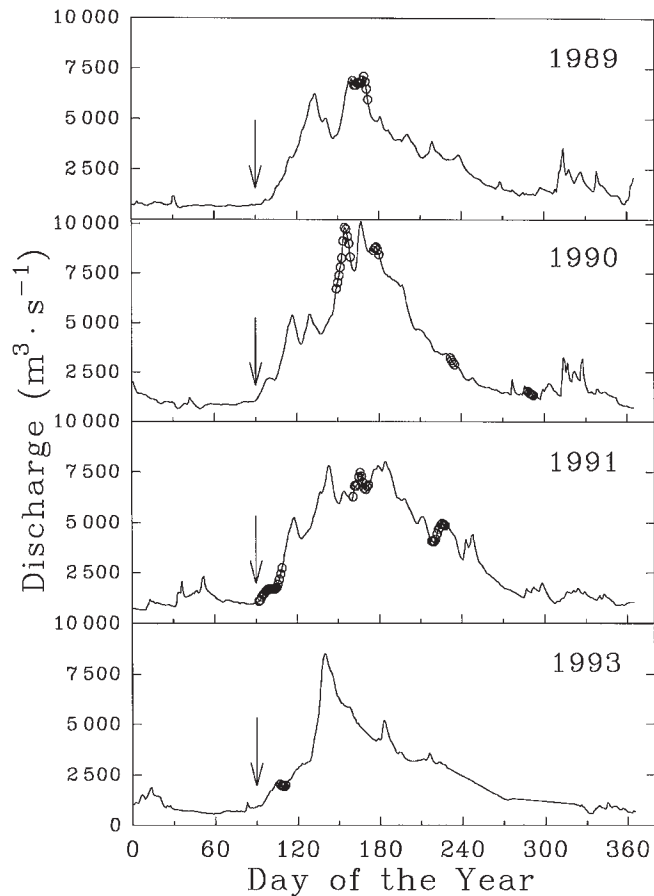
Received May 17, 1996. Accepted February 25, 1997.
J13479

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Fig. 1. Daily discharge ($\text{m}^3 \cdot \text{s}^{-1}$) of the Fraser River at Hope for 1989, 1990, 1991, and 1993 (the data were obtained from Water Survey, Environment Canada). The arrow indicates the beginning of the annual freshet in April. The circles represent the periods during which the cruises were conducted. Not all of the data from these cruises are presented in this study.



(Fulton 1973). Grazing by this copepod has been shown to have a large impact on the development of the spring bloom (Parsons et al. 1969a; Harrison et al. 1983; Yin et al. 1996).

In this study, we present changes over short time scales (days) in the vertical distribution of salinity, temperature, nutrients, phytoplankton biomass, and zooplankton abundance for 1988, 1992, and 1993. The objectives of the study were to examine if there is interannual variability in the timing of the spring bloom in the Strait of Georgia and how the onset and the course of the spring bloom are affected by the interannual variability in physical conditions such as river discharge and winds. We also examined how the timing of zooplankton grazing due to ontogenetic migration interacted with physical processes and affected the course of the spring bloom.

Before describing the methods and results, we will examine the general pattern of daily changes in river discharge, winds, and tidal ranges for the Strait of Georgia over a few years and present a conceptual model to illustrate how wind events and the timing of zooplankton grazing interact and affect the spring bloom.

River discharge, winds, and tidal cycles for the Strait of Georgia

The hydrodynamics in the Strait of Georgia are largely

determined by runoff, winds, and tides (LeBlond 1983), which in turn determine biological processes in the Strait. There are two periods each year during which tidal ranges are minimal (ca. 2 m) (Yin 1994). One period occurs in March, and the other is in autumn. Because the tidal cycle is due to astronomical forces, the pattern is repeated every year. The beginning of the Fraser River spring freshet usually occurs at the beginning of April (1989, 1990, 1991, and 1993) (Fig. 1). These years can be viewed as normal years. Winds are more variable from year to year (Yin 1994). Therefore, in March when tidal mixing is reduced and river discharge remains constant and low before the spring freshet begins, winds become a critical factor in determining the stability of the water column in the Strait of Georgia. If winds are weak at this time, an estuarine plume can form. If strong winds occur, however, the estuarine plume may be destroyed by mixing. 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 period of time long enough to allow a bloom to develop. For example, in 1991, winds were reduced in March (the wind speed exceeded $4 \text{ m} \cdot \text{s}^{-1}$ only for 3 days), and the spring bloom developed in late March and early April. This bloom was then interrupted during a wind event (Yin et al. 1996).

Conceptual model of the spring bloom development

In the Strait of Georgia, the annual vertical migration of the predominant zooplankton species occurs independent of the spring bloom (Fulton 1973; Harrison et al. 1983). Therefore, there will be an interactive effect between wind events and zooplankton grazing during the course of the spring bloom. Suppose the model starts with phytoplankton biomass, measured as particulate organic nitrogen (PON), being low and NO_3 being high within the euphotic zone (Fig. 2). If the conditions are favorable for phytoplankton growth, NO_3 will decrease and PON will increase at the same rate. If there are no physical interruptions and no grazing, PON will increase steadily (a bloom occurs), as indicated by the broken line, until NO_3 is exhausted (Fig. 2A). If a wind event occurs during the spring bloom (indicated by the arrows), the bloom will be interrupted, resulting in an increase in NO_3 concentration and a decrease in PON resulting from wind mixing. After the interruption, how fast the spring bloom recovers depends on the magnitude and duration of the wind event. Assuming the timing of the peak in zooplankton migration occurs at a fixed window in time because of their ontogenetic nature (indicated by the arrow in Fig. 2B), zooplankton grazing can have dramatically different effects on the development of the spring bloom, depending on its stage. When the bloom is at a stage that can produce sufficient biomass to balance zooplankton grazing, biomass (PON) will not increase, but NO_3 will continue to decrease until it is exhausted (Fig. 2B). Thus, phytoplankton and zooplankton are in phase. When a wind event occurs prior to the peak in grazing, biomass will be reduced because of mixing (Fig. 2C). As a result, primary production cannot meet the grazing demand when the peak migration of zooplankton occurs. Consequently, phytoplankton biomass will decrease, and at the same time, NH_4 concentrations will increase because of zooplankton grazing; little NO_3 will be utilized (Fig. 2C), as the amount of NH_4 produced by zooplankton activity is sufficient to meet the utilization of nitrogen by phytoplankton. These features were observed during the slow recovery of the spring bloom in 1991

(Yin et al. 1996). Therefore, when a wind event interrupts the spring bloom just before the peak in grazing, the effects can be detrimental to the recovery of the spring bloom. We present observations that support these conceptual models.

Materials and methods

Three cruises in the central Strait of Georgia were conducted during May 31 – June 9, 1988; April 6–15, 1992; April 19–22, 1993. The sampling stations were mainly in the central strait (Fig. 3). For information on the hydrodynamical features pertaining to this study area, see reviews by LeBlond (1983) and Harrison et al. (1983).

The vertical profiling system that produced continuous vertical profiles of depth, salinity, temperature, fluorescence, and nutrients (NO_3 , NH_4 , PO_4 , and SiO_4) is described in Jones et al. (1991). The methods for phytoplankton counts, chlorophyll *a* (chl *a*), and ^{14}C uptake as well as the depth integration (0–20 m) for biomass and primary production were described previously (Harrison et al. 1991). Nitrate (plus nitrite) and ammonium were determined following the procedures of Wood et al. (1967) and Slawyk and MacIsaac (1972), respectively.

