

Nutrient and plankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia

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ABSTRACT: High discharge rates from the Fraser River create a riverine plume front that moves daily and fortnightly with the tides in the Strait of Georgia. During a spring-neap tidal cycle in July 1987, a study of nutrient and plankton dynamics including vertical profiles of temperature, salinity, fluorescence, nutrients (NO_3 , NH_4 , PO_4 , SiO_4 and urea), zooplankton, phytoplankton and bacterial biomass and primary and heterotrophic productivities was conducted at 3 stations, one situated in the riverine plume and two at the inner and outer estuarine plume. Primary productivity was highest in the outer part of the estuarine plume and lowest in the riverine plume. Bottom to surface daytime vertical zooplankton hauls revealed no differences in species composition among the 3 stations, but euphausiids were significantly more abundant in the estuarine plume, where phytoplankton abundance was also the highest. During post-neap tides, nitrate was undetectable, a subsurface chlorophyll maximum was present and productivity was high in the estuarine plume. During the post-spring tidal period, nutrient concentrations were elevated, maximum chlorophyll concentrations occurred near the surface and primary productivity increased approaching neap tides. Utilizable nitrogen sources ($\text{NO}_3 + \text{NH}_4 + \text{urea}$) and phosphate concentrations in the river were similar to concentrations in the riverine plume, while silicate was significantly higher in the river. Therefore, in late July, nutrient enrichment of the surface waters of the plume, resulting in high primary productivity at the plume boundaries and beyond, appears to be mainly due to entrainment as the freshwater moves over the seawater.

INTRODUCTION

Large rivers can have a significant impact on biological processes in the coastal zone (Meybeck 1982). These rivers may carry nutrients and pollutants and consequently may influence large areas of the coast when a riverine plume is formed.

The Fraser River empties into the southern portion of the Strait of Georgia, a partially enclosed basin on the west coast of Canada, lying between the mainland of British Columbia and the southern half of Vancouver Island (Fig. 1). The circulation and stratification of the southern portion of the Strait are strongly affected by the large freshwater discharge (up to $8 \times 10^3 \text{ m}^3 \text{ s}^{-1}$) of the Fraser River, particularly during the May to July freshet period (Stronach 1981, Crean et al. 1988). Tides are mixed semi-diurnal with a maximum daily range of 5 m.

There are 2 plumes formed by the Fraser River. The riverine plume is the plume formed daily by the river flowing into the Strait. A small riverine plume (salinity

0 to 10 ‰) is formed during neap tides and it expands daily until the largest riverine plume is reached during spring tides. During the next 7 d transition from spring to neap tides, the size of the riverine plume decreases. The extent of the plume varies primarily with the damping effect of the tides, but is also influenced by winds. The estuarine plume (salinity 10 to 15 ‰) is defined as remnants of previous riverine plumes, which are being transported by the residual circulation of the Strait of Georgia as well as wind. The estuarine plume contains enhanced nutrient concentrations due to entrainment of nutrients at the toe of the salt wedge (R. Kostaschuk pers. comm.), as well as deepwater entrainment along the bottom of the freshwater lens.

Early studies of the plankton dynamics of the Fraser River plume revealed that phytoplankton bloomed at the edge of the plume and zooplankton were displaced further seaward (Parsons et al. 1969a, b). The latter study was conducted from February to May with twice-monthly sampling. More recent studies on phytoplankton production, abundance and distribution by Stock-

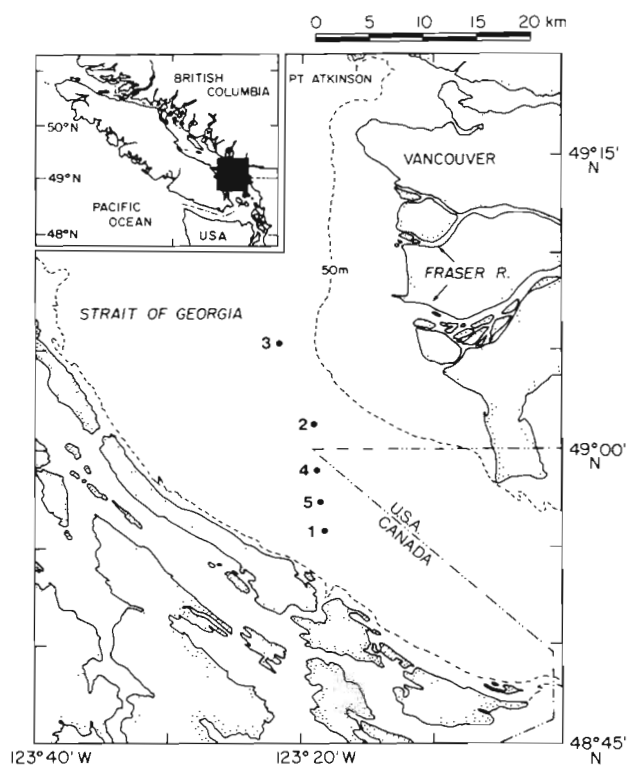


Fig. 1. Study area showing the Fraser River plume in the southern portion of the Strait of Georgia and the 3 main stations (Stn 1 = outer part of the estuarine plume, Stn 2 = inner estuarine plume and Stn 3 = riverine plume). Stns 4 and 5 are additional zooplankton sampling stations. Inset shows study area in relation to the southern coastline of British Columbia

ner et al. (1979) over a 2 yr period with monthly sampling (except during winter) revealed that the plume boundaries were very productive (> 4 to $5 \text{ g C m}^{-2} \text{ d}^{-1}$). Despite these studies (see review by Harrison et al. 1983), our understanding of the nutrient and plankton dynamics of the Fraser River plume remains poor (Parsons et al. 1980, Stockner et al. 1980), partially because of the inappropriate temporal sampling scales (monthly or twice-monthly) used to study such a dynamic system. To date there have been no systematic studies on the daily changes in nutrients and plankton in the Fraser River plume.

The objective of this study was to examine the nutrient and plankton dynamics in the Fraser River plume, and to focus particularly on the plume boundary, the most productive area. One of the key questions we address is whether the main source of nutrient enrichment for this area is river input or entrainment. We conducted an intensive daily sampling program over an 11 d study period (spring-neap tidal cycle) in which nutrients, bacteria, microflagellates, phytoplankton, zooplankton and rate processes such as heterotrophic and primary production were measured. The results of

^{15}N uptake experiments and the proportion of primary production derived from new nitrogen (nitrate) vs recycled nitrogen (ammonium and urea) are reported elsewhere (Cochlan unpubl.).

MATERIALS AND METHODS

Sampling. The cruise was conducted from 20 to 31 July 1987 off the mouth of the Fraser River in the Strait of Georgia, British Columbia, Canada (Fig. 1). A more detailed account of sampling methods and analyses is given in Clifford et al. (1989). At the beginning of the cruise, continuous horizontal mapping of surface temperature and salinity (InterOcean 514A CSTD), in vivo fluorescence (Turner model 111 fluorometer) and nitrate plus nitrite (Technicon AutoAnalyzer®) was carried out on board using seawater pumped from ca 1.0 m. These underway measurements aided in the selection of 3 major sampling stations (Fig. 1) and the determination of the plume boundaries.

At each of the 3 stations, continuous vertical profiles (0 to ca 20 m) of temperature, salinity, fluorescence, and selected nutrients were obtained 3 or 4 times during the 11 d cruise. A darkened hose (1.5 cm ID) was fixed to an InterOcean CSTD probe, and as the probe was lowered (ca 1 m min^{-1}), water was pumped to the deck of the research vessel with an mRoy FR162-144 diaphragm pump (flow rate ca 1 l min^{-1}). Water from the vertical profiles was continuously pumped through a fluorometer and the AutoAnalyzer® to determine in vivo fluorescence, nitrate plus nitrite, and silicate concentrations. These data were logged onto a computer and plotted in real-time. On one occasion, bottle casts were conducted at 2 stations (A and B) in the river to obtain samples for nutrient profiles.

