

BENTHIC ALGAL ECOLOGY AND PRIMARY
PATHWAYS OF ENERGY FLOW ON THE
SQUAMISH RIVER DELTA, BRITISH COLUMBIA

by

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ABSTRACT

Benthic algal ecology and primary pathways of energy flow were considered on the Squamish River delta at the head of Howe Sound, a fjord-type estuary. The study elucidated the structure and function of major autotrophic components of the estuarine ecosystem. Benthic algae were investigated with regard to species composition and distribution and the capacity for energy conversion, input to the system and storage. Comparisons were made with existing information on the vascular plant component of the ecosystem.

The benthic algal community was studied by regular field sampling of major macroalgae and microalgal associations with a monitoring of physical-chemical environmental factors. Presence of an alga in the estuary was a function of its osmoregulatory capabilities. Establishment and temporal-spatial distribution patterns were controlled by substrate-habitat preference and availability and the interaction of light, interspecies competition, desiccation, temperature and salinity, light being of greatest importance. *Carex lyngbyei* Hornem., the dominant vascular plant, had a significant effect on distribution of benthic algae through light restriction during its summer growth period and action as a substrate during the winter. Total species diversity, biomass and distributional area of benthic algae were greatest at the latter period.

The effect of ecosystem structure on function was investigated by analysis of energy flux through major benthic algal producers. Comparisons were made of the total amount of energy input attributable to benthic algae and vascular plants. The importance of an algal producer to energy flux $\cdot m^{-2}$ was a function of either high primary productivity, photosynthetic efficiency and caloric content, or in the case of diatom dominated microalgal associations, high caloric content alone. Distribution, reflecting the presence of suitable substrate-habitat, modified this pattern. Macroalgae having high energy input $\cdot m^{-2}$ (*Monostroma oxyspermum* (Kutz.) Doty, *Pylaiella littoralis* (Lyngb.) Kjell.) were of minimum importance to total energy input. Two microalgal associations (Association E, diatom dominated, Association G, *Ulothrix flacca* (Dill.) Thur. dominated), each with low energy input $\cdot m^{-2}$ but with wide distribution and high photosynthetic efficiency and caloric content contributed a total of 84% of available energy attributable to benthic algae.

Benthic algae account for a maximum of ca. 7% of total energy input to the delta ecosystem compared to ca. 90% by vascular plants and 3% by addition of organic matter. The majority of energy for the detrital based ecosystem comes from vascular plants and becomes available after a lag period allowing decomposition. Benthic algae are significant to the ecosystem as a readily

available, continually present energy source requiring little or no breakdown for utilization and not for total energy input.

Energy is available as either dissolved or particulate organic matter. Of the latter, *ca.* 49% is removed to the estuary, 33% incorporated into the sediments of the delta and 18% used by consumers in the delta ecosystem.

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INTRODUCTION

Estuaries and their associated deltas and marshes form a biologically important transition zone between the marine and freshwater environments (Odum 1971, Remane and Schlieper 1971). Their vulnerability to industrial development (dredging, land fill, dyking and pollution) has frequently been discussed (Odum 1971, Perkins 1974). Also, the value of shallow-water and intertidal marshes of estuaries as feeding and nursery areas for commercially important fish and shellfish (Anonymous 1972, Perkins 1974) and as a source of organic matter (detritus) for ecosystems of adjacent coastal waters (Melchiorri-Santolini and Hopton 1972, Heinle and Flemer 1976) has been noted.

Estuaries are among the most highly productive of natural ecosystems. Most information relating to the autotrophic components (primarily benthic algae) of estuarine ecosystems has been gathered from coastal plain salt marshes on the east coast of the United States (Pomeroy 1959, Williams 1962, Gallagher and Daiber 1973, 1974, Sullivan 1977), Canada (Hatcher and Mann 1975), England (Carter 1932, 1933, Hopkins 1966) and South Africa (Day 1950, Day *et al* 1952, 1953). Fjord-type estuaries of Norway and Denmark have also provided considerable information (Grontved 1960, Nienhuis 1971, Gargas 1972). A summary of existing literature on the benthic algal component of estuaries

is given by Pomeroy (1974) and that for vascular plants by Keefe (1972) and Turner (1976).

Past research in estuarine ecosystems has generally been directed to structure (species composition and distribution-abundance) with little attention paid to function (energy and material flow through the system). The work by Teal (1962) on a salt marsh ecosystem in Georgia is the best documented study of energy flow. A similar approach is needed for other types of estuaries to gain a full understanding of their importance and operation.

The present study was formulated to provide some indication of the structure and function of the little studied fjord-type estuaries common to British Columbia. The Squamish River estuary was selected as "typical" of these in view of its physical and biological similarity (Levings *et al.* 1976). Particular emphasis is placed on the autotrophic components of the intertidal marshes.

Field and laboratory experiments were designed to:

- a.) identify factors limiting or controlling distribution and primary production of benthic algae; b.) determine the amount of energy flowing into and through vascular plants and benthic algae and the role of each in the ecosystem (i.e. primary pathways of energy flow); c.) delineate the magnitude of seasonal and annual pathways of energy flow; and d.) determine the importance

of the tidal marsh as an energy source for estuarine organisms as well as those of adjacent coastal waters. Data from these question areas, when combined, may have a predictive value regarding the effects of environmental alteration on energy flow and ecosystem function.

This study represents the first attempt at gaining an understanding of ecosystem function in a fjord-type estuary, a very complex, dynamic environment. Understanding the primary pathways of energy flow from vascular plants and benthic algae in such a system is highly important, for it is the base upon which the remainder of the ecosystem is built.

STUDY AREA

The Squamish River estuary ($49^{\circ}41' \text{ N}$, $123^{\circ}10' \text{ W}$) is located approximately 48 km north of Vancouver, British Columbia at the head of Howe Sound (Fig. 1). The area is representative of a turbid outwash fjord (Burrell and Matthews 1974) and is bounded on both sides by steep mountains.

The entire Squamish estuary has been affected by industrial development and physical alteration (Anonymous 1972). The most significant has been the construction of a river training dyke running the length of the estuary (Fig. 2), and the establishment of two rather distinct habitats (Pomeroy and Stockner 1976). The region west of the dyke is under strong freshwater influence as a result of the redirection of virtually the entire flow of the Squamish River to this area. In comparison, the region to the east of the dyke is now a relatively stable habitat displaying marine conditions, resulting from blockage of the east arm of the Squamish River and formation of the Central Basin (Fig. 2).

The Squamish estuary has been separated into West, Central and East deltas on the basis of major physiographic features (training dyke and Central Basin (Fig. 2). Of these, the seaward portion of the Central delta best fits the two main requirements for this study. Firstly, since the delta is located within an area

Figure 1. Southern coast of British Columbia showing the location of Howe Sound with the Squamish estuary at the head.