Zooplankton samples were obtained using a bongo net towed vertically at approximately $1 \text{ m}\cdot\text{s}^{-1}$. Filtering efficiency of the nets was determined using a calibrated flow meter. Vertical hauls were made from 50 m to the surface. Samples were preserved in 5% borax-buffered formalin for later identification and enumeration.

Observed hourly tidal heights were provided by the Tides and Current Section, Institute of Ocean Sciences, Sidney, B.C. The discharge data for the Fraser River at Hope were obtained from the Water Survey, Environment Canada, Vancouver, B.C. The wind data were recorded at the Vancouver International Airport and provided by the Atmospheric Environment Service, Environment Canada, Vancouver, B.C.

Results

1993 April cruise

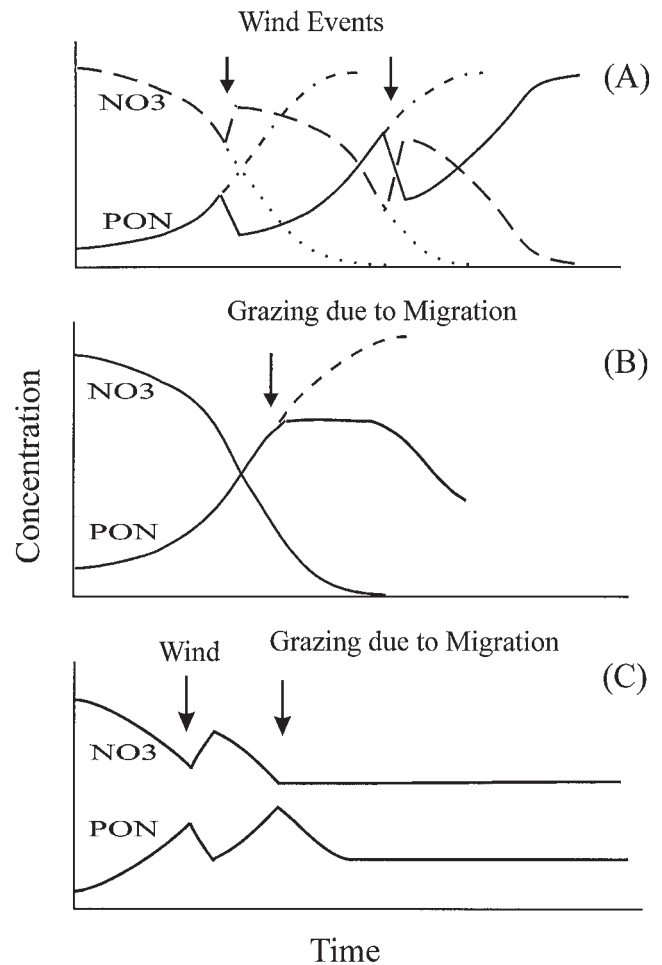
River discharge was very low during March 1993 (Fig. 1). A rapid increase in the volume of the discharge at the beginning of April marked the beginning of the annual freshet.

NO_3 concentrations ranged from 2 to $10 \mu\text{M}$ at the surface and were less than $19 \mu\text{M}$ at 20 m except at station M2 (Table 1). NH_4 concentrations were above $1 \mu\text{M}$ at almost all the stations and sometimes above $2 \mu\text{M}$. Chlorophyll *a* ranged between 8.7 and $61 \text{ mg}\cdot\text{m}^{-2}$ (Table 1). The differences in NO_3 concentration between the surface and 20 m (just below the photic zone) were between 4 and $19 \mu\text{M}$, which were considered to represent the consumption of NO_3 by phytoplankton (Table 1). Total zooplankton abundance was over 1000 animals· m^{-3} at most stations (Table 2). Copepods were the most abundant animals (ranging between 57 and 89% of total zooplankton) followed by euphausiids. Among the copepods, the most abundant species was *Pseudocalanus* spp. However, *N. plumchrus* is much larger and represented the greatest proportion of total zooplankton biomass. Most *N. plumchrus* were stages C4 and C5 (C4 is 3–6 times and C5 is 10–20 times greater than *Pseudocalanus* spp. in dry weight, respectively), and the euphausiids were all larvae and juveniles.

1992 April cruise

A rapid increase in river discharge occurred just prior to the cruise and was followed by a rapid decrease during the cruise (Fig. 4A). Wind speeds were $<3 \text{ m}\cdot\text{s}^{-1}$ (Fig. 4B). The cruise began during a spring tide and ended during a neap tide.

Fig. 2. Conceptual model to illustrate how wind events and timed grazing affect the development of the spring bloom. (A) The effect of wind events. The two arrows indicate the occurrence of wind events. The solid and short broken lines represent the changes in PON and NO_3 concentrations, respectively, if there are interruptions by wind events. The long broken and dotted lines indicate a steady increase and decrease without any interruption for PON and NO_3 , respectively. (B) The effect of grazing due to the ontogenetic migration of zooplankton without any wind events during the spring bloom. (C) The effect of the interaction of wind events and vertical zooplankton migration on the spring bloom (NO_3 concentrations and biomass PON). The arrows indicate either a wind event or a peak in grazing. The spring bloom has been delayed because of wind mixing before the peak in grazing occurs. As a result, grazing exceeds primary production so that biomass decreases and NO_3 is not depleted.



Salinity was <20 at the surface at station S2 on April 7–15 (Fig. 5), indicating the presence of the riverine plume. The recent freshwater influence had not yet reached P6 and S1 on April 7 because the salinity at the surface was only slightly lower than at depth. The estuarine plume expanded to P6 on April 13–15 (Fig. 5), reflecting the rapid increase in river discharge before the cruise (Fig. 4A). Temperature in the upper layer increased with time at each station during April 6–15, and the vertical gradient became larger (Fig. 5). This phenomenon indicates that the water column had stabilized during April 6–15.

Fig. 3. Map of the study area indicating stations for 1988 (×), 1992 (●), and 1993 (Δ). The stations in 1992 were the same as in 1991, except some stations in 1991 were not visited in 1992.