Usually after each vertical profile, water samples were collected from 6 depths selected on the basis of light penetration (usually 100, 55, 30, 10, 3 and 1 % of surface irradiance [I_0]), using 5 l PVC Niskin bottles equipped with silicone rubber springs to eliminate toxicity from amber rubber tubing (Price et al. 1986). Subsamples were taken for the measurements described below and experiments were initiated within 1 h of collection.

Nutrients. Subsamples were removed with an acid-washed syringe and gently filtered through combusted (460°C for 4 h) Whatman GF/F filters (mounted in 25 mm Millipore Swinex® filter holders) into acid-washed polyethylene bottles. All nutrients were determined using a Technicon AutoAnalyzer® II. Nitrate plus nitrite, ammonium and silicate samples were analyzed immediately on board ship, while phosphate and urea were stored frozen (-20°C) until analysis ashore. Nitrate plus nitrite and ammonium were deter-

mined following the procedures of Wood et al. (1967) and Slawyk & MacIsaac (1972), respectively. Urea was determined by the diacetyl monoxime thiosemicarbazide technique described by Price & Harrison (1987). Silicate was determined following Armstrong et al. (1967), and phosphate according to Hager et al. (1968).

Chlorophyll, particulate organic carbon and nitrogen. Samples for chlorophyll *a* (chl *a*), normally 500 ml, were filtered onto Whatman GF/F filters and stored frozen in a desiccator and analyzed ashore. Chl *a* was extracted for 24 h in 90 % acetone and analyzed by *in vitro* fluorometry (Parsons et al. 1984). 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 1106 elemental analyzer, using the dry combustion method (Sharp 1974).

Samples for dissolved carbon were stored frozen until processing, when they were defrosted at room temperature. Total dissolved carbon and dissolved inorganic carbon were measured using a Beckman Tocamaster model 915-B. Dissolved organic carbon (DOC) was calculated as the difference between the 2 measurements.

³H-thymidine uptake by bacteria. Bacterial production assays followed Fuhrman & Azam (1980, 1982). Duplicate killed (3.7 % formaldehyde, final concentration) and active 10 ml samples were placed in 30 ml syringes and 15 nM ³H-thymidine (methyl-³H-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 addition of 10 ml ice-cold 10 % trichloroacetic acid (TCA) and samples filtered through 0.22 µm Millipore filters. Each filter was washed twice with 5 ml ice-cold TCA and placed in a scintillation vial. The filter was dissolved by adding 1 ml ethyl acetate, and then 10 ml scintillation fluor was added to each vial. Samples were counted using a Beckman LS3801 liquid scintillation counter, and quench correction was by the channels-ratio method. The factor used to convert the rate of thymidine uptake to bacterial production was 1.2×10^{18} (Fuhrman & Azam 1982).

¹⁴C uptake. Carbon uptake rates were measured by adding 2.0 µCi NaH¹⁴CO₃ to duplicate samples in borosilicate glass bottles. After thorough mixing, the bottles were incubated for ca 4 h (generally 11:00 to 15:00 h Pacific Daylight Time, PDT) in simulated *in situ* deck incubators corresponding to the light levels from which the samples were taken (achieved with different layers of neutral density screening). Samples from >10 % light depth were cooled with flowing surface seawater, while samples <10 % light depth were incu-

bated at a temperature similar to the *in situ* temperature of their depth of collection. Incubations were terminated by filtration (<100 mm Hg) onto Whatman GF/F glass-fibre filters. Filters were placed into scintillation vials containing 0.2 ml of 0.5 N HCl, which removed inorganic ¹⁴C. After 2 h, 10 ml Aquasol II scintillation fluor was added to each vial. Hourly productivity rates were converted to daily rates by dividing the total 4 h carbon uptake by the percentage that the incubation period represented of the daily irradiance (05:30 to 22:00 h). Zero time blanks were used to correct for cell and bottle adsorption of ¹⁴C. Samples were counted on an Isocap 300 liquid scintillation counter and quench correction was by the channels-ratio method. Carbon uptake rates were determined according to Parsons et al. (1984).

Bacterial counts. Water samples were preserved with 1 % formaldehyde (final concentration) at the time of sampling. Immediately prior to assay in the lab, each sample was treated with 0.001 M Na₄P₂O₇ for 30 min and then sonicated at 100 W for 30 s. This procedure facilitates detachment of bacteria from particulates and results in a random distribution of bacteria in the sample (Velji & Albright 1986). After staining with DAPI, the samples were filtered (<100 mm Hg) onto 0.2 µm Nuclepore membrane filters and the bacteria were counted using epifluorescent microscopy (Porter & Feig 1980). Calculated biovolumes (based on mean length and width of cells) were converted to bacterial carbon values as described by Vald   & Albright (1981).

Microflagellate counts. Five ml samples (preserved as described for bacteria) were filtered (<100 mm Hg) onto 2 µm Nuclepore filters which were prestained with Iragalan black, and the microflagellates (<10 µm) were stained with DAPI. The filters were examined using an epifluorescent microscope. Cells containing chlorophyll were identified as autotrophic eucaryotic microflagellates, and emitted blue fluorescence with Zeiss filter set 48 77 01 (BP 365/10, FT310 and LP395) or orange fluorescence when filter set 48 77 09 (BP 450–490, FT 510 and LP 520) was used (Sherr & Sherr 1983). Heterotrophic microflagellates fluoresced blue (filter set 48 77 01 [BP 365/10 and LP395]), but had no autofluorescence due to their lack of chlorophyll. Total microflagellate numbers were calculated as the sum of autotrophic and heterotrophic microflagellates.

Phytoplankton counts. Samples (200 ml) for phytoplankton species analysis were preserved in Lugol's solution (Parsons et al. 1984) and stored in the dark until analysis. Ten ml subsamples were settled (24 h) and counted on an inverted microscope following Uterm  hl (1958). Cell volumes were determined by measuring the dimensions of at least 10 cells and then using simple geometric shapes to represent the species.

Zooplankton counts. Triplicate zooplankton samples

were obtained at stations representing the riverine plume and the inner and outer estuarine plume (Stns 3, 2 and 1, respectively). Day or night vertical hauls were made with a 303 μm mesh SCOR net (60 cm dia.) from the 1 % light depth to the surface, and from the bottom to the surface at a towing speed of ca 1 m s^{-1} . In addition, samples were taken from the bottom to surface at 2 stations (Stns 4 and 5), intermediate between the inner and outer estuarine plume stations. Samples were preserved in 4 % buffered formalin following the techniques described by Parsons et al. (1984).

Samples were then enumerated for the groups Amphipoda, Euphausiia, Chaetognatha, Hydromedusae, Copepoda and larval fish. Where possible the entire sample was enumerated for these groups but when densities were prohibitive, subsampling was performed following Griffiths et al. (1984) and a minimum of 100 individuals of each group were counted. The first 100 copepods in each sample were identified to species (Gardner & Szabo 1982) with a dissecting microscope.

In order to compare the densities of the populations between stations, means of the populations were compared using a Student's *t*-test at a level of significance of 0.05 (Sokal & Rohlf 1981). If the equality of variance assumption was violated, data was transformed and the *F*-test again performed. If the equality of variance assumption was still violated, the non-parametric Mann-Whitney *U* test was performed on the transformed data set. Utilization of the Mann-Whitney *U* test on a heteroscedastic data set may result in a type II error (Sokal & Rohlf 1981).