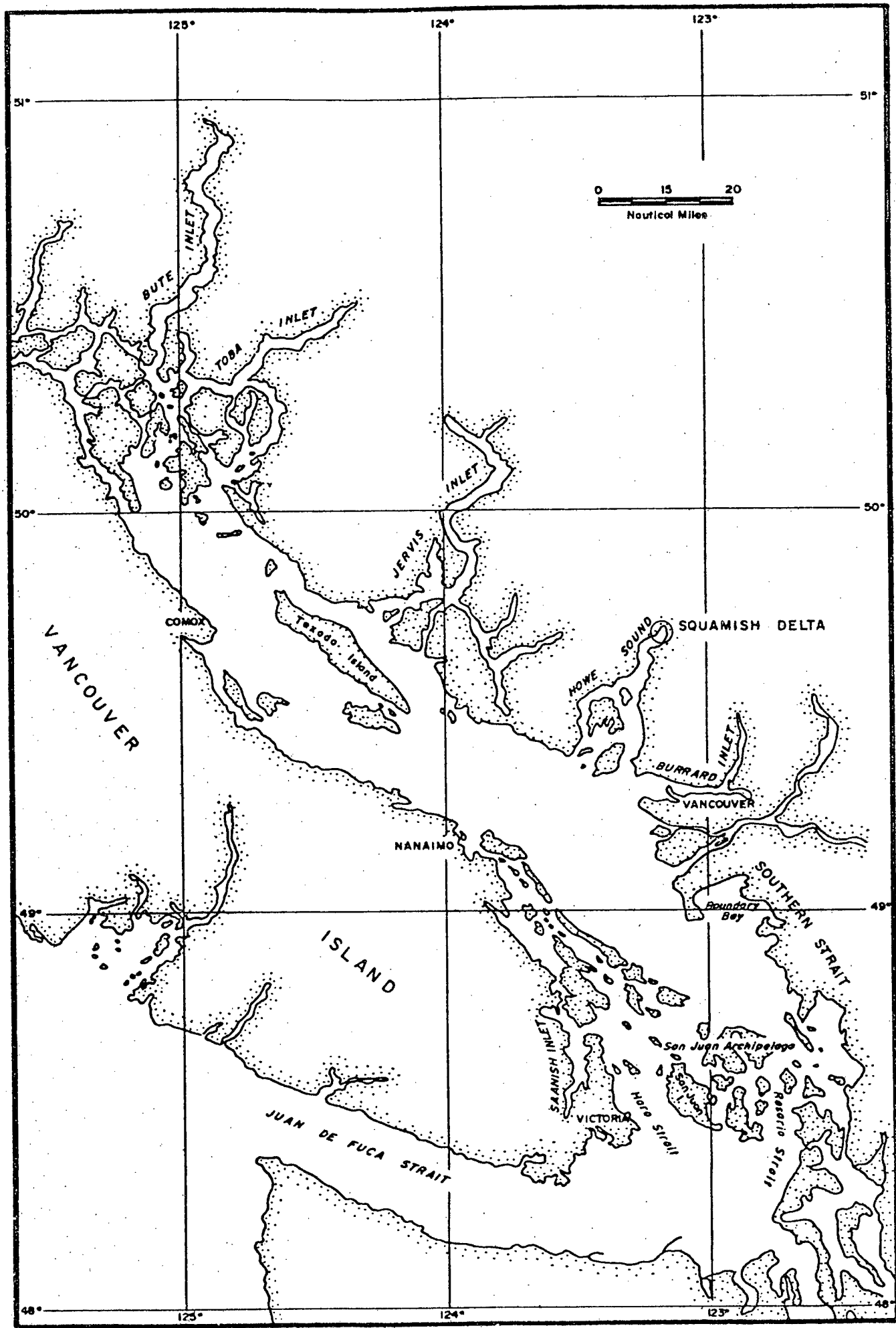
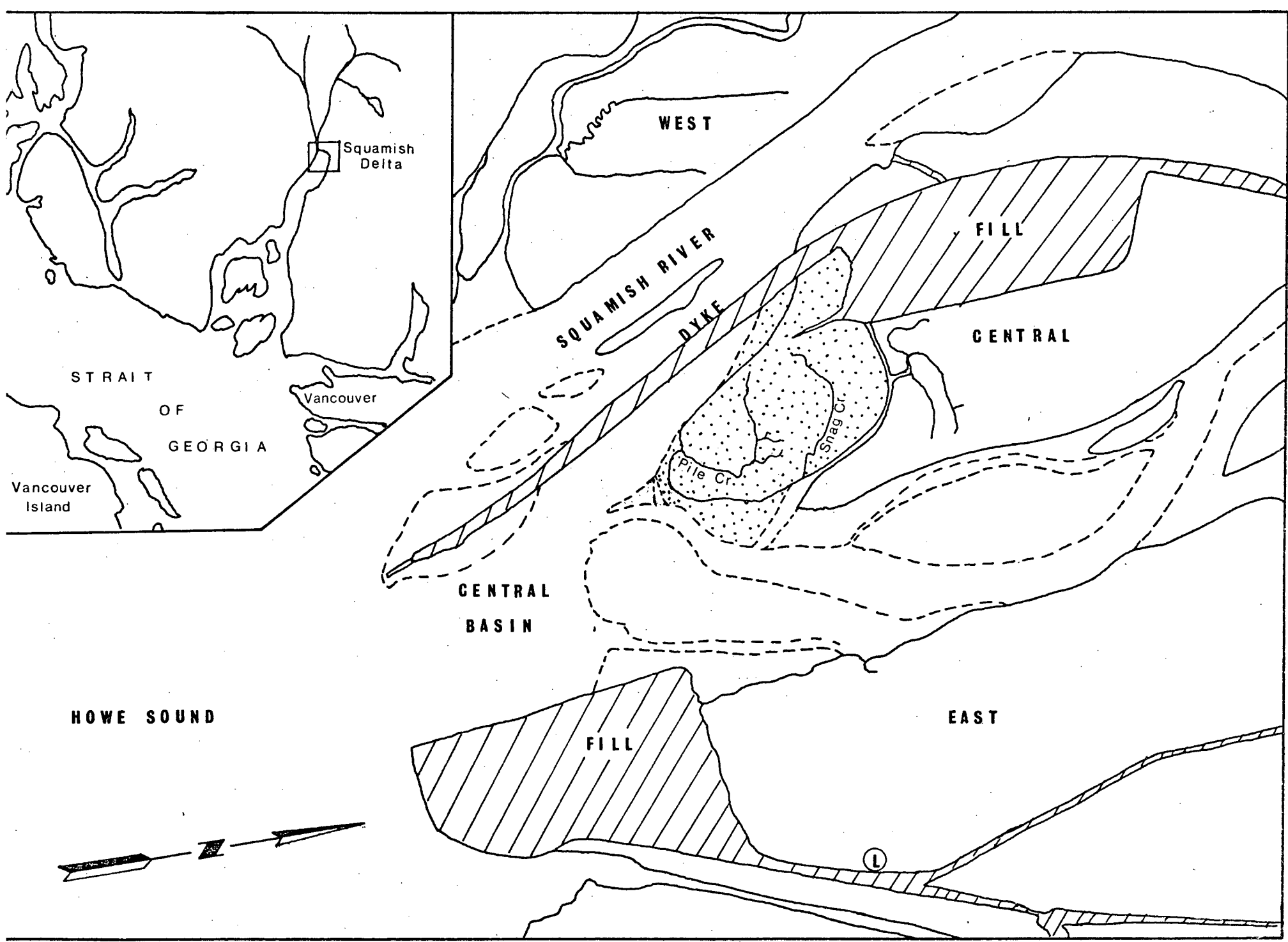