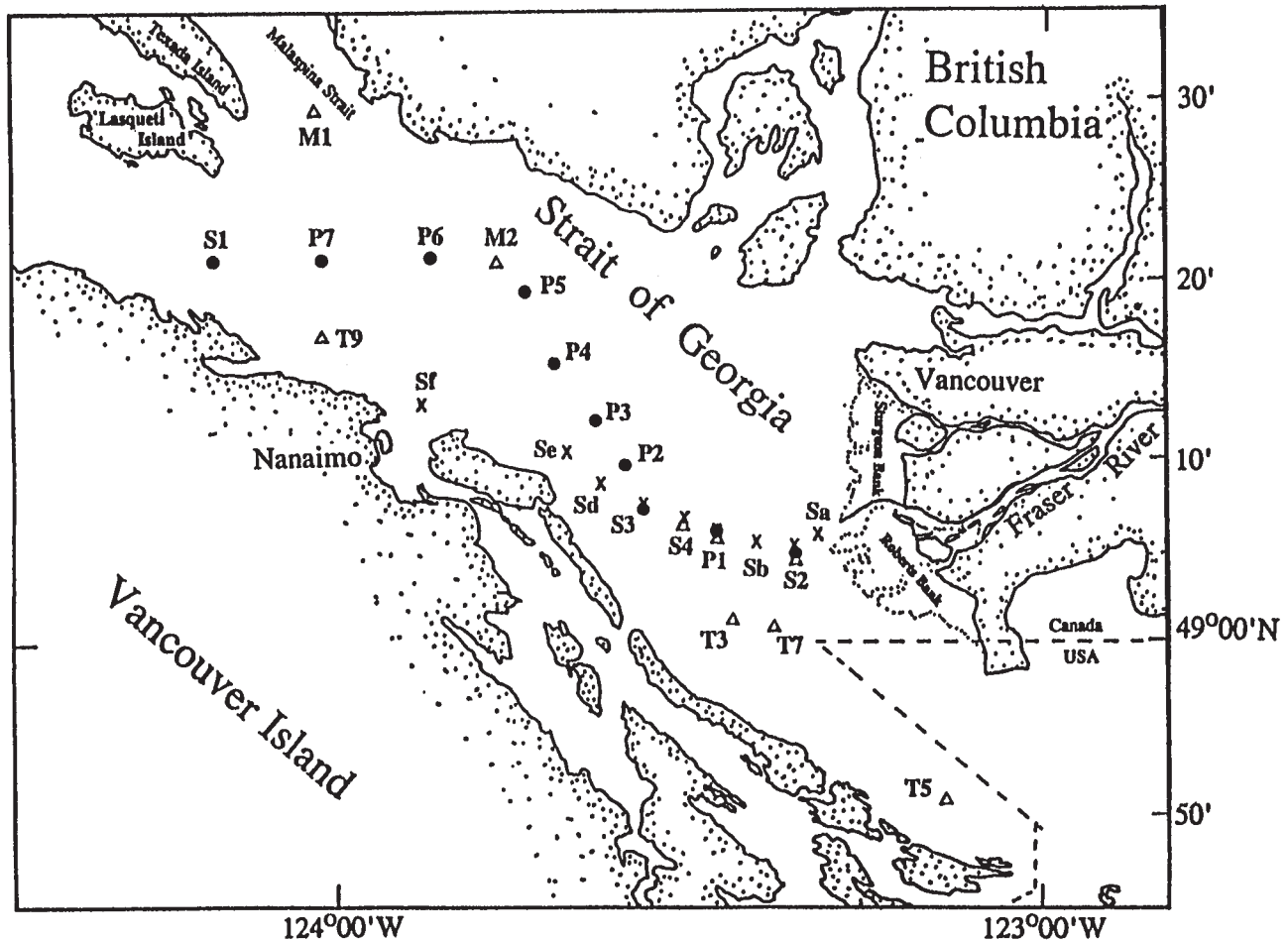


Table 1. Nutrients (NO_3 and NH_4) and integrated (0–20 m) chl *a* at eight stations (see Fig. 3) in the Strait of Georgia during April 19–22, 1993.

	Station							
	P1	S2	S4	T5	T7	T9	M1	M2
NO_3 (μM)								
0 m	5.8	8.7	2.5	10	7.1	2	3.3	2.1
20 m	18	16	17	14	15	11	14	21
20–0 m	12	7.5	14	4.1	8	11	10	19
Chl <i>a</i> ($\text{mg}\cdot\text{m}^{-2}$)	20	37	61	8.7	41	26	13	26
NH_4 (μM)	1.9	1.7	0.7	2.2	1.9	1.4	2.7	1.1

Note: NO_3 concentration (20–0 m) is the difference between 0 and 20 m, representing consumption of NO_3 by phytoplankton. NH_4 concentration is depth averaged (0–20 m).

On April 7, NO_3 concentrations in the water column were around $5 \mu\text{M}$ at the surface, higher than at an intermediate depth at stations S2, P3, and S1 (Fig. 6), reflecting the sharp increase in river discharge prior to April 6 and possibly the spring tide that resulted in an increased entrainment near the river mouth (Yin et al. 1995b). NO_3 concentrations decreased very slowly in the upper layer and remained undepleted at all the stations during the entire 10-day cruise. NO_3 concentrations at 20 m were mostly below $20 \mu\text{M}$. The difference in

NO_3 concentrations between the surface and the deep water (20 m) was more than $10 \mu\text{M}$ at most stations and indicated that a large amount of NO_3 had been utilized prior to the cruise. NH_4 concentrations were usually higher than $1 \mu\text{M}$ and sometimes exceeded $4 \mu\text{M}$ at intermediate depths on April 12–14 (Fig. 7). Both chl *a* (Fig. 8) and primary production (Yin 1994) were low except at P6 on April 7, but they increased during April 13–15, particularly chl *a*. The increase coincided with the sharp drop in river discharge and the neap tide. Chlorophyll *a* appeared to be higher at station S2 than at other stations during April 8–13.

1988 June cruise

Winds were weak during the cruise period, and river discharge declined rapidly after the annual maximum during the same period, although the river discharge was still high (Fig. 9).

The estuarine plume was well developed in the sampling region with the halocline penetrating to a depth of about 10 m (Fig. 10), indicating a large freshwater influence by the annual maximum river discharge. Fluorescence was at a maximum at the surface on June 1. Fluorescence progressively increased vertically downwards and developed into a subsurface maximum during June 6–7 (Fig. 11). The increase in fluorescence was coupled with a decrease in nitrate (Fig. 11). On June 1, NO_3 concentrations were above $5 \mu\text{M}$ at the surface at

Table 2. Total zooplankton abundance and relative abundance of major zooplankton species (% of total zooplankton abundance) at eight stations (see Fig. 3) in the Strait of Georgia during April 19–22, 1993.

	Stations							
	P1	S2	S4	T5	T7	T9	M1	M2
Total zooplankton (animals·m ⁻³)	140	641	1107	1215	1312	787	1027	1350
Total copepods (%)	57	87	64	80	89	69	85	64
<i>Neocalanus plumchrus</i> (%)	19	15	13	21	7	14	44	8
C1–C3	0.7	5.5	2.0	7.1	3.1	0.7	9.5	0.8
C4	4.1	3.9	3.6	7.6	1.4	2.8	23	1.3
C5	14	5.5	7.0	5.9	2.4	11	11	5.6
<i>Pseudocalanus</i> spp. (%)	14	40	17	39	60	22	45	9.8
<i>Euphausiia pacifica</i> (%)								
Zoea	2.2	0	4.8	2.3	1.5	1.8	1.2	1.4
Protozoa	14	0	9.6	5.5	1.4	11	0.7	0.6
Juvenile	0	5.4	0	0	0	0	0	0
Adult	0	0.1	0	0	0	0	0	4.1

Note: Other copepods included *Acartia* sp., *Calanus* sp., *Metridia* sp., and *Oithona* spp. and they are not included in this table.

station S2 (near the river mouth) and increased seaward, reaching almost 10 μM at station Sf (Fig. 11), whereas on June 4 and 6, NO_3 concentrations had decreased and were undetectable at the surface at station Sf. By June 7, a subsurface minimum in NO_3 at an intermediate depth (7 m) at stations S2 and S3 (10 m) was observed (Fig. 11).

Phytoplankton biomass and production were high during this cruise, with chl *a* ranging from 44 to 67 $\text{mg}\cdot\text{m}^{-2}$ at stations S2, S3, S4, and Sf and daily primary production, from 1190 to 2990 $\text{mg}\text{C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Table 3). The phytoplankton assemblage was made up almost entirely of three genera of diatoms: *Thalassiosira* spp., *Skeletonema costatum*, and *Chaetoceros* spp. (Table 4). *Thalassiosira* spp. accounted for 70% or more (range from 26 to 87%) of the total phytoplankton volume at four stations during the entire cruise.