RESULTS

Horizontal transects and tides

Horizontal mapping was used to determine the extent and boundaries of the riverine and estuarine plumes and as an aid in selecting 3 main stations; the riverine plume (Stn 3) and the inner and outer estuarine plume (Stns 2 and 1, respectively; Fig. 1). Moving from the riverine plume to the estuarine plume during a horizontal transect resulted in a slight decrease in temperature, but a marked increase in salinity (Fig. 2). Pronounced oscillations in salinity during the horizontal transect occurred in the vicinity of the plume boundary, probably due to internal waves (see arrows in Fig. 2). On several other occasions the crest of the internal waves could be seen clearly at the surface from the bridge of the ship. The wavelength of the salinity oscillations ranged from 0.25 to 1.0 km, estimated from visual observations when the internal waves reached the sea surface and from the horizontal profile of salinity (Fig. 2).

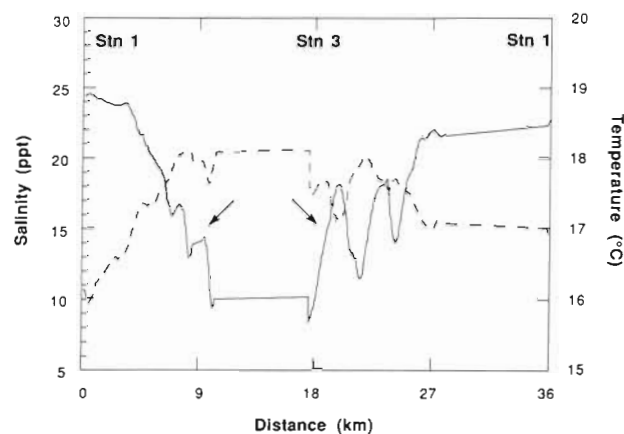


Fig. 2. Horizontal profile of temperature (— — —) and salinity (—) for the transect starting at Stn 1 (outer estuarine plume), proceeding into the plume (Stn 3) and then returning to Stn 1. Seawater was collected from a depth of 1 m through a fitting in the ship's hull. Arrows indicate pronounced oscillations in salinity, probably due to internal waves at the riverine plume boundary (Stn 2)

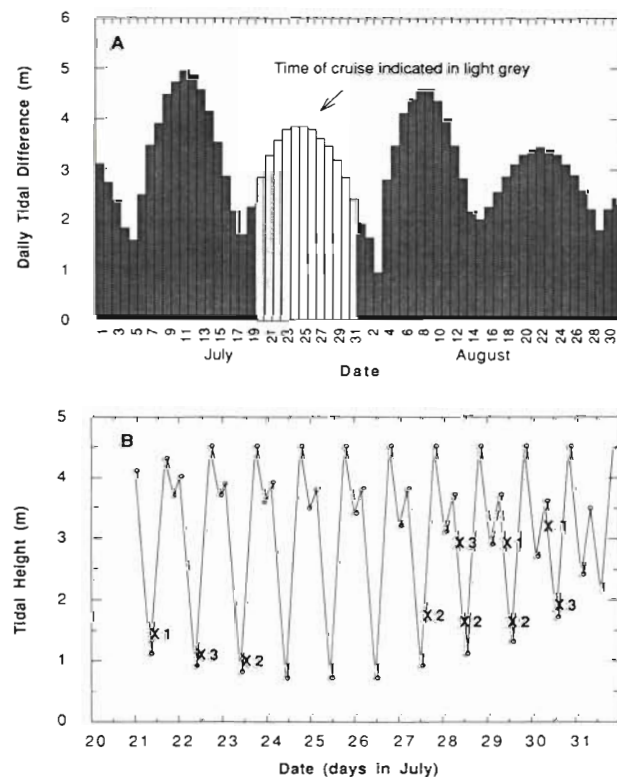


Fig. 3. (A) Maximum daily tidal difference at Point Atkinson for July and August 1987, with the time of the cruise indicated in light grey. (B) Tidal height during the study period, showing the mixed semi-diurnal nature of the tides. The times of the primary productivity stations at Stns 1, 2 and 3 (X1, X2, X3) in relation to the tidal cycle are indicated

The maximum daily difference in the tidal height is shown in Fig. 3A for the cruise period and when the primary productivity stations were conducted (Fig. 3B). The daily difference in tidal height is mainly due to the

difference in the height of the low tide between spring and neap tides. The study began 2 d after the neap tide and ended 3 d before the next neap tide. The study period has been divided into 2 periods, post-neap and post-spring, for the periods before and after 24 July, respectively. The difference in the tidal height between neap and spring tides for the study period was about 2 m, which was less than the spring-neap cycle before or after it (Fig. 3A).

Nutrients and hydrographic features

Stn 3 is representative of the riverine plume, which was strongly influenced by the river discharge. During the post-neap period, salinity increased rapidly down to 3 m, while the temperature decreased slowly with depth (Fig. 4). During the post-spring period, the increase in salinity occurred more abruptly in steps and the pycnocline was deeper (6.5 m) in the mid-portion of the post-spring period. The surface temperature was higher in the post-spring period. Nitrate in the top 5 m ranged from 1 to 4 μM during the post-neap period,

while during the post-spring it reached a minimum at 3 to 4 m, near the bottom of the plume. Vertical profiles of ammonium and urea generally showed higher concentrations of these nutrients in the surface layer of the riverine plume (0 to 2 m; Table 1, Fig. 4) than in the river water (Table 2). Nitrate and phosphate were similar in the river and riverine plume. However, silicate was higher in the river than at Stn 3, indicating that the river was the source of the high silicate concentrations observed at Stn 3.

Stn 2 represents the inner boundary of the estuarine plume. Due to the dynamic nature of the plume, parameters at Stn 2 fluctuated considerably because the riverine plume moved back and forth across this station. Therefore, on some occasions, Stn 2 was within the outer edge of the riverine plume, and at other times in the inner portion of the estuarine plume and thus similar to Stn 1.

The post-neap period was sampled once and the post-spring period was sampled 3 times on consecutive days at Stn 2 (only 2 d are shown in Fig. 5). During the post-neap period, there was no pronounced pycnocline. During the post-spring sampling sequence, steep

Table 1. Means \pm 1 SD in temperature (T), salinity (S), nutrients, and chl *a* for the post-neap and post-spring portions of a spring-neap tidal cycle at 3 stations (Stns 1 and 2 = outer and inner estuarine plume and Stn 3 = riverine plume) in the Fraser River plume. A dash means no measurements were taken. ND: not detectable

Stn	Tidal cycle	Depth (m)	T (°C)	S (‰)	NO ₃	NH ₄	Urea ($\mu\text{g-at. l}^{-1}$)	PO ₄	SiO ₄	Chl <i>a</i> (mg m^{-3})	n
1	Post-neap	0–1	17.2 \pm 0.3	22.6 \pm 0.9	ND	–	–	–	–	0.43 \pm 0.11	2
	Post-spring	0–1.5	15.8 \pm 0.7	23.2 \pm 0.5	1.2 \pm 1.6	0.07 \pm 0.06	0.43 \pm 0.13	0.36 \pm 0.10	8.6 \pm 5.8	0.97 \pm 0.40	4
2	Post-neap	0–1	17.4 \pm 1.3	23.3 \pm 1.3	ND	–	–	–	–	1.37	2
	Post-spring	0–1	18.5 \pm 0.7	10.7 \pm 2.8	2.3 \pm 0.2	0.55 \pm 0.24	1.39 \pm 1.02	0.56 \pm 0.20	42.4 \pm 4.5	0.63 \pm 0.28	6
3	Post-neap	0–1	16.1 \pm 0.6	14.5 \pm 2.4	2.9 \pm 1.1	–	–	–	–	1.55	2
	Post-spring	0–1	18.7 \pm 0.7	13.8 \pm 2.8	1.8 \pm 0.9	0.54 \pm 0.30	1.43 \pm 1.03	0.43 \pm 0.15	38.1 \pm 14.3	0.30 \pm 0.03	4