Figure 2. Squamish River estuary, British Columbia, showing physiographic details of the delta (---- indicates extent of sand/mud flats exposed at low tide; dotted area of the Central delta indicates study region; L indicates location of light meter).



removed from the unsettling and complicating effects of direct river flow, more accurate studies relating to annual primary production, nutrient cycling, removal and deposition of particulate organic matter and other parameters required for the formulation of energy budgets may be undertaken. Secondly, the area chosen drains through two major tidal creeks, thus facilitating the measurement of organic and nutrient removal.

The study area of $ca. 1.27 \times 10^5 \text{ m}^2$ is characterized by an intertidal zone of extensive, low elevation marshlands in combination with sand/mud flats. The area has been separated into three recognizable zones by Levings (1974). The lower intertidal zone (0.0-1.5 m above chart datum (O.D.)) has sand/mud sediments free of vascular plants. Marshlands supporting vascular plant communities common to developing alluvial lands are indicative of the mid-intertidal zone (1.6-3.0 m O.D.). The transition between this zone and the lower intertidal is generally delineated by a natural embankment ranging in height from 0.3-1.8 m. A dense overhanging mat of *Carex lyngbyei* Hornem. rhizomes is common, extending out into the low intertidal sand flats for approximately 0.2 m (Levings 1974). The mid-intertidal marshland is dominated by extensive sedge meadows of *C. lyngbyei* and *Eleocharis palustris* (L.) R. and S. dissected by tidal creeks (Lim and Levings 1973). Die-off of sedge occurs gradually beginning in late August and by December a mat of dead vegetation is present.

A gradation exists from sedge to grasses on the higher levels of the upper intertidal lands (3.1-4.5 m O.D.). Deciduous shrubs and mixed coniferous trees such as Douglas fir (*Pseudotsuga menziesii* (Mirbel) France) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) occupy the infrequently flooded landward portion of the delta above the intertidal. Orloci (1961) and Krajina (1970) indicate the Squamish delta as being within the coastal western hemlock zone of the Pacific coastal meso-thermal forest region.

Climate in the study area is classed as moderate maritime with a mean annual precipitation of 203 cm (Hoos and Vold 1975). Average monthly air temperatures range from near 0 C in January to 17 C in July. Steep mountains and a frequent industrial haze layer effectively reduce duration and intensity of sunlight. Wind patterns are typical of those prevailing in many British Columbia fjords (Hoos and Vold 1975). Strong northerly outflows, common during December and January, frequently reach $56-64 \text{ km}\cdot\text{h}^{-1}$ and may persist for 3-5 days. Southerly inflow winds (October to March) are less persistent but more frequent than northerly winds. A diurnal sea breeze circulation ($25-37 \text{ km}\cdot\text{h}^{-1}$), resulting from strong thermal heating in the interior, is evident during the summer. Strong amplification of winds occurs in the immediate vicinity of the Squamish estuary on sunny days, being attributed to valley winds or overheated air in the estuary rising up the steep mountain sides

(Anonymous 1972). Discussion of wind and other climatic factors are given by Stathers (1958) and Hoos and Vold (1975).

The Squamish River system drains 2500 km² of the westerly slopes of the Coast Mountains in southern British Columbia. Annual discharge patterns are characteristic of glacier fed systems with a mean annual flow rate of ca. 292 m³·s⁻¹. During the high runoff period (May through August), peak flows of ca. 658 m³·s⁻¹ are common (June, July) (Bell 1975). Minimum flow rates (ca. 71 m³·s⁻¹) generally occur in March. A second pronounced runoff can occur in the fall as a result of heavy rains or premature snow melt.

The Squamish River is heavily laden with glacial sediments at the time of maximum runoff (June-July). River water is carried around the dyke and sediments become deposited at the delta front. Bell (1975) indicates an average rate of delta front advancement approaching 6.0 m·yr⁻¹. Sediments of the delta are classed as Fluvial (alluvial)-Glacial Marine with a slope of less than 5% (Anonymous 1972). Coarser sediments become deposited on the upper portions of the delta. Finer colloidal particles (glacial flour) flocculate with the mixing of fresh and marine waters and settle towards the seaward portion of the delta. Data on minerology, sediment distribution and grain size are provided by Matthews *et al.* (1966) and Bell (1975).

Tides affecting the delta are of the mixed type typical of the Pacific Coast with two high and two low periods in a tidal day. Tidal amplitude varies from 0 to 4.8 m O.D. with mean tidal range being 3.2 m O.D. (Anonymous 1972). During periods of strong winds and high runoff, these limits can be greatly exceeded. Thus, the extent and duration of exposure and coverage of the intertidal region can be extremely variable.

MATERIALS AND METHODS

Field studies were conducted from June 1974 through August 1975. Sampling was done weekly or biweekly from June to September 1974 and 1975. For the period September 1974 through April 1975, sampling was done monthly. Station locations for physical, chemical and biological factors appear in Figure 3.

I. Physical-Chemical FactorsA. Salinity, temperature, precipitation, light.

Field determinations of salinity and temperature at high tide were made at the surface and at 1 and 2 m. A YSI Model 33 SCT meter was used June-August 1974, followed by a Beckman Model RS5-3 SCT meter for subsequent work. Salinity of samples collected in the field was determined using a Bissett-Berman Salinometer (Model 6230) on return to the laboratory.