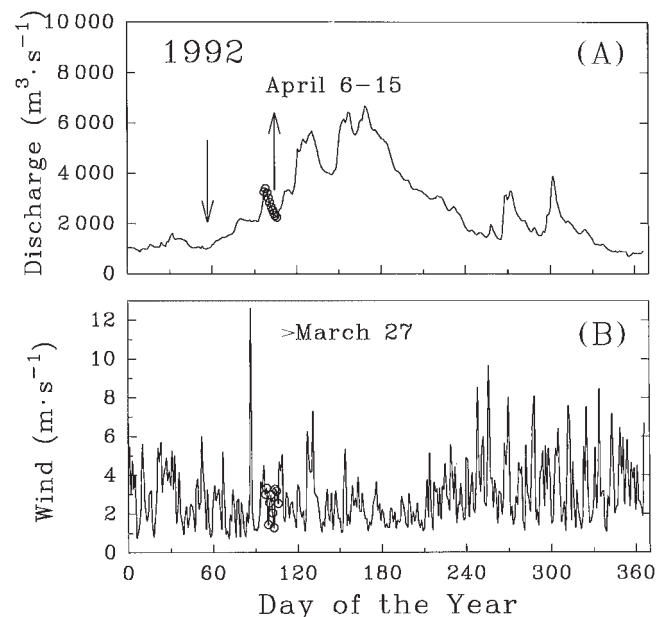
Discussion

The spring bloom in 1993

The Fraser River discharge was smaller during March and April of 1993 than in 1992, possibly because of warm weather in the winter of 1992, an El Niño year. Winds were not particularly strong during March and April prior to the cruise. The spring bloom could develop during March and particularly during April when the annual freshet started (Parsons et al. 1969a). Chlorophyll *a* and nutrient data indicate that the spring bloom had occurred before the mid-April cruise.

NO_3 concentrations at a depth of 20 m in the strait are usually higher than 20 μM in June (Clifford et al. 1992) and are close to 25 μM at the surface in winter (Stephens et al. 1969). Lower concentrations of NO_3 (<17 μM) at 20 m and the vertical difference in NO_3 concentrations between the surface and 20 m in April 1993 indicated consumption of NO_3 in the water column by phytoplankton (assuming that the water column was homogeneously mixed and NO_3 concentrations were 20 μM at the beginning of spring). However, chl *a* values were not high enough to account for this consumption of NO_3 . For example, at station S2 the vertical difference in NO_3 was 7.5 μM , and chl *a* was 37.3 $\text{mg}\cdot\text{m}^{-2}$. In comparison, at P1 the

Fig. 4. (A) The Fraser River discharge and (B) wind speed for 1992. The arrow in (A) indicates the beginning of the spring freshet in March. The circles indicate the cruise period during April 6–15.

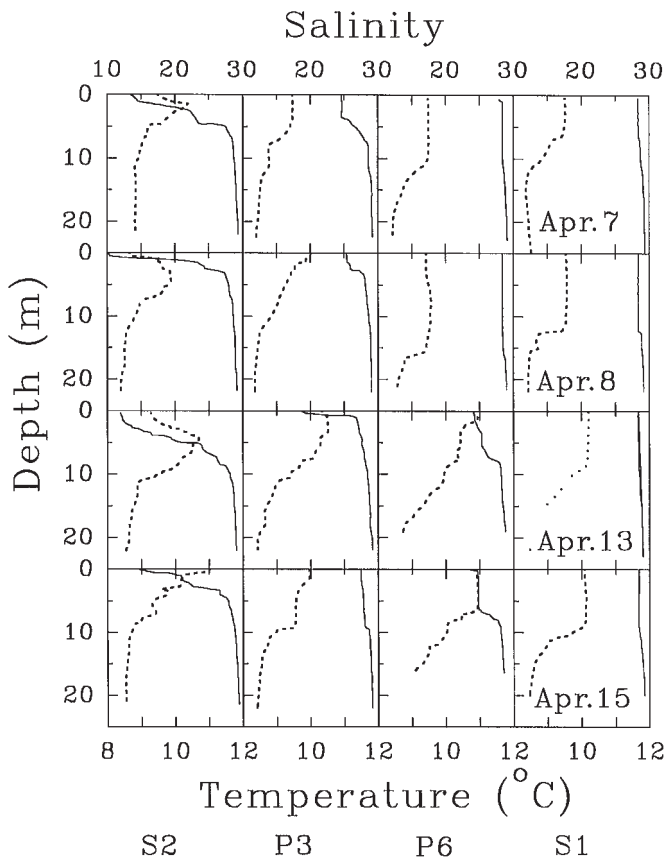


difference was 12 μM , but chl *a* was only 20 $\text{mg}\cdot\text{m}^{-2}$, indicating more loss of utilized NO_3 from phytoplankton. In addition, NH_4 concentrations were high. Features such as undepleted NO_3 and high NH_4 , similar to observations of the spring bloom in 1991 (Yin et al. 1996), indicate that zooplankton grazing was responsible for the increase in NH_4 . This was supported by high abundance of the large copepod *N. plumchrus* and the smaller copepod *Pseudocalanus* spp.

The early spring bloom in 1992

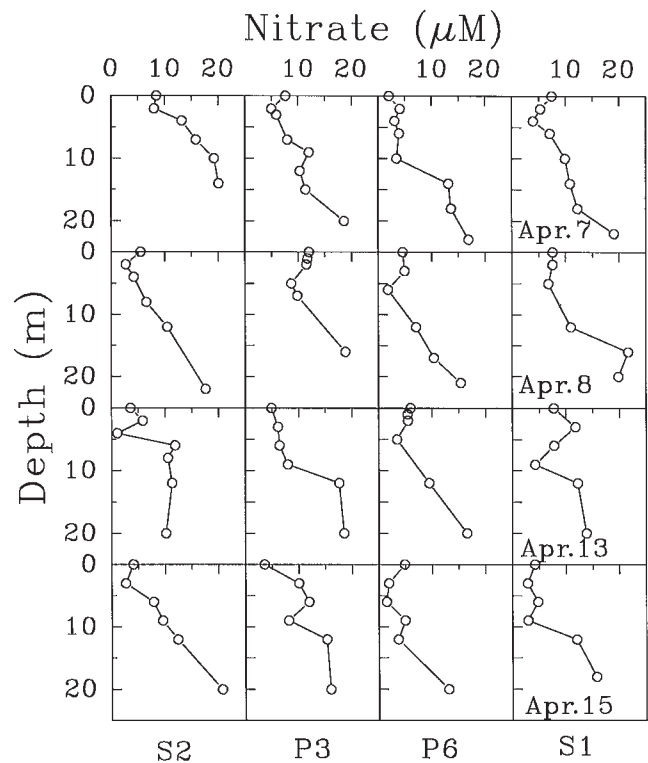
Large differences in the concentrations of NO_3 (Fig. 6), silicate, and phosphate (Yin 1994) between the surface and the deep water (20 m) indicated a large consumption of nutrients and that the spring bloom had occurred prior to the cruise in

Fig. 5. Vertical profiles of salinity (solid line) and temperature (broken line) at four stations along the transect (see Fig. 3) during April 6–15, 1992.