Table 2. Nutrient concentrations ($\mu\text{g-at. l}^{-1}$) at: (A) ca 100 m (Stn A), and (B) ca 1 km (Stn B) downstream of the discharge pipe of the Annacis Island sewage treatment plant located 5 km upstream from the mouth of the south arm of the Fraser River. Salinity was constant (< 1 ‰) with depth at each station

Stn	Depth (m)	NO ₃	NH ₄	Urea	PO ₄	SiO ₄
A	0	2.33	0.18	0.69	0.45	63.7
	2	2.25	0.14	0.60	0.61	64.0
	4	2.25	0.11	0.71	0.71	63.8
	6	2.25	0.12	0.74	0.88	64.5
	8	2.17	0.16	0.71	0.45	63.8
	10	2.17	0.13	0.77	0.95	64.4
B	0	2.17	0.03	0.71	0.48	64.6
	5	2.17	0.04	0.80	0.48	64.2
	10	2.17	0.10	0.82	0.48	64.5

temperature and salinity gradients occurred down to 3 m, indicating that the riverine plume was covering this station (Fig. 5). Surface salinities decreased from 24 ‰ during post-neap to < 10 ‰ during post-spring conditions. Water temperatures in the top meter were higher (and similar to the temperature of the river) in the post-spring period than during post-neap conditions. Nitrate was undetectable down to 6.5 m during post-neap conditions, but generally > 2 μM in the surface waters during the post-spring cycle. Silicate was always high (> 40 μM) in surface waters, and reached a minimum at 3 m (the bottom of the riverine plume) and then increased with depth. Urea, phosphate and ammonium were also higher in the surface water than at the bottom of the plume (about 3 m).

At the outer portion of the estuarine plume at Stn 1, the bottom of the pycnocline occurred deeper during

← POST-NEAP POST-SPRING →

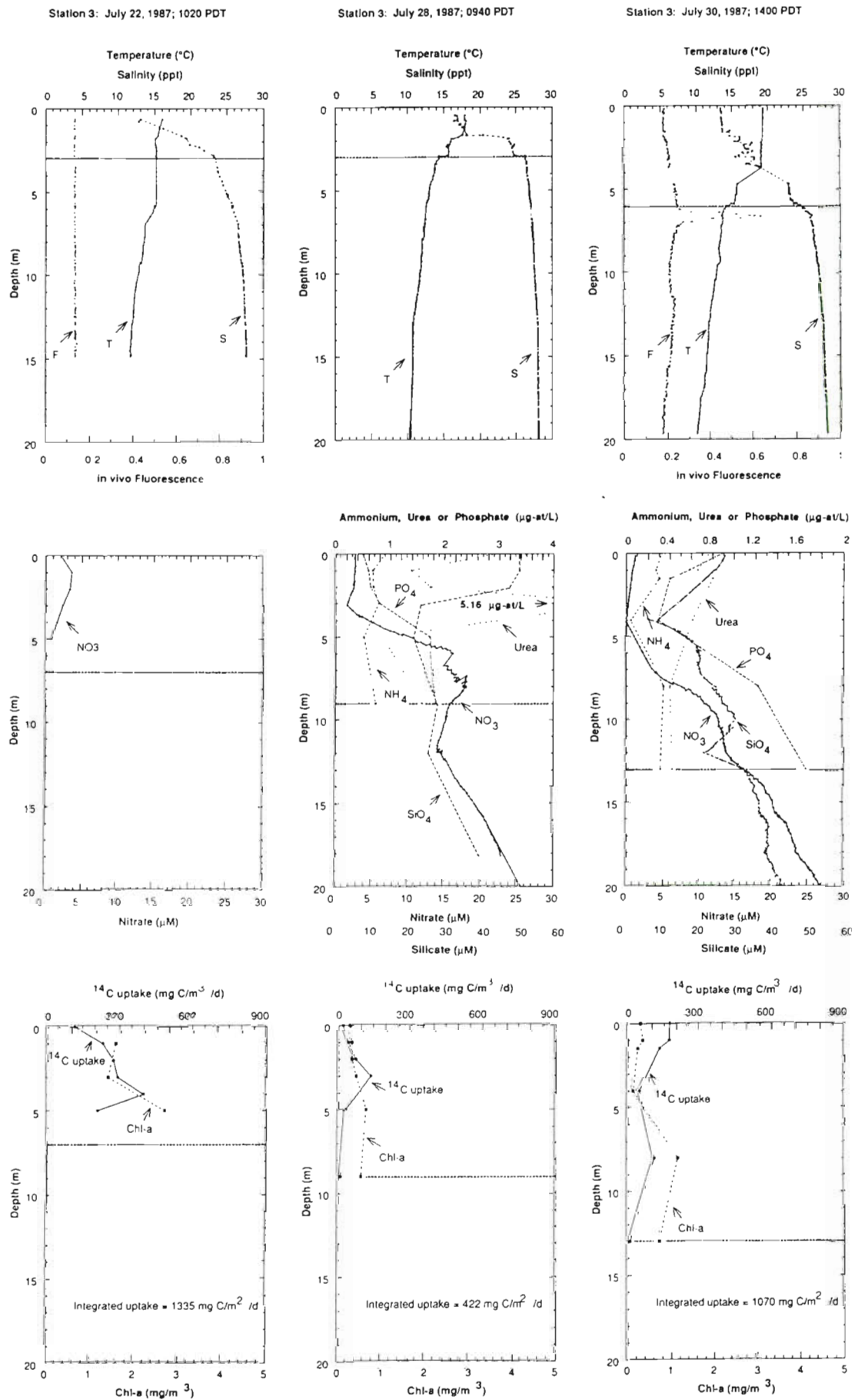


Fig. 4. Temperature (T), salinity (S), fluorescence (F), nutrients (NO₃, SiO₄, PO₄, NH₄ and urea), chl *a* (Chl-*a*) and ¹⁴C primary productivity (¹⁴C uptake) for the riverine plume station (Stn 3) during post-neap (before 24 July) and post-spring (after 24 July) tidal conditions. The depth of the bottom of the pycnocline is drawn as a broken line on the T and S profiles, and the 1% light depth is drawn as a broken line on the nutrient, chl *a* and ¹⁴C uptake profiles to facilitate comparisons among stations