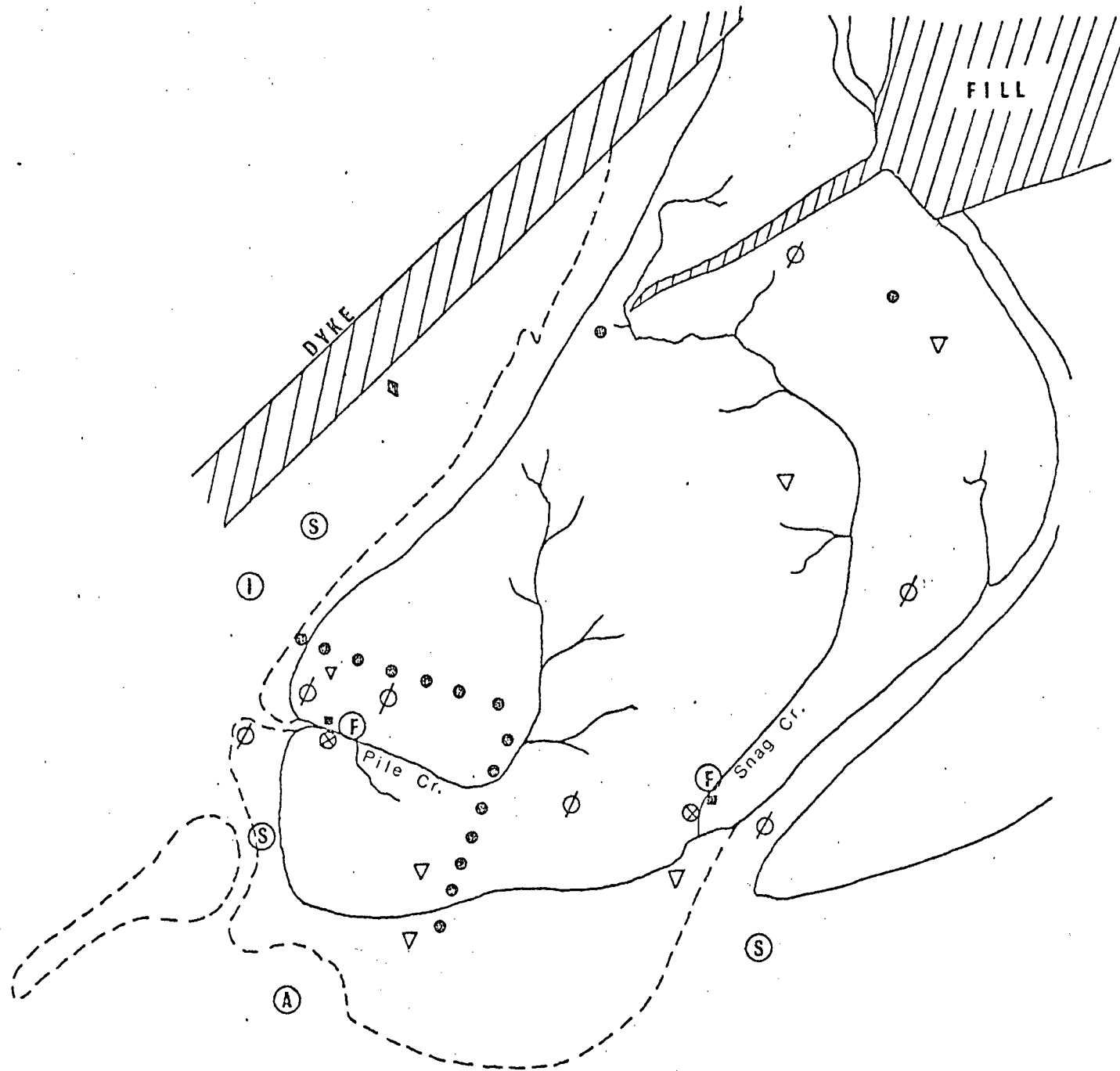
Temperature determinations in tidal pools were made with standard mercury thermometers.

Air temperature and precipitation data were obtained from the Squamish-St. Davids monitoring station of the Atmospheric Environment Service (AES) located just north of Squamish.

Daily incident solar radiation ($\text{g cal} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$) was recorded on a Belfort Pyranometer situated, to prevent vandalism, at Squamish Terminals on the East delta (Fig. 2). Days were identified as sunny or

Figure 3. Detailed map of Central delta showing sampling stations, ---- indicates extent of sand/mud flats exposed at low tide.

- Ⓕ tidal creek flow rates
- Ⓐ light attenuation with depth
- Ⓢ salinity-temperature stations
- ◆ seasonal nutrients
- nutrient loss from tidal creeks
- ∅ sedimentation and sediment organics
- ▽ addition of particulate organic matter
- removal of particulate organic matter
-delta surface
- ⊗ removal of particulate organic matter
-tidal creeks



CENTRAL BASIN

overcast based on data from the AES station and from pyranometer tracings. On overcast days, solar energy was assumed to be entirely photosynthetically available radiation (PAR = 400-700 nm) (Szeicz 1966). However, due to the reduction in atmospheric filtering on sunny days, the value obtained from the pyranometer was multiplied by 0.47 to determine PAR (Vollenweider 1974). Monthly PAR estimates were derived using weekly pyranometer charts.

A Montedoro-Whitney underwater photometer (Model LMT-8a) was used to measure percent light attenuation with depth in the water column (Fig. 3). Percent light reduction at the sediment surface by marsh vegetation was determined using a simple hand-held Gossen light meter.

B. Alkalinity, pH, nutrients.

Samples of water to be used for incubation in primary production experiments collected at the edge of the delta were analysed for pH and alkalinity using an Orion Digital pH meter, Model 801. Carbonate alkalinity for use in productivity equations was determined according to Strickland and Parsons (1972). Analyses were done within 6 h of collection.

Sample collection and subsequent analyses for ortho-phosphate, ammonia, nitrate and nitrite were done using methods of Strickland and Parsons (1972). Samples were transported to the laboratory in ice chests and

immediately frozen until analysis, conducted within 4 wk.

Surface water samples were taken on the east side of the dyke at monthly intervals at high slack water for seasonal nutrient analyses (Fig. 3).

Nutrient losses from Pile and Snag creeks were monitored at 3-4 month intervals. Samples were taken when the tide fell below the marsh surface, again at about mid-ebb tide, and finally near low slack water at a point 10 m from the creek mouths (Fig. 3). Background nutrient levels present prior to ebb tide were determined from samples taken over the delta on the preceeding high tide. Values were corrected for background concentrations and combined with information on flow rates of the creeks to provide estimates of nutrients "leached" from the sediment and carried off the delta over an ebb tide.

C. Sediment and organic deposition patterns.

Four sediment cores (5 cm diam.) were taken in June 1974 from the seven major sediment-habitat types on the delta (Fig. 3, see Appendix V for area descriptions). The cores were extruded, wrapped in aluminum foil and returned to the laboratory for analysis. Cores were initially sectioned longitudinally to expose surfaces undisturbed by the coring process. Annual layers, identified by differences in sediment particle size and presence of vascular plant remains, were

measured and separated. Each layer was taken, mixed thoroughly and the wet weight determined. Four weighed subsamples were then taken from which moisture and organic content were determined by drying to constant weight at 100 C, weighing and ashing in a muffle furnace 4 h at 500 C. Multiplication of the ash-free dry weight (i.e. organic content) by 0.5 gave estimates of g C·g dry wt sediment⁻¹, as organic matter was assumed to be 50 % carbon based on estimates given by Westlake (1963).

Estimates of sedimentation during freshet were made by securing centimeter rulers vertically to solid substrates and recording depth changes over time.