April 1992. However, low biomass of phytoplankton indicated that the utilized nutrients had not accumulated as phytoplankton biomass but was most likely due to export to organisms of higher trophic levels via grazing. A striking phenomenon was that the remaining nutrients decreased slowly over time, although they were not high. Therefore, low biomass and production were not due to limitation by nutrients. The Fraser River freshet began in early March 1992 (the El Niño year), 1 month earlier than in the previous 4 years. Winds in March were weak. These conditions must have favored an earlier onset of the spring bloom. However, there were 2 days in March where wind speeds were $5.2 \text{ m}\cdot\text{s}^{-1}$ on March 7 and $12.6 \text{ m}\cdot\text{s}^{-1}$ on March 27. Relative to the stability of the water column during their respective times, mixing energy generated by winds on these days could have been destructive to the stratification, particularly on March 27. It is likely that the spring bloom started in late February or early March and was interrupted by the March 7 wind event. During the March 27 wind event, there must have been much NO_3 mixed up into the surface layer, which matched the prediction of a model run for the same region, which showed that nutrient profiles were almost completely homogeneous after a constant wind speed of $10 \text{ m}\cdot\text{s}^{-1}$ of 48 h duration (St. John et al. 1993). Extremely calm weather and a rapid increase in river discharge followed this wind event. These conditions favored a fast recovery of the spring bloom. However, chl *a* concentrations were low 10 days (April 6) after this wind event, probably because of

Fig. 6. Vertical profiles of nitrate at four stations along the transect (see Fig. 3) during April 6–15, 1992.



zooplankton grazing by *N. plumchrus* in the surface layer. The grazing suggestion was also supported by other evidence such as a slow decrease in NO_3 and PO_4 concentrations (Yin 1994) and high NH_4 concentrations in the water column during the entire period of April 6–15. In addition, urea was abnormally high ($1\text{--}3 \mu\text{M}$; Yin 1994). The grazing after the wind event resulted in low phytoplankton biomass, undepleted nutrients, and subsequent slow utilization by phytoplankton during the cruise (April 6–15), which fits the conceptual model (Fig. 2C).

The delayed spring bloom or a secondary bloom in 1988

The temporal increase in fluorescence, decrease in NO_3 , and high phytoplankton biomass and production indicated the development of a bloom during the June cruise period in 1988. The question is whether this bloom was the spring bloom or a secondary bloom (referring to a bloom that occurs because of resupply of nutrients due to mixing after winter nutrients are depleted during the primary spring bloom).

The combined evidence from the results during the cruise indicates that this bloom could be a delayed spring bloom. In the Strait of Georgia, the spring bloom occurs earlier (March–April) in the estuarine plume near the river mouth than in adjacent waters (Parsons et al. 1969a; Stockner et al. 1979; Yin et al. 1996). Correspondingly, NO_3 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, NO_3 in the estuarine plume will be utilized, resulting in a low or undetectable concentration during June (Parsons et al. 1970; Harrison et al. 1991). Because the river outflow carries a higher NO_3 concentration in June (Yin et al. 1995a), NO_3 concentration is higher near the river mouth and decreases

Fig. 7. Vertical profiles of ammonium at four stations along the transect (see Fig. 3) during April 6–15, 1992.

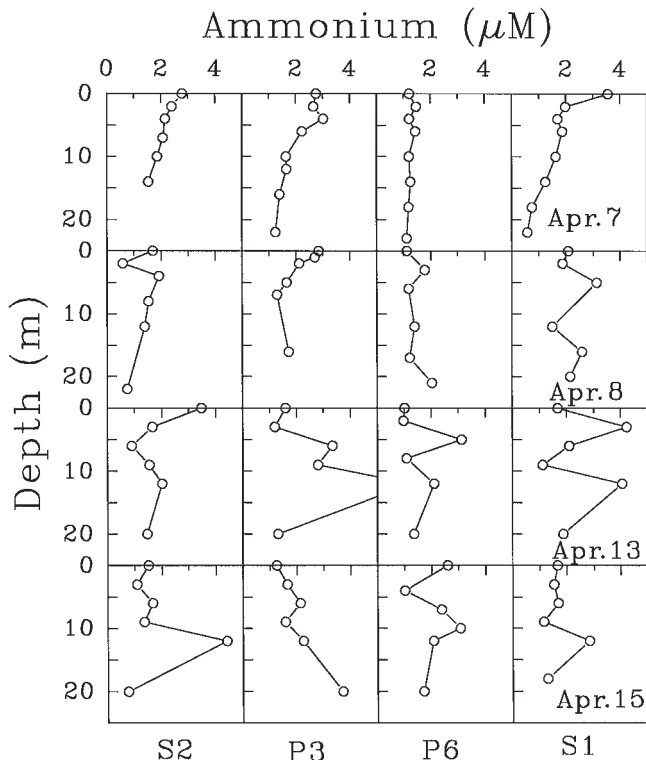
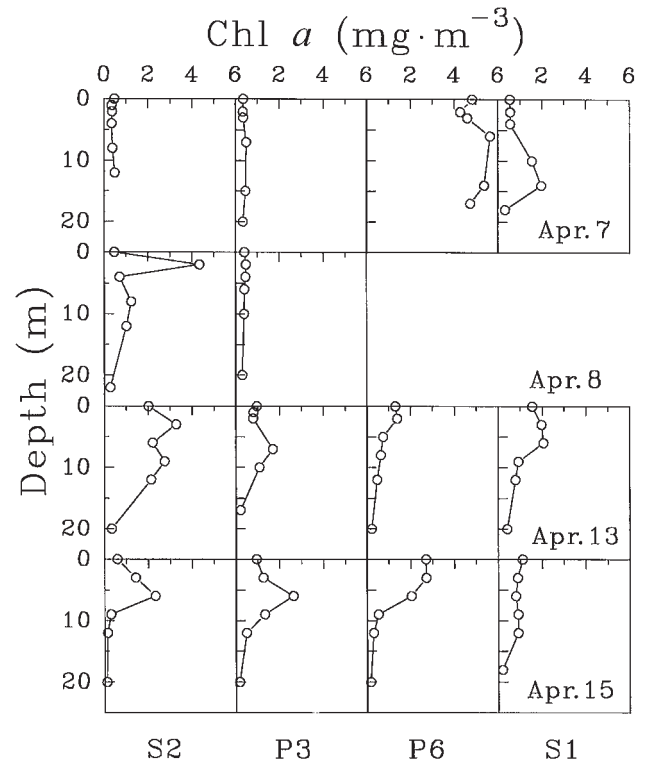