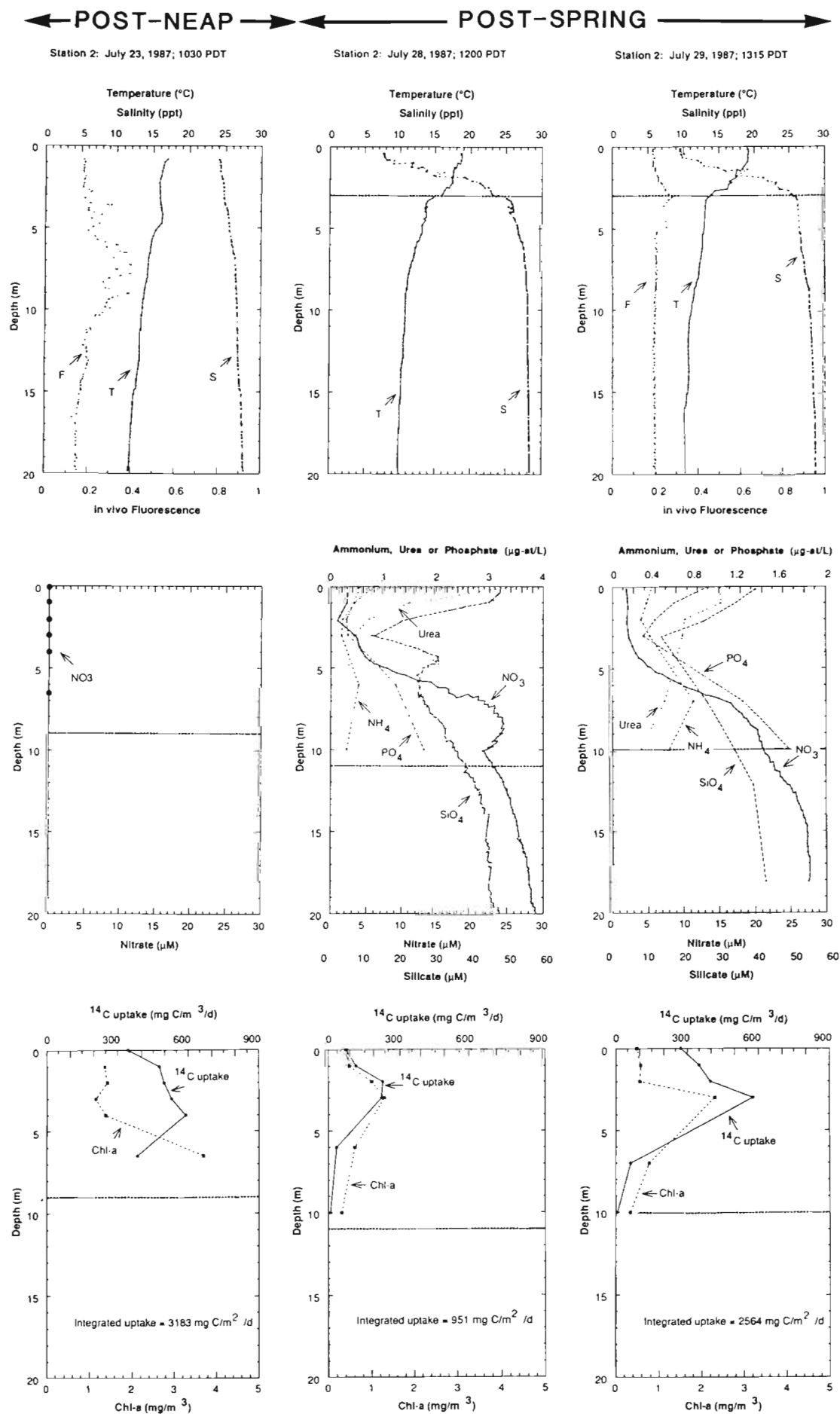


Fig. 5. Same as Fig. 4, except for Stn 2, the inner estuarine plume station

← POST-NEAP → ← POST-SPRING →

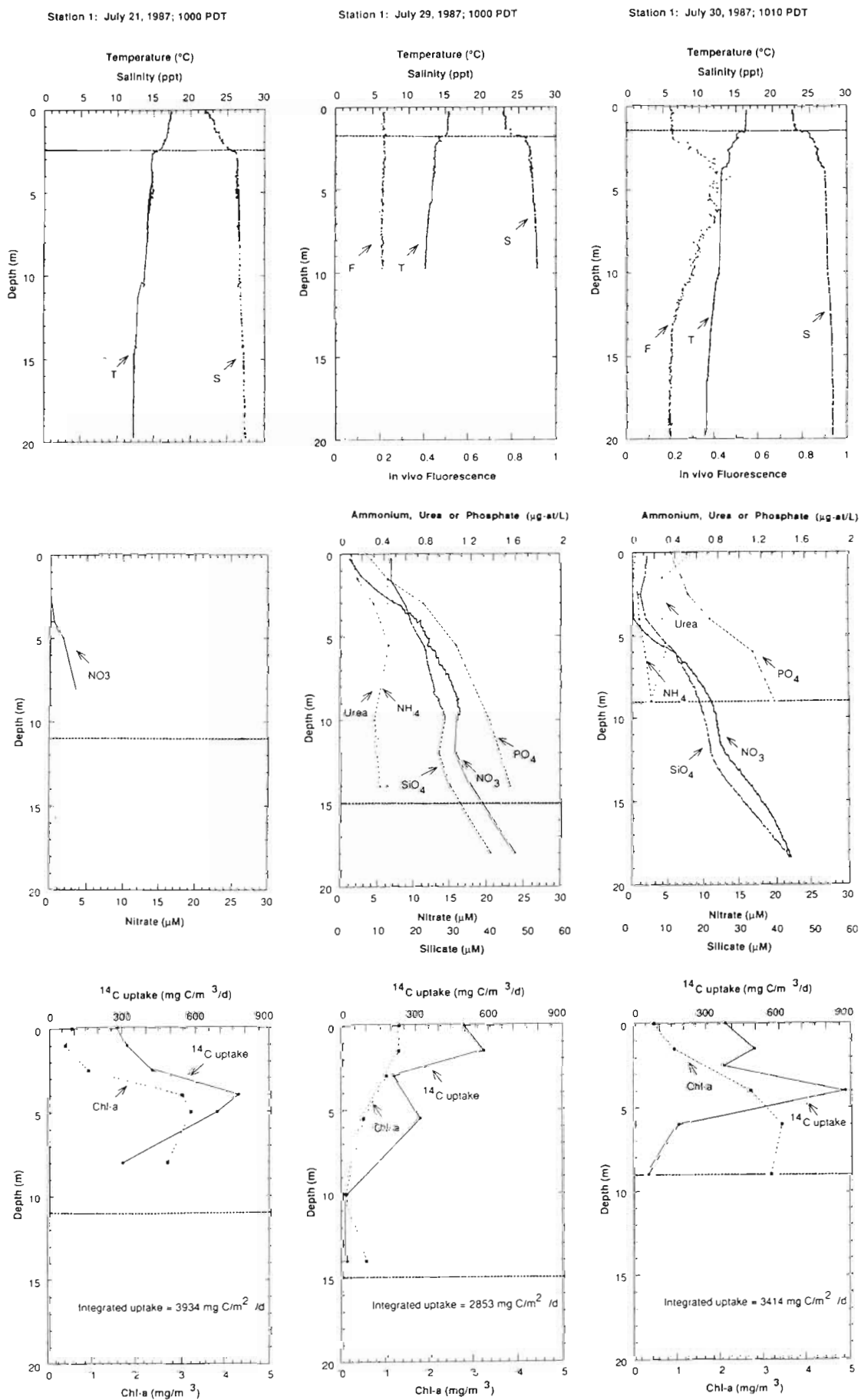


Fig. 6. Same as Fig. 4, except for Stn 1, the outer estuarine plume station

the post-neap than the post-spring portion of the tidal cycle (Fig. 6). Nitrate was undetectable down to 2.5 m during post-neap conditions (Fig. 6). Higher surface nitrate concentrations occurred during the post-spring period (29 July), but the following day, nitrate was either exhausted by the phytoplankton or advected to another area, and silicate was also lower.

Phytoplankton biomass and productivity

There were no obvious differences in species composition with depth among the stations and between post-neap and post-spring periods of the tidal cycle (Fig. 7A, B). The diatoms *Skeletonema costatum* and *Chaetoceros* spp. (particularly *C. compressus*) domi-

nated in terms of relative biovolume (72 %) (Fig. 7A). Other prominent *Chaetoceros* spp. were *C. socialis*, *C. radicans*, *C. debilis* and *C. septentrionalis*. In terms of species abundance, the dominant species were very different from the species that made up the bulk of the phytoplankton biomass. A small prasinomonad (an eukaryotic picoplankter), *Micromonas pusilla*, dominated (5×10^6 cells l^{-1} ; 40 % of total cell numbers), followed by *Chrysochromulina* spp., *Skeletonema* and *Chaetoceros* spp. (Fig. 7A). However, since *M. pusilla* is so small (a $2 \mu m^3$ sphere), its contribution to the total biovolume of the phytoplankton community becomes almost negligible compared to the much larger chain-forming diatoms. Similarly, some *Thalassiosira* spp. were not very abundant (5×10^4 cells l^{-1}), but they often contributed 5 to 10 % of the biovolume of the phytoplankton community. The *Thalassiosira* spp. were mainly composed of *T. nordenskiöldii*, *T. rotula* and *T. aestivalis*. A detailed description of the species composition of the phytoplankton community is given in Clifford et al. (1989).