D. Tidal creek flow rates.

Flow rates were determined for Pile and Snag creeks at 20 min intervals over an ebb tide in April and June 1975. A pole, marked off in 5 cm intervals, was secured in place vertically in the deepest part of the creek bed. On the following day, measurements of flow rate (F) were begun when the level of the creek fell below the marsh surface. The time (T) in seconds for a wooden block 4 x 6 cm to travel a distance (L) of 1 m and the width (W) and depth (D) in m of water in the creek were noted. The sections of the creeks chosen for the determination of flow rates (Fig. 3) approximated rectangles; thus an equation based on the volume of a rectangle was derived:

$$F \text{ (l}\cdot\text{s}^{-1}) = \frac{(L \times W \times D)}{T} \times 10^3 \quad (1)$$

Where: 10^3 = factor for expressing $\text{m}^3\cdot\text{s}^{-1}$ as $\text{l}\cdot\text{s}^{-1}$.

II. Biological Factors

A. Distribution (coverage) area), biomass.

Four quadrat samples (0.06 m^2) of a macroalgal species or a microalgal association were randomly selected from within the coverage area. Sediments were scraped to a depth of 0.2 cm for diatom associations. Macroalgal samples were cleaned of vascular plant material and sediment prior to analysis. Samples were oven dried at 100 C to constant weight, ground and redried 2 h prior to dry weight determinations. Three equally weighted sub-samples were then removed and treated in the same manner as organic matter in the sediment cores (part I C, preceeding). Standing crop biomass was expressed as $\text{g C}\cdot\text{m}^{-2}$.

Distribution or coverage area for each macroalgal species and microalgal association was estimated using a combination of ground survey and aerial photographs. Plots were made from these data showing seasonal distribution of algae for fall, winter, spring, and summer.

B. Primary production.

Two methods were employed for the determination of benthic algal primary production. The first was the radioactive carbon (^{14}C) technique based on uptake

and fixation of CO_2 . The second was the dissolved oxygen method based on an equivalence of oxygen evolved and organic material produced. The basic techniques are described in detail by Strickland and Parsons (1972) and Vollenweider (1974).

The ^{14}C technique was used to obtain seasonal production estimates for reasons of greater accuracy in waters having high dissolved organic content and high nutrient concentrations such as were present at Squamish (Strickland and Parsons 1972). Gross production values, unattainable by the ^{14}C method, are desirable for the construction of energy budgets. Dissolved oxygen production data provided an experimental basis for extrapolating ^{14}C values which were assumed to approximate net production (Parsons and Takahashi 1973).

Carbon-14 method. Water samples for incubation were collected at the edge of the delta (Fig. 3) and filtered through a $10\mu\text{m}^2$ mesh Nitex screen. Productivity bottles (two 135 ml light and one 135 ml dark) were filled and a sample of algae, *ca.* 0.5 cm^2 , cleaned of extraneous organic matter and sediment, was added to each bottle. In mud and sand microalgal associations, the 0.5 cm^2 sediment sample was scraped to a depth of 0.2 cm and added to the bottles. Production bottles were inoculated with 1 ml of radio-isotope stock solution $100\mu\text{Ci } ^{14}\text{C-NaHCO}_3$ in 10 ml sterile water (pH 9.5) (New England Nuclear) diluted with 75 ml distilled deionized water, using an automatic pipette.

Control sets without algal material were run to account for metabolic activity of micro-organisms passing through the screen. Each day a production experiment was done, the number of disintegrations per minute (dpm) per ml were determined by placing 1 ml stock solution into each of three vials containing 15 ml of Aquasol (New England Nuclear, Liquid Scintillation Cocktail).

Sample incubation was done at two depths throughout the study. During the late spring and summer, when daytime low tides predominated leaving the algae either totally exposed or in shallow pools, bottles were incubated in tidal pools *ca.* 15 cm deep. However, during the fall and winter, when high tides occurred during the day, bottles were suspended as described by Pomeroy (1974) at *ca.* 15 cm below the surface in the area of the delta. The values obtained from these incubations are referred to as surface production. In addition, bottles were suspended at 1 m. The production values obtained, when combined with information on tide cover, provided more accurate daily production estimates. All incubations, of *ca.* 4 h duration, were done *in situ*, generally between 1000 and 1400 h.

Following incubation, 2 drops concentrated formalin were added to each bottle before return to the laboratory, with analyses done within 3 h. The control sets were filtered onto Sartorius 0.45 μm^2 pore diameter cellulose acetate filters which were then exposed to fumes of conc. HCl for 10 min to removed any active CO_2

precipitated as carbonate. Filters were then placed in scintillation vials with 15 ml Aquasol. Bottles containing microalgal associations from sand/mud substrates were shaken and allowed to settle 10 sec when much of the heavier sediment particles settled. The supernatant was filtered onto Sartorius filters and treated as described. Macroalgal samples were removed from the bottles by filtering onto pre-weighed Sartorius filters. Intact algae (thalli, large filaments) were removed from the filters, blotted dry and exposed to conc. HCl fumes, blotted dry again and weighed (wet wt.). Small filamentous algae and sand/mud microalgal associations were treated as for macroalgae except the material was removed by scraping. All algal material thus treated was placed in glass scintillation vials with 1 ml Protosol (New England Nuclear) and digested for 24 h at 50 C. Subsequently, 15 ml of specially prepared scintillation fluor [5.5 g PPO plus 50 mg POPOP (New England Nuclear) to 1 l with 1:2 (v/v) 2-ethoxyethanol, toluene] (UNESCO 1973) was added to each vial.

Dissolved organic material (DOM) released from algae during ^{14}C incubation periods may represent a significant portion of the total daily ^{14}C uptake and production (Sieburth 1969). To account for this loss and possible underestimates of production, filtrates collected from ^{14}C production light bottles (Watt 1965) were treated to remove active inorganic carbon dioxide and retain volatile organic material exuded during

production (carbohydrates, nitrogenous, polyphenolic materials). Modifying the method of Sieburth (1969), four replicates of 2 ml filtrate from each light bottle were placed in glass scintillation vials, acidified with 0.2 ml 3 % phosphoric acid and purged 15 min with pure nitrogen, followed by the addition of 15 ml Aquasol. Tests were also run on filtered water without added algal material to check for background levels of dissolved organic material.

The activities of stock solution, control sets, algal samples and light bottle filtrates were determined on a Packard Tri-Carb Liquid Scintillation Spectrophotometer (Model 3375).

The equation used to convert dpm to mg ^{14}C -DOM released was:

$$\text{mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1} = \frac{\frac{L_{\text{dpm}} \times 67.5}{\text{mg algae (wet wt.)}} \times \xi \text{CO}_2 \times 1.05}{L_t \times a} \times F \times D_w \quad (2)$$

where: L_{dpm} = dpm in 2 ml sub-sample from light bottle; 67.5 = factor to express dpm/135 ml bottle; ξCO_2 = total CO_2 in bottle as mg C (Strickland and Parsons 1972); 1.05 = isotope correction factor; L_t = PAR during incubation/daily PAR; a = absolute activity (dpm) of added isotope stock; F = conversion factor for wet to dry wt. of algae; D_w = dry wt. of algae ($\text{mg} \cdot \text{m}^{-2}$).