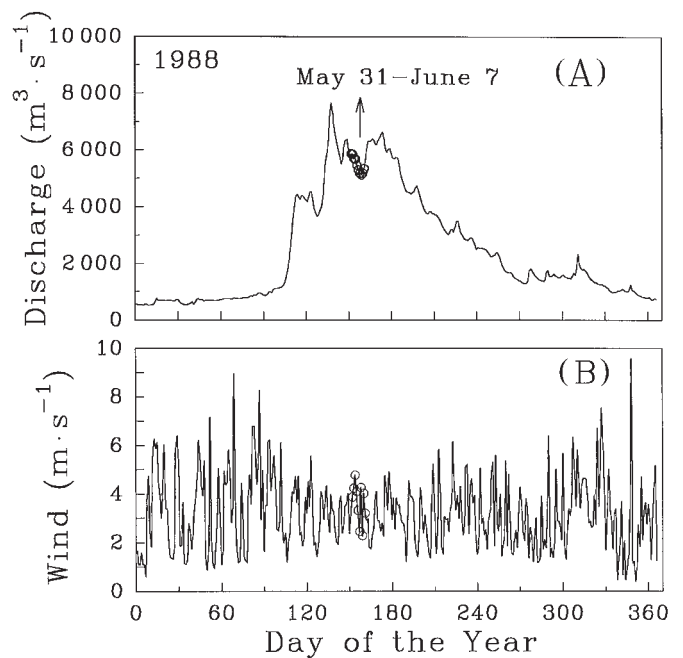
Fig. 8. Vertical profiles of chlorophyll *a* at four stations along the transect (see Fig. 3) during April 6–15, 1992.



seaward at the surface of the estuarine plume. Frequently, a subsurface NO_3 minimum at an intermediate depth will form when the riverine plume (carrying NO_3) spreads over the estuarine plume (with lower or undetectable NO_3), particularly near the river mouth (Yin et al. 1995a). In comparison, the observations during May 31 – June 7, 1988 showed that NO_3 increased seaward at the surface along the transect at the beginning of the cruise. A subsurface NO_3 minimum in the water column appeared at the end of the cruise. More importantly, NO_3 concentrations were high (close to $15 \mu\text{M}$) at stations Sd, Se, and Sf away from the river mouth on May 31 (Yin 1994). Phytoplankton biomass and production during this cruise were comparable with the spring bloom of 1991 (Yin et al. 1996). Silicate concentrations also decreased over time, especially at stations S3 and Sf (Yin 1994). A minimum in the silicate concentration occurred at an intermediate depth (ca. 6 m), and its position coincided with the fluorescence maximum (Yin 1994). This indicates that the developing 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 are closely followed by *S. costatum* (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 4). Therefore, the seaward increase of NO_3 concentration, high NO_3 concentrations at the beginning of the cruise, the appearance of the subsurface minimum of NO_3 , and species composition suggested a delayed spring bloom. The question now is why the spring bloom would be delayed.

An examination of the river discharge and wind speeds in

Fig. 9. (A) Fraser River discharge and (B) wind speed for 1988. The circles indicate the cruise period, June 1–7.



1988 (Fig. 9) 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 not start until late April and early May. However, it is known that the recruitment of copepodite stages of *N. plumchrus* from the deep water to the

Fig. 10. Vertical profiles of salinity along the transect from the river mouth (S2) across to the other side of the strait (Sf) (see Fig. 3) during June 1–7, 1988.

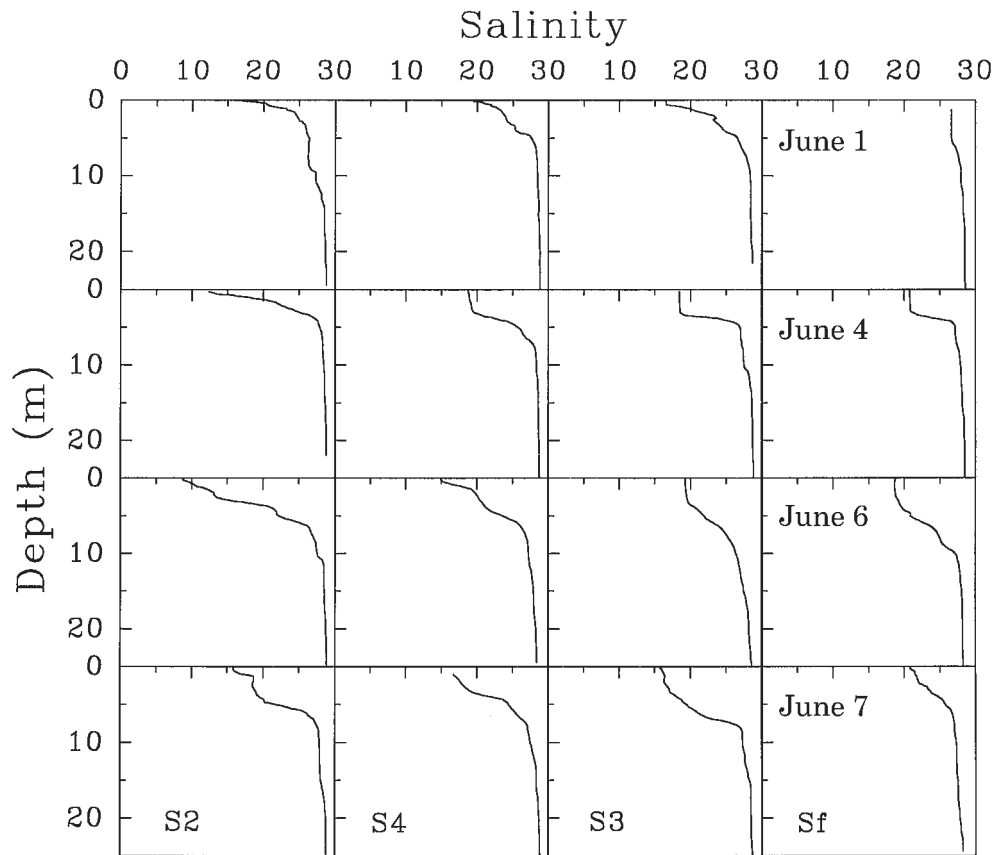


Table 3. Mean integrated chl *a* and primary production (PP) at four stations during May 31 – June 9, 1988.

Station	Chl <i>a</i> (mg·m ⁻²)	PP (mg C·m ⁻² ·day ⁻¹)
S2 (<i>n</i> = 4)	43.5 (30.4–56.1)	1190 (150–2770)
S3 (<i>n</i> = 4)	58.7 (12.6–101)	1830 (843–2540)
S4 (<i>n</i> = 1)	67.1	2540
Sf (<i>n</i> = 4)	47.7 (26.2–72.8)	2990 (1240–5000)

Note: The values are depth integrated and then averaged over *n* days. Ranges are given in parentheses.

surface reaches a peak during February and March with the peak in grazing in April (Fulton 1973). It was likely that grazing by this abundant copepod had suppressed the early development of the spring bloom during this period, as shown in the conceptual model (Fig. 2C). The full development of the spring bloom could not occur until the grazing pressure on phytoplankton was relieved. The low abundance of *N. plum-chrus* in the upper 10-m water layer during the time series at S4 (Yin 1994) suggests that this species had descended to deeper waters. Low ammonium concentrations (<1 μM) during the entire cruise, and even lower than 0.5 μM at the end of the cruise (compared with the other cruises), also supported the idea that grazer abundance was not great enough to suppress this bloom. Winds (mostly below 4 m·s⁻¹) from mid-April to the end of May 1988 were not strong enough to increase NO₃ to the high concentrations observed at several stations, such as Sf on June 1. In addition, there was a neap

tide at the beginning of the cruise, indicating minimal tidal mixing. In a recent study, the spring diatom bloom was not observed in the northern Strait of Georgia, possibly because of strong winds (Haigh and Taylor 1991). The evidence presented above suggested that the bloom in early June 1988 was a delayed spring bloom, although it is not possible to rule out that this bloom was a secondary bloom.