In the plume at Stn 3, chl *a* and primary productivity were low throughout the water column during the post-neap period and even lower during the post-spring period. A narrow chlorophyll maximum occurred on 30 July at 6.5 m (Fig. 4).

In the inner estuarine plume at Stn 2 there was a deep chlorophyll maximum during the post-neap period, similar to Stn 1, and the integrated primary production was highest during this period. The chlorophyll maximum occurred near the surface during the early post-spring period and integrated primary productivity was low and similar to Stn 3 (riverine plume). Later in the post-spring period, chl *a* and primary productivity increased, but never to the high values observed during the post-neap period (Table 3).

In the outer estuarine plume at Stn 1 there were subsurface maxima in chlorophyll and primary productivity at 4 to 5 m, and the highest integrated primary productivity occurred during the post-neap period (Fig. 6). During the post-spring period, maximum chlorophyll and primary productivity occurred at the surface, but the following day, subsurface maxima occurred at Stn 1.

Heterotrophic biomass and production

Post-neap and post-spring values for DOC and total microflagellates at Stn 3 were similar to Stns 1 and 2 (Table 3), and there was no consistent pattern in any of these parameters with depth (Clifford et al. 1989). There was a trend towards higher heterotrophic productivity and bacterial numbers in the riverine plume

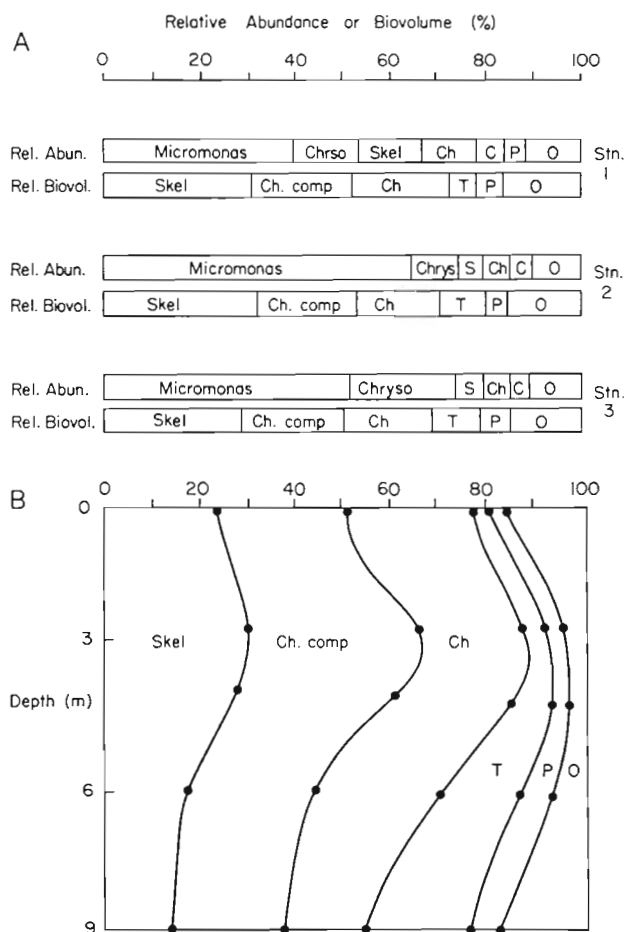


Fig. 7. (A) Composition of the phytoplankton community at 0 m at Stn 1 (29 July), Stn 2 (29 July), and Stn 3 (30 July), expressed as relative abundance or biovolume (%). Abbreviations are: *Micromonas* = *Micromonas pusilla*; *Skel* or *S* = *Skeletonema costatum*; *Chrs* = *Chrysochromulina* spp.; *Ch. comp* = *Chaetoceros compressus*; *Ch* = *Chaetoceros* spp.; *T* = *Thalassiosira* spp.; *C* = cryptomonads; *P* = pennate diatoms; *O* = others. (B) Vertical profile of the composition of the phytoplankton community at Stn 1 on 30 July, expressed as relative biovolume (%)

Table 3. Means \pm 1 SD of chl *a*, ^{14}C uptake by phytoplankton, dissolved organic carbon (DOC), ^3H -labelled thymidine bacterial production (^3H prod.), total bacterial cell counts, total microflagellates, autotrophic microflagellates and heterotrophic microflagellates at the 3 plume stations (Stns 1 and 2 = outer and inner estuarine plume, and Stn 3 = riverine plume) during post-neap and post-spring tidal conditions. Chl *a* and ^{14}C were integrated to the 1% light depth. Mean values are shown in parentheses. (For integrated chl *a* and ^{14}C uptake, post-neap, $n = 1$, for post-spring Stns 1 and 2, $n = 2$ and for Stn 3, $n = 3$)

Stn	Tidal cycle	Chl <i>a</i> (mg m^{-2})	Total phytoplankton ($\times 10^7 \text{ l}^{-1}$)	^{14}C uptake ($\text{g C m}^{-2} \text{ d}^{-1}$)	DOC (mg l^{-1})	^3H prod. ($\times 10^8 \text{ cells l}^{-1} \text{ d}^{-1}$)	Total bact. ($\times 10^9 \text{ l}^{-1}$)	Total $\mu\text{flag.}$ ($\times 10^7 \text{ l}^{-1}$)	Auto. $\mu\text{flag.}$ ($\times 10^7 \text{ l}^{-1}$)	Hetero. $\mu\text{flag.}$ ($\times 10^7 \text{ l}^{-1}$)
1	Post-neap	16.2	0.61 ± 0.39	3.9	8.0 ± 4.8	6.5 ± 2.6	4.0 ± 2.6	6.4 ± 3.7	5.1 ± 3.7	1.3 ± 1.2
	Post-spring	14.5 ± 9.6	0.55 ± 0.58	3.2 ± 0.4	7.6 ± 4.5	12.3 ± 8.5	5.4 ± 1.2	17.7 ± 10.3	9.3 ± 9.1	3.7 ± 4.3
2	Post-neap	10.3	0.47 ± 0.15	3.2	5.9 ± 2.6	86.3 ± 20.7	7.0 ± 1.9	12.1 ± 3.8	11.0 ± 3.1	1.3 ± 1.2
	Post-spring	8.2 ± 1.9	0.62 ± 0.94	1.5 ± 0.9	7.2 ± 2.9	29.3 ± 40.8	6.1 ± 2.3	9.0 ± 8.7	6.4 ± 6.3	2.6 ± 2.6
3	Post-neap	7.0	0.84 ± 0.57	1.3	6.8 ± 4.7	41.2 ± 28.5	8.0 ± 2.8	4.3 ± 3.0	3.0 ± 2.6	1.3 ± 1.2
	Post-spring	6.2 ± 2.8	0.55 ± 0.63	0.76 ± 0.48	7.2 ± 3.7	28.1 ± 44.3	6.1 ± 2.7	9.1 ± 5.1	4.7 ± 4.0	3.1 ± 3.1

and its boundaries (Stn 3) than in the outer portion of the estuarine plume, but the differences were not significant ($p > 0.05$).

Surface zooplankton densities

Zooplankton densities in the photic zone were extremely variable, which is to be expected in such an energetic physical environment (Figs. 8 & 9). Densities of amphipods and euphausiids were significantly ($p \leq 0.05$) higher at night than day in the photic zone at the inner and outer estuarine plume stations, suggesting the occurrence of vertical migration at these 2 stations. Vertical migration was not evident in the riverine plume because day and night densities were not significantly ($p > 0.05$) different.