The equation used to convert dpm to mg particulate C fixed $\cdot m^{-2}$ was:

$$\text{mg C} \cdot m^{-2} \cdot \text{day}^{-1} = \frac{R \times \Delta \text{CO}_2 \times 1.05}{\text{Lt} \times a} \times F \times D_w \quad (3)$$

where: R = dpm/unit wet wt light bottle - dpm/unit wet wt dark bottle.

Estimates of total net primary production were then made by combining the values from Equation 2 on organic exudates (DOM) and Equation 3 on particulate organics (POM) (Parsons and Takahashi 1973, Sellner *et al.* 1976).

Dissolved oxygen method. At intervals throughout the study, primary production was determined with a modified light and dark bottle dissolved oxygen (DO) technique (Strickland and Parsons 1972). Algal samples of *ca.* 4 cm² were added to 300 ml DO bottles (2 light, 1 dark) containing water pretreated as described for the ¹⁴C method with control sets minus algae and incubated as described.

Production values are expressed as mg O₂ $\cdot l^{-1}$ (Strickland and Parsons 1972) and converted to mg C $\cdot m^{-2}$ day⁻¹ using the equation:

$$\text{mg C} \cdot m^{-2} \cdot \text{day}^{-1} = \frac{\text{mg O}_2 \cdot l^{-1} \times 0.3 \times C}{\text{Lt}} \times W \quad (4)$$

where: 0.3 = correction factor for O₂ content in 300 ml bottle; C = conversion factor for mg O₂ to mg C (macroalgae PQ = 1.20, C = 0.278; microalgae

with higher fat content $PQ = 1.25$, $C = 0.300$
 (Westlake 1963)); $Lt = PAR$ during incubation/daily
 PAR ; $W = \text{dry wt of algae} \cdot m^{-2} / \text{dry wt of algae}$
 incubated.

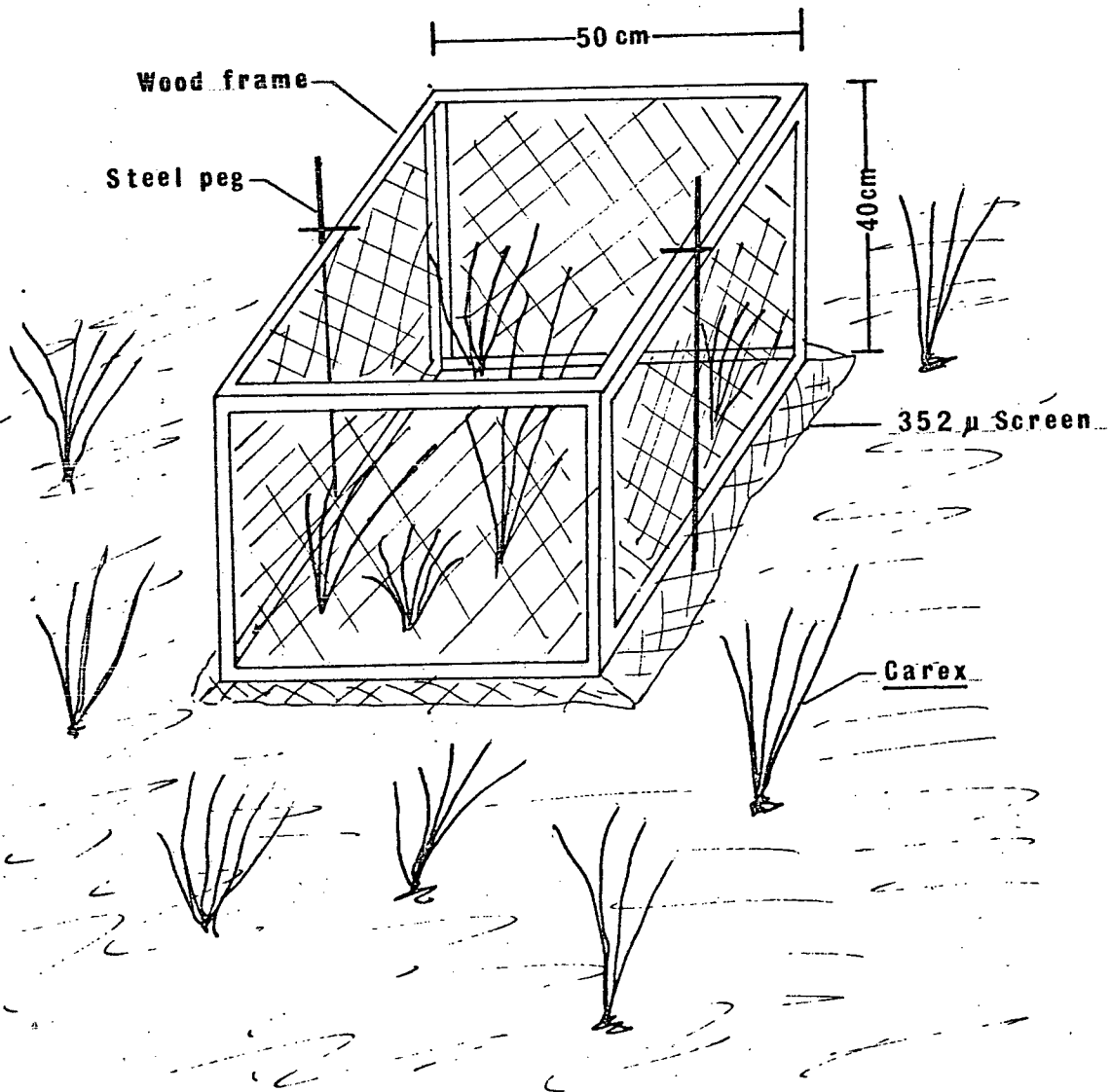
C. Removal, deposition of particulate organic matter (POM).

For removal of POM (intact macroalgae, microalgae and detrital material--dead organic matter of plant or animal origin with associated micro-organisms (Mann 1972)) during floodtide and its addition to the water column, two sampling transects were selected at the delta front, one on the western sector and one on the eastern (Fig. 3). Seven stations were sampled along each, covering the major algal growth forms and habitats. Samplings were also made in the upper intertidal.

Wooden cages ($50 \text{ cm}^2 \times 40 \text{ cm}$ high) covered on four sides with $352 \mu m^2$ Nitex screening were used (Fig. 4). The mesh size allowed relatively free water movement into the cages for "normal" removal of POM but restricted entry of larger plant material. The cages were initially placed on the sand/mud flats at the seaward edge of the delta and secured with steel pegs. Prior to the incoming tide reaching the level where the cages were located, two 1 l water samples were taken outside the cage for analysis of "background" POM (amount before the tide reaches a specific level on the delta) and microscope examination. Subsequently, when the incoming tide reached a predetermined depth and thus a known water

Figure 4. Diagram of cage used for studies of particulate organic removal in place on the delta.