Temporal variability

Two previous studies have examined the occurrence of the spring bloom in the Strait of Georgia (Parsons et al. 1969a; Stockner et al. 1979). However, in both studies, monthly sampling was used. When daily sampling and continuous vertical profiles of nutrients and chl *a* were used in our study, it showed just how dynamic the system is in the strait. Daily or at least biweekly measurements of nutrients, chl *a*, and zooplankton are needed to determine their response to tides, winds, and river discharge. The development of a moored underwater fluorometer should give us the temporal resolution over the February to June time period to better characterize the development and decline of the spring bloom in the future.

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 chain. One example is the delayed spring bloom in the waters of

Fig. 11. Vertical profiles of fluorescence (solid line) and NO₃ (broken line) along the transect from the river mouth (S2) across to the other side of the strait (Sf) (see Fig. 3) during June 1–7, 1988.

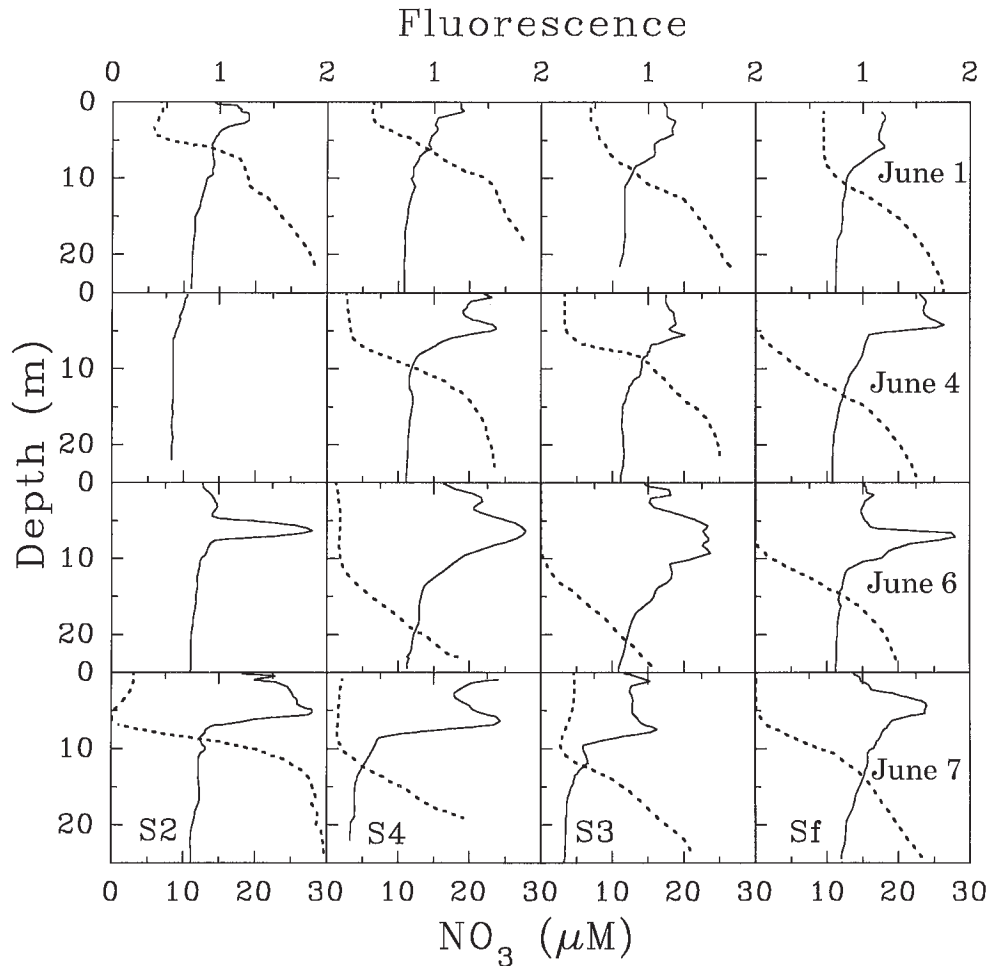


Table 4. Mean abundance and relative biovolume (% of total phytoplankton biovolume) of major phytoplankton genera, *Skeletonema costatum*, *Thalassiosira* spp., and *Chaetoceros* spp., at the surface or at a depth of 1–2 m at four stations (see Fig. 3) during May 31 – June 9, 1988.

		<i>Thalassiosira</i> spp.	<i>Chaetoceros</i> spp.	<i>S. costatum</i>
S2 (n = 5)*	Abundance (10 ³ cells·L ⁻¹)	33	130	160
	Relative biovolume (%)	74	9	7
S4 (n = 2)	Abundance (10 ³ cells·L ⁻¹)	220	530	67
	Relative biovolume (%)	78	15	1
S3 (n = 2)	Abundance (10 ³ cells·L ⁻¹)	220	740	310
	Relative biovolume (%)	81	9	3
Sf (n = 4)	Abundance (10 ³ cells·L ⁻¹)	260	600	750
	Relative biovolume (%)	72	9	7

*n, number of days that were averaged.

western Europe in the 1970s because of much stronger northerly winds in the springtime in the 1970s than in the 1950s (Dickson et al. 1988). The delayed spring bloom resulted in a decline in phytoplankton and zooplankton biomass.

In the Strait of Georgia, the zooplankton community, which is dominated by copepods in the spring, plays an important role in the food chain. These zooplankton include *N. plumchrus* (Fulton 1973), *Pseudocalanus* spp., *Calanus marshallae*,

C. pacificus, and *Metridia pacifica* (LeBrasseur et al. 1969). Of these species, the *N. plumchrus* population has the highest biomass (Harrison et al. 1983), which is supported by the 1991 (Yin et al. 1996) and 1993 data. As the conceptual model shows (Fig. 2C), when the spring bloom is at an early stage, grazing pressure from migrating zooplankton will hinder the development of the spring bloom. A windy spring would extend the duration of spring bloom, and this effect could be

cascaded to juvenile fish, including juvenile salmon entering the strait during this period, and affect the return of adults in later years.

The interaction of zooplankton and winds in the spring has a great impact on juvenile fish. Larval fish of most species in the strait start feeding from spring to early summer. Each species is thought to have its own entry time "window" for food. For example, herring start spawning in the strait during March, and the juvenile herring remain in the Strait of Georgia until autumn (Ketchen et al. 1983). Newly hatched larvae of lingcod (*Ophiodon elongatus*) 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 salmon (*Oncorhynchus nerka*) appeared to grow significantly during their residence time in the strait (Healey 1978). Their diet was found to include copepods in the early larval fish stage (Parsons et al. 1969b), although Healey (1978) favored more epibenthic and neritic species. In the Gulf of St. Lawrence, most fish species have a relatively fixed spawning period (Ware 1975), and larval fish abundance was shown to be positively correlated to mesozooplankton biomass in Baie-des-Chaleurs (de Lafontaine et al. 1991). There have been few studies on the relationship between zooplankton as food and juvenile fish in the strait. However, the coincidence of the period of these feeding windows with the spring bloom and the annual Fraser River freshet (June–July) suggests that timing of the spring bloom development must be a significant factor 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.

Acknowledgements

We would like to thank Peter Clifford, who conducted ¹⁴C uptake experiments and other measurements. Thanks are extended to the Department of Fisheries and Oceans for providing ship time, and the officers and crew of C.S.S. *Vector* for their assistance. Comments by Dr. James Cloern were helpful. Xiaodan Liu enumerated zooplankton samples for the 1993 cruise. This research was funded by a Natural Sciences and Engineering Research Council of Canada strategic grant. The Research Fellowship to support K.Y. was kindly provided by the Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., Canada.