Copepods were dominated by 4 genera: *Acartia*, *Calanus*, *Pseudocalanus* and *Metridia*. Due to the high variability in their abundance, there were no significant differences amongst stations, except for *Metridia* spp. which was significantly ($p \leq 0.05$) more abundant at night than daytime in the outer estuarine plume.

Densities of the various hydromedusae were low at most stations except for the riverine plume station,

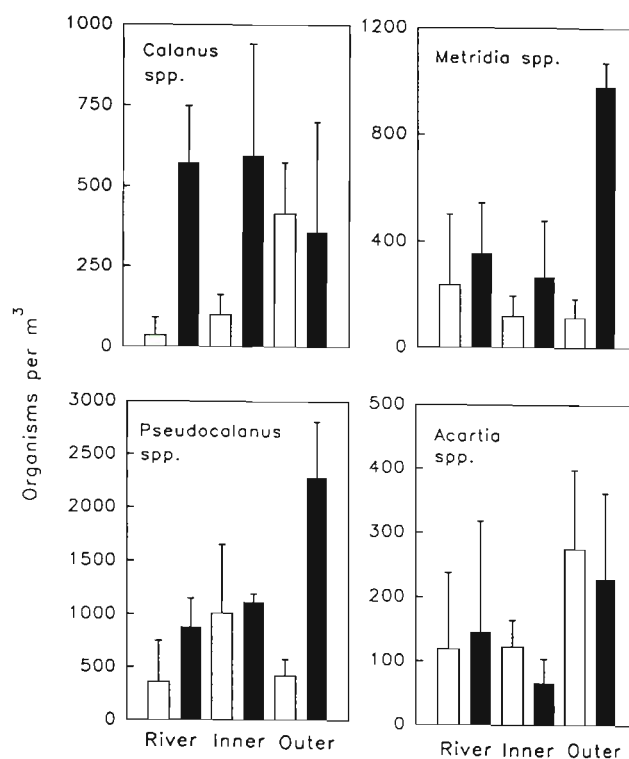


Fig. 8. Mean abundance of copepods per m^3 in the photic zone, obtained from vertical hauls during 28 to 31 July 1987 at the riverine plume (Stn 3), and the inner (Stn 2) and outer (Stn 1) portion of the estuarine plume. Black bars: night; open bars: daytime hauls. Error bars represent ± 1 SD

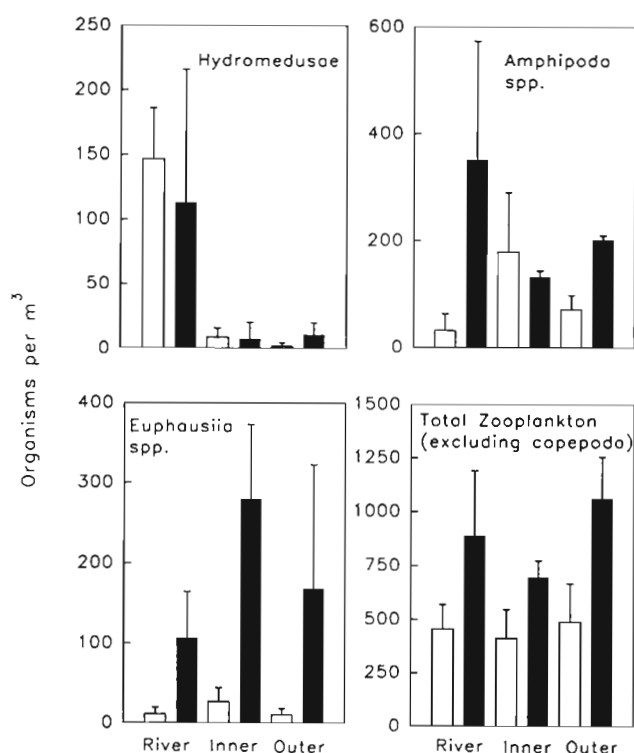


Fig. 9. Mean abundance of other zooplankton (excluding copepods) per m^3 in the photic zone, obtained from vertical hauls during 28 to 31 July 1987 at the riverine plume (Stn 3), and the inner (Stn 2) and outer (Stn 1) portion of the estuarine plume. Black bars: night; open bars: daytime hauls. Error bars represent ± 1 SD

where they were significantly ($p \leq 0.05$) more abundant than in the estuarine plume.

Deepwater zooplankton densities

Densities of euphausiids were significantly ($p \leq 0.05$) higher at the outer estuarine plume station than at the riverine plume station and the intermediate stations (Stns 4 and 5) closest to the inner estuarine plume station (data not shown). High densities at the estuarine plume stations suggest that orientation to the increase in primary production in this region may be occurring. Densities of *Pseudocalanus* spp. at the intermediate station (Stn 4) closest to the inner estuarine plume station were significantly ($p \leq 0.05$) different from either the riverine plume station or the outer estuarine plume stations. As with the species composition of the surface layer there was no difference in species composition amongst stations. Over the entire water column *Metridia* spp. dominated the copepod community, followed by *Pseudocalanus*, *Oithona* and *Acartia*.

DISCUSSION

Nutrients

There have been few nutrient measurements in the Fraser River and the riverine plume. This paper reports the first ammonium and urea values for the plume, the first continuous profiles of nitrate and silicate and the first series of daily measurements of nutrients to show the dynamic nature of the plume. All nutrient concentrations (except silicate) were generally higher in the riverine plume than in the river. Thus, in late July the nutrient enrichment of the surface waters at these stations was probably due primarily to entrainment of nutrient-rich deep water as the river flowed seaward, and not due to the nutrients in the river water as suggested by Stockner et al. (1979, 1980). Silicate was the only nutrient that had higher concentrations in the river ($> 60 \mu\text{M}$) than in the plume (ca $40 \mu\text{M}$). In fact, vertical profiles of silicate and salinity were most useful in tracing the plume and determining its thickness. The nutrient concentrations of the Fraser River reported here and by others (Hall et al. 1974, Clark & Drinnan 1980, Drinnan & Clark 1980) easily fall within the range reported for other major unpolluted rivers of the world (Meybeck 1982).

In the riverine plume, nutrients do not appear to be limiting, although on 30 July a high density, narrow band of phytoplankton at the bottom of the plume reduced nitrate at 4 m to undetectable concentrations (Fig. 4). In the estuarine plume, nitrate and ammonium reached undetectable concentrations occasionally in the top 4 m, indicating that nitrogen most likely limited primary production on some days at this station. Silicate was also surprisingly low ($2.2 \mu\text{M}$ at 2.5 m) on 30 July, considering that it was $14 \mu\text{M}$ on the previous day.

Primary productivity

High primary productivity at the plume boundary was observed by Parsons et al. (1969b) and in more recent studies (Stockner et al. 1979, Parsons et al. 1981). In our study, significantly (Mann-Whitney test, $p \leq 0.05$) higher values (2 to $4 \text{ g C m}^{-2} \text{ d}^{-1}$) were observed in the outer part of the estuarine plume than in the riverine plume (Table 3; Figs. 4 & 6). These values are higher than Parsons et al. (1969b) found for mid-May, but less than August values of Stockner et al. (1979) which often were in excess of $4 \text{ g C m}^{-2} \text{ d}^{-1}$. The primary production values were temporally variable and generally the highest values occurred during the post-neap portion of the tidal cycle at all 3 stations (Table 3).