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volume in the cages, 1 l water samples were taken from inside for the above noted analyses. The cages were rinsed and then moved back to an area of the delta not yet reached by the incoming tide where the sampling procedure was repeated.

Samples for microscope examination were preserved in Lugol's solution and examined using the Utermohl (1958) sedimentation technique. Identification of algae as to planktonic and benthic, the relative dominance and estimates of the proportion of macroalgae, microalgae and detritus were made. One liter water samples were filtered onto pre-ashed and weighed Whatman GFC glass fiber filters. Analysis for organic content was as previously described.

The organic content was estimated by:

$$\text{mg C removed} \cdot \text{m}^{-2} \cdot \text{flood tide}^{-1} = \frac{C_1 - C_b \times V}{a} \quad (5)$$

where: C_1 = mg C $\cdot$ l $^{-1}$ inside cage; C_b = mg C $\cdot$ l $^{-1}$ background level outside cage; V = water volume inside cage (l); a = area of enclosure (m $^{-2}$).

To study removal of POM via tidal creeks on an ebb tide, measurements were done in the major creeks when the water level fell to the surface of the marsh. Stations were established ca. 10 m back from the mouths of Snag and Pile creeks (Fig. 3). Two 1 l samples were taken at high (15 cm below water surface) and low (near creek bottom) water level, with determination of organic

content and microscope examination carried out as described. Estimates of the total amount of POM leaving the marsh through tidal creeks on an ebb tide were possible by combining data on $\text{g C} \cdot \text{l}^{-1}$ with that on flow rates.

The addition of POM was determined monthly by measurements of amounts deposited on the mud/sand flats and on the marshland over a tidal cycle. Sampling sites were located in the low, mid, and upper intertidal zones (Fig. 3). Large size plastic petri dishes of known area were secured with their openings $\text{ca. } 3 \text{ cm}$ above the surface of the sediment at one low tide and retrieved on the following low tide. The sample was split, with half being used for microscope examination and half for determination of organic content as described. Results are expressed as $\text{mg C deposited} \cdot \text{m}^{-2} \cdot \text{tidal cycle}^{-1}$.

D. Caloric equivalents.

Caloric equivalents were determined for the major benthic algal producers, vascular plants, detritus, sediment organics and material removed from and deposited on the delta. Sediments with microalgal associations and detrital deposits were scraped to a depth of 0.5 cm . Material collected from removal and deposit sites (Fig. 3) was returned to the laboratory in ice chests within 3 h where it was immediately centrifuged to remove excess water. The samples were placed in plastic bags and frozen until analysis could be performed (up to 10 mo

after collection).

At the time of analysis, macroalgae and vascular plant material were lightly washed in distilled water to remove sediment particles. All samples were dried to constant weight at 80 C rather than 100 C to reduce the probability of denaturing proteins or volatilizing energy rich materials (Paine 1971). Samples were ground to a fine powder. For sediment organics and microalgal associations with low caloric content/g material, a known amount of benzoic acid standard was added to the sample to bring the value to a readable level. Replicates were taken for each sample and burned in a Phillipson Microbomb Calorimeter to determine cal·g dry wt⁻¹. Applying organic content to caloric value, estimates were made of g cal·g organic material⁻¹.

Equivalents were not determined for dissolved organic matter due to technical limitations. Values derived for the corresponding algae were used and are considered to be minima since the exudates are known to have higher caloric values than are intact cells with cellulose or silica walls (Paine 1971).

E. Algal, plant and detritus utilization by amphipods.

Abundant gammarid amphipods (*Anisogammarus confervicolus* (Stimpson)), an important food source for salmonids (Anonymous 1972), were associated with vascular plants, benthic algae and detritus in the field. Studies were undertaken to determine the importance of these

to both adult (sexually mature) and juvenile in terms of protection and a source of food.

Field Studies. Observations were made on the relationship of amphipods and cover type at low tide on each sampling date. Each macroalga and microalgal association was examined as well as detrital material. A detailed examination of a section of the marshland was made (30 x 30 m grid in the mid-intertidal zone) noting associations at 1 m intervals. Observations were made as to whether or not amphipods were actively feeding (mouth parts being manipulated) on the plant material with which they were associated. Collections were made and amphipods placed immediately in 10 % formalin. Subsequently, the gut was removed and opened for microscope examination to relate gut appearance to food consumed.

Laboratory studies. Amphipods collected in May and June 1975 for cover preference studies were fed on a mixture of decayed vascular plants, macroalgae and detritus collected from the study area while being acclimated for 1 wk at 15 ‰ S. Subsequently, the amphipods were placed in a tray containing separate clumps of each material in ca. 2 cm water at normal room light. The number of amphipods associated with each clump was noted after 5 min. The short time interval was selected to avoid the onset of feeding activity following a fright/cover response.

Experiments were conducted in the laboratory to indicate food preference by starving field collected amphipods acclimated to 15 ‰ S. Trays were set up as described for cover studies, but were covered with black plastic sheeting to insure a "safe" feeding situation. The number of amphipods actively feeding on each food source was noted after 10 min.

Cover and feeding experiments were repeated a number of times, varying the arrangement of materials in the trays and the point at which the amphipods were introduced.

Fatty acid spectra comparison. Past studies show that algae display characteristic fatty acid spectra in the C_{14} - C_{22} range (McIntyre *et al.* 1969). Thus, experiments were designed to identify gut contents and thus food source based on fatty acid spectra. Determinations were made of the various food sources as well as starved amphipods, amphipods fed on a single food source and amphipods collected from the field. The extraction method used was a modification of those suggested by McIntyre *et al.* (1969), Jeffries (1972) and Schultz and Quinn (1973).

Ten g tissue (air dry wt) was ground and placed in a flask with 100 ml of chloroform : methanol (2 : 1 v/v), acidified with 2 ml conc. HCl. Extraction proceeded for 24 h at 15 C, after which the contents of the flask were gravity filtered through a Whatman # 1 filter paper previously leached with the chloroform : methanol acid

solution. The filtrate was concentrated in a rotary evaporator and the residue dissolved in 10 ml petroleum ether and transferred to a vial. Methylation followed with 1 ml diazomethane for 30 min. The extract was then dried under N_2 gas in a water bath (30 C). The sample was solubilized with 2 ml petroleum ether and analyzed immediately for total fatty acid content on a Hewlett Packard Gas Chromatograph (Model 5711 A-F.I.D.). The instrument had flame ionization detectors and was fitted with a stainless steel Support Coated Open Tubular column (49 m x 2.5 mm inside diameter), packed with diethylene glycol succinate. Detector and injection temperatures were held at 200 C and column temperature at 180 C isothermal. A 5 μ l sample was injected and an integrator provided retention times and relative abundance of fatty acids.

III. Analysis of factors influencing primary production

A stepwise multiple regression analysis (TRIP) was run on the UBC 370 computer to test the effect of certain environmental factors--salinity, light intensity, temperature, nitrate, phosphate and ammonia--on net production. Since it cannot be assumed that any of these factors operate independently to control production (Zaneveld 1969), TRIP was chosen as appropriate.