References

- Clifford, P.J., Harrison, P.J., Yin, K., St. John, M.A., Goldblatt, R., and Varela, D. 1992. Plankton production and nutrient dynamics in the Fraser River plume, 1991. Manuscr. Rep. No. 59. Department of Oceanography, University of British Columbia, Vancouver.
- Cloern, J.E. 1991. Annual variations in river flow and primary production in south San Francisco Bay estuary (USA). In *Estuaries and Coasts: Spatial and Temporal Intercomparisons*. Proceedings of the 19th Symposium of the Estuarine and Coastal Sciences Association, Sept. 4–8, 1989, University of Caen, France. Edited by M. Elliott and J.-P. Ducrottoy. Olsen & Olsen, Fredensborg, Denmark. pp. 91–96.
- de Lafontaine, Y., Demers, S., and Runge, J. 1991. Pelagic food web interactions and productivity in the Gulf of St. Lawrence: a perspective. In *The Gulf of St. Lawrence: small ocean or big estuary?* Edited by J.-C. Therriault. Can. Spec. Publ. Fish. Aquat. Sci. No. 113. pp. 99–123.
- Dickson, R.R., Kelly, P.M., Colebrook, J.M., Wooster, W.S., and Cushing, D.H. 1988. North winds and production in the eastern North Atlantic. *J. Plankton Res.* **10**: 151–169.
- Erga, S.R., and Heimdal, B.R. 1984. Ecological studies on the phytoplankton of Korsfjorden, western Norway. The dynamics of a spring bloom seen in relation to hydrographical conditions and light regime. *J. Plankton Res.* **6**: 67–90.
- Fulton, J.D. 1973. Some aspects of the life history of *Calanus plumchirus* in the Strait of Georgia. *J. Fish. Res. Board Can.* **30**: 811–815.
- Haigh, R., and Taylor, F.J.R. 1991. Mosaicism of microplankton communities in the northern Strait of Georgia, British Columbia. *Mar. Biol.* **110**: 301–314.
- Harrison, P.J., Fulton, J.D., Taylor, F.J.R., and Parsons, T.R. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. *Can. J. Fish. Aquat. Sci.* **40**: 1064–1094.
- Harrison, P.J., Clifford, P.J., Cochlan, W.P., Yin, K., St. John, M.A., Thompson, P.A., Sibbald, M.J., and Albright, L.J. 1991. Nutrient and phytoplankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia. *Mar. Ecol. Prog. Ser.* **70**: 291–304.
- Healey, M.C. 1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. *Fish. Mar. Serv. Tech. Rep. No.* 788.
- Jones, D.M., Harrison, P.J., Clifford, P.J., Yin, K., and St. John, M.A. 1991. A computer-based system for the acquisition and display of continuous vertical profiles of temperature, salinity, fluorescence and nutrients. *Water Res.* **25**: 1545–1548.
- Ketchen, K.S., Bourne, N., and Butler, T.H. 1983. History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia. *Can. J. Fish. Aquat. Sci.* **40**: 1095–1119.
- LeBlond, P.H. 1983. The Strait of Georgia: functional anatomy of a coastal sea. *Can. J. Fish. Aquat. Sci.* **40**: 1033–1063.
- LeBrasseur, R.J., Barraclough, W.E., Kennedy, O.D., and Parsons, T.R. 1969. Production studies in the Strait of Georgia. Part III. Observations on the food of larval and juvenile fish in the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 51–61.
- Legendre, L., Demers, S., and Lefavre, D. 1988. Biological production at marine ergoclines. In *Marine Interfaces Ecohydrodynamics*. Proceedings of the 17th International Liege Colloquium on Ocean Hydrodynamics, University of Liege. Edited by J.C.J. Nihoul. Elsevier Oceanogr. Ser. No. 42. pp. 1–29.
- Malone, T.C., Crocker, L.H., Pike, S.E., and Wendler, B.W. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Mar. Ecol. Prog. Ser.* **48**: 235–249.
- Mann, K.H. 1993. Physical oceanography, food chains, and fish stocks: a review. *ICES J. Mar. Sci.* **50**: 105–119.
- Parsons, T.R., Stephens, K. and LeBrasseur, R.J. 1969a. Production studies in the Strait of Georgia. Part I. Primary production under the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 27–38.
- Parsons, T.R., LeBrasseur, R.J., Fulton, J.D., and Kennedy, O.D. 1969b. Production studies in the Strait of Georgia. Part II. Secondary production under the Fraser River plume, February to May, 1967. *J. Exp. Mar. Biol. Ecol.* **3**: 39–50.
- Parsons, T.R., LeBrasseur, R.J., and Barraclough, W.E. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: a review. *J. Fish. Res. Board Can.* **27**: 1251–1264.
- Philips, A.C., and Barraclough, W.E. 1977. On the early life history of the lingcod (*Ophiodon elongatus*). *Fish. Mar. Serv. Res. Dev. Tech. Rep. No.* 756.
- Slawyk, G., and MacIsaac, J.J. 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. *Deep-Sea Res.* **19**: 521–524.

- Sournia, A., Birrien, J.-L., Douvillé, J.-L., Klein, B., and Viollier, M. 1987. A daily study of the diatom spring bloom at Roscoff (France) in 1985. I. The spring bloom with the annual cycle. *Estuarine Coastal Shelf Sci.* **25**: 355–367.
- Stephens, K., Fulton, J.D., and Kennedy, O.D. 1969. Summary of biological oceanographic observations in the Strait of Georgia, 1965–1968. Tech. Rep. Fish. Res. Board Can. No. 110.
- St. John, M.A., Marinone, S.G., Stronach, J., Harrison, P.J., Fyfe, J., and Beamish, R.J. 1993. A horizontal resolving physical–biological model of nitrate fluxes and primary productivity in the Strait of Georgia. *Can. J. Fish. Aquat. Sci.* **50**: 1456–1466.
- Stockner, J.G., Cliff, D.D., and Shortreed, K.R.S. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. *J. Fish. Res. Board Can.* **36**: 657–666.
- Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. *J. Fish. Res. Board Can.* **32**: 2503–2512.
- Wood, E.D., Armstrong, F.A.J., and Richards, F.A. 1967. Determination of nitrate in seawater by cadmium–copper reduction to nitrite. *J. Mar. Biol. Assoc. U.K.* **47**: 23–31.
- Yin, K. 1994. Dynamics of nutrients and phytoplankton production in the Strait of Georgia estuary, British Columbia, Canada. Ph.D. thesis, University of British Columbia, Vancouver.
- Yin, K., Harrison, P.J., Pond, S., and Beamish, R.J. 1995a. Entrainment of nitrate in the Fraser River plume and its biological implications. I. Effects of salt wedge. *Estuarine Coastal Shelf Sci.* **40**: 505–528.
- Yin, K., Harrison, P.J., Pond, S., and Beamish, R.J. 1995b. Entrainment of nitrate in the Fraser River plume and its biological implications. II. Effects of spring vs. neap tides and river discharge. *Estuarine Coastal Shelf Sci.* **40**: 529–544.
- Yin, K., Harrison, P.J., Goldblatt, R.H., and Beamish, R.J. 1996. Spring bloom in the central Strait of Georgia: interactions of river discharge, winds and grazing. *Mar. Ecol. Prog. Ser.* **138**: 255–263.