The reason for the low productivity at the riverine plume station is not apparent. It does not appear to be due to light limitation caused by the turbidity of the riverine plume. While the top meter of the plume has a significantly ($p \leq 0.05$) higher extinction coefficient than at Stn 1, the extinction coefficient for the whole euphotic zone was not significantly ($p \geq 0.05$) different between Stns 1 and 3 (Table 4). Although the riverine

Table 4. Mean \pm 1 SD extinction coefficients (k) and 1 % light depths at 3 stations (Stns 1 and 2 = outer and inner estuarine plume, and Stn 3 = riverine plume) in the Fraser River plume during a spring-neap tidal cycle. Larger values of k indicate greater light attenuation

Stn	Tidal cycle	$k_{0-15\text{ m}}$ (m^{-1})	$k_{0-1\text{ m}}$ (m^{-1})	1 % light depth (m)
1	Post-neap	0.41	0.62	11
	Post-spring	0.36 ± 0.06	0.39 ± 0.04	12
2	Post-neap	0.44	0.69	9
	Post-spring	0.37 ± 0.01	0.76 ± 0.03	11
3	Post-neap	0.52	0.89	7
	Post-spring	0.37 ± 0.04	0.89 ± 0.23	11

plume attenuates light in the top 2 m at Stn 3, the 1 % light depths at Stns 1 and 3 were the same since the light attenuation due to the turbidity of the riverine plume at Stn 3 is offset by the increased phytoplankton biomass at Stn 1. The depth of mixing (defined by the depth of the pycnocline) at Stn 3 was deeper than Stn 1.

This study clearly demonstrates the importance of choosing the correct temporal scale in resolving the rapid changes occurring in this riverine plume front. The primary productivity of the plume and its boundaries are temporally variable. At Stn 2, productivity was measured for 3 consecutive days at the same stage of the tidal cycle (Fig. 3B). On two of those days, productivity was $0.95\text{ g C m}^{-2}\text{ d}^{-1}$, while on the third day it increased dramatically to $2.6\text{ g C m}^{-2}\text{ d}^{-1}$ (Fig. 5; Clifford et al. 1989). Similar variability can also be seen at Stn 3 (Fig. 4). What remains to be resolved on future cruises is the temporal variability over a 24 h period at the same station.

Phytoplankton community

We found that a very small prasinomonad, *Micromonas pusilla*, dominated in terms of cell numbers (2×10^6 to 2×10^7 cells l^{-1}), followed by *Chrysochromulina* spp. and *Skeletonema costatum*. However, *M. pusilla* was nearly insignificant in terms of biomass ($< 1\%$ biovolume) and it even grows more slowly (maximum doubling time is about 15 h; Cochlan 1989) than most of the larger chain-forming diatoms that were dominant

in the plume. *M. pusilla* was more abundant in the surface waters of the riverine plume and the inner estuarine plume (16.2 and 21.8×10^6 cells l^{-1} , respectively) than in the outer portion of the estuarine plume (7.6×10^6 cells l^{-1}). At all stations it was 2 to 5 times more abundant in surface waters than at the 1 % light depth at about 10 m (3×10^6 cells l^{-1} ; Clifford et al. 1989). However, past studies have found that *Skeletonema* is usually the most abundant phytoplankter throughout the Strait of Georgia (Shim 1977, Harrison et al. 1983, Spies & Parsons 1985) and therefore *M. pusilla* may have been missed in previous studies. In terms of phytoplankton biomass (biovolume), fast-growing centric diatoms such as *S. costatum*, *Chaetoceros* spp. and *Thalassiosira* spp. clearly dominated. We found *Chaetoceros compressus* dominated in the plume while previous studies found that *Chaetoceros debilis* dominated throughout the Strait (Harrison et al. 1983). *Chaetoceros convolutus*, a diatom suspected of killing salmon in fish farms, was present primarily in the lower half of the photic zone at all stations but only in low numbers (about 5×10^3 cells l^{-1} ; Clifford et al. 1989). It is not surprising that fast-growing diatoms such as *Skeletonema*, which can double 2 to 3 times a day (Harrison et al. 1976), dominated the phytoplankton biomass in this tidally influenced riverine front. Near the boundaries of the riverine plume, phytoplankton receive a fairly continual supply of nutrients probably due to entrainment, with highest supply rates during spring tides. Therefore the plume operates somewhat like a continuous flow culture at a high variable dilution rate and seldom encounters nutrient limitation.

Bacteria and heterotrophic production

Albright (1983a, b) has previously observed that both bacterial numbers and their productivities are greatest in the Fraser River plume water, the salinity of which lies intermediate between that of the river and the Strait of Georgia waters. He suggested that the mixing of the 2 parent waters resulted in a plume water that was enriched with organic matter compared to the water from the river and the Strait. The 2 main sources of these organics are allochthonous matter added by the river and primary production in the estuary. However, as Albright (1983a, b) previously noted, there is no clear correlation between primary production of the estuary and heterotrophic bacterial productivity. The data presented herein also show no correlation with dissolved organic nitrogen (Clifford et al. 1989), DOC or primary productivity (Table 3). Instead, the data suggest an inverse relationship between heterotrophic and primary productivities. Based on these data, it

would appear that the relationship between the heterotrophic bacteria and their use of organic substrates is complex and is likely the result of many physical, chemical and biological processes which interact as the 2 parent waters mix.

Zooplankton community

The dominance of *Pseudocalanus*, *Metridia*, *Calanus* spp. and *Acartia* in the euphotic zone is typical of the summer copepod community for the Strait of Georgia (Harrison et al. 1983). Copepod densities differed significantly ($p \leq 0.05$) between day and night in the euphotic zone only at the outer estuarine plume station for *Pseudocalanus* and *Metridia* spp. Thus, diel vertical migrations were not occurring in the regions defined as the inner plume and the riverine plume for these species. The lack of vertical migration by *Metridia* and *Pseudocalanus* spp. (which are known vertical migrators) in the riverine and inner estuarine plume may be due to factors such as food (phytoplankton), increased turbidity, or decreased salinity.

Amphipod species exhibited diel vertical migrations in the riverine plume (densities significantly different at $p \leq 0.05$). No significant differences between densities in the euphotic zone (day vs night) were observed in regions defined as the inner and outer estuarine plume, suggesting active orientation or physical aggregation in these regions.

Comparisons between the riverine and estuarine plumes

The riverine plume is characterized by higher nutrients (particularly silicate) in the surface waters compared to the estuarine plume during the post-spring period (Table 1). In late July, this nutrient enrichment of the surface waters appears to be the result of entrainment of deeper water and not due to the nutrients in the river water, since the nutrients in the river were lower than concentrations in the riverine plume (except for silicate). Surface temperatures were generally higher and salinities were much lower in the riverine plume than the estuarine plume, due to the influence of the river water. Chl *a* concentrations, phytoplankton abundance and primary productivity were also lower. This was not due to the increased turbidity of the riverine plume, but it may be due to the increased vertical mixing (deeper pycnocline) at this station. The opposite trend to primary production was observed for heterotrophic bacterial production and bacterial cell numbers, with higher values in the plume than beyond the plume. Heterotrophic microflagellates

and larvaceans, which are known bacterial grazers (King 1982), were similar and higher, respectively, in the riverine plume than at Stn 1. These data suggest more bacterial grazing at Stn 3, since larvaceans were 5 times more abundant than at Stn 1. Zooplankton distributions were variable, with the apparent lack of vertical migration for some vertically migrating species in regions of high production. Therefore, zooplankton behavioral responses appear to be resulting in aggregation to high densities of food particles. This is evident for *Pseudocalanus* and *Metridia* spp. as well as for amphipods, in the inner estuarine plume.

During this study we examined nutrient and plankton dynamics on a daily basis over a spring-neap tidal cycle (fortnightly variability). Further research is required to determine temporal variability at 2 more scales, a shorter and a longer temporal scale than in our study. Short-term variability at one station over a 24 h tidal cycle must be studied as well as long-term (seasonal) variability. The latter would require studying a spring-neap tidal cycle each month from spring to fall, in order to determine how the pronounced seasonal cycle in the amount of freshwater discharged by the Fraser River would affect nutrient and plankton dynamics.

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