RESULTS

I. Physical-Chemical FactorsA. Salinity, temperature, light.

Daily means and monthly estimates of photosynthetically available radiation (400-700 nm) reaching the study area appear in Table 1. Maximum values occurred in July 1975, with the minimum in January 1975.

Light attenuation in the water column adjacent to the delta was greatest during the maximum river flow period (June, July) (Fig. 5). Values immediately below the surface averaged *ca.* 50% of incident radiation whereas illumination at 2 m was as low as 2%. Minimum light attenuation occurred during the winter with 90% of incident radiation recorded just below the surface. Illumination at 1 m averaged *ca.* 30% of incident radiation and *ca.* 15% at 2 m (Fig. 5).

Reductions in the amount of incident radiation reaching the sediment surface on the marshland were evident with increased height of vascular plants (Table 2). Stands of *Carex lyngbyei* had a much greater shading effect at the sediment surface than did *Eleocharis palustris*. For the former, percent total incident radiation reaching the sediment was lowest at times of peak growth (*ca.* 6-14% in July) and upon formation of the dead vegetation mat in November (*ca.* 2%). In comparison, the growth form of *E. palustris* permitted much more light penetration, with a minimum of 37%

Table 1. Photosynthetically available radiation (400-700 nm) reaching the study area.

Month	Daily mean (g cal·cm ⁻²)	Monthly estimate (kcal·cm ⁻² ×10 ³)
1974		
June	255.0	7.65
July	250.0	7.75
August	149.0	4.63
September	154.0	4.62
October	101.0	3.03
November	30.8	0.92
December	28.9	0.90
1975		
January	20.0	0.63
February	29.8	0.83
March	26.0	0.81
April	94.2	2.83
May	210.6	6.53
June	264.6	7.94
July	266.4	8.26
August	134.2	4.16

Figure 5. Light attenuation with depth in water column adjacent to the delta (data appear in Appendix 1).

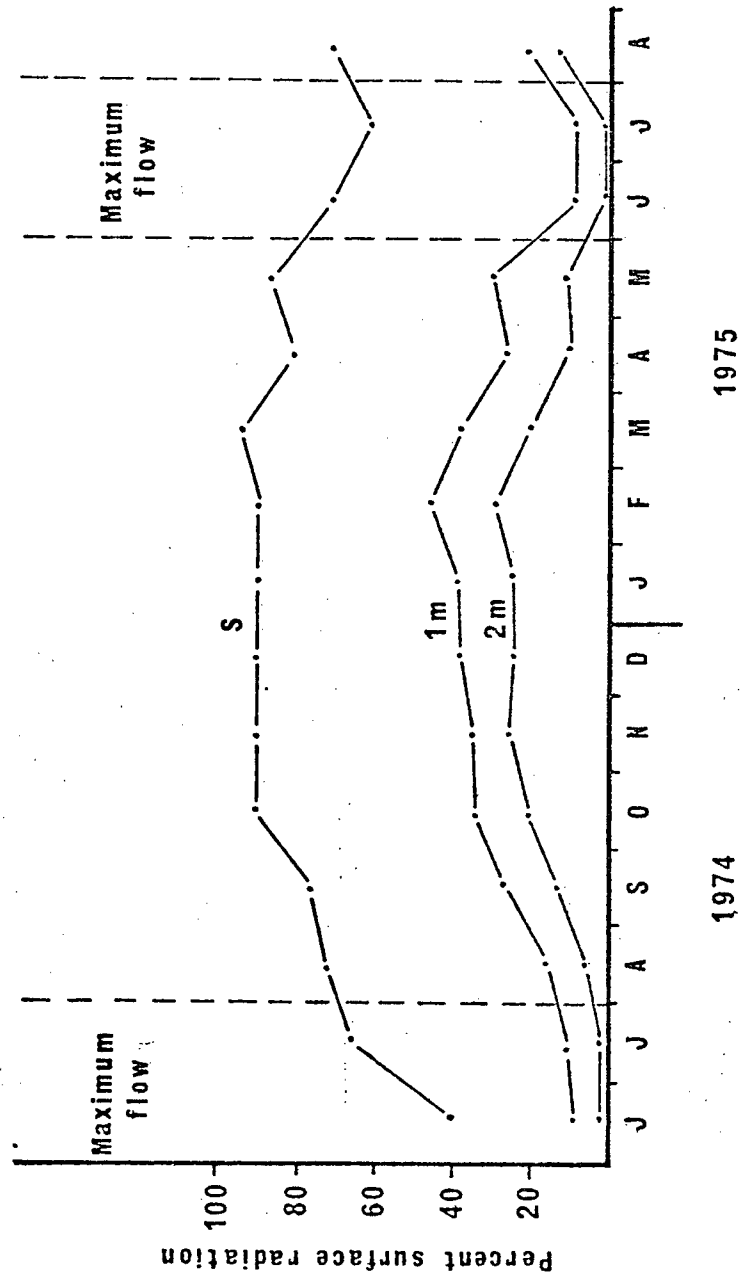


Table 2. Shading of the delta surface by attached vascular plants. Light attenuation as percent incident radiation

Date	<i>Carex lyngbyei</i>		<i>Eleocharis palustris</i>	
	height (cm)	% incident radiation	height (cm)	% incident radiation
1974				
19 July	50	14	15	60
	60	14	30	48
	110	6	-	-
27 August	40	26	15	58
	60	12	40	44
	80	10	-	-
13 September	20	24	15	60
	40	10	40	50
	50	6	-	-
17 October	20	20	15	49
	30	12	20	37
	40	10	-	-
November - Prostrate mat of dead vegetation (ca. 15 cm high) with 2% of surface radiation noted.				
1975				
19 March	5	46	5	80
16 April	5	40	5	80
	10	30	10	65
	15	25	-	-
14 May	10	35	10	70
	15	25	15	60
	20	15	-	-
20 June	20	20	15	60
	40	15	20	48
	60	12	-	-
18 July	40	20	20	55
	65	14	30	44
	100	8	-	-
10 August	40	25	20	55
	50	20	35	42
	85	12	-	-

incident radiation recorded in October (Table 2).

Air temperatures during the day were highest in August and lowest in January and February (Fig. 6a). Daytime water temperatures just below the surface averaged 10 C during the high runoff period (May-August), with winter values near 5 C (Fig. 6b). Temperatures at 1 m were 1 C higher than surface for most of the study (Appendix II).

Monthly precipitation increased from 18 cm in September 1974 to 71 cm in December (Fig. 6a), with a general decrease to August 1975. Seasonal variation in freshwater runoff caused distinct salinity patterns in the estuary (Fig. 6c). A low salinity layer (3 m or more) was present during the period of high runoff. The mean surface salinity was ca. 2-3 ‰ with an increase of only 1-2 ‰ over 1 m. A second period of reduced salinities occurred in November-December concurrent with a time of high precipitation (Fig. 6a, c). Salinity values through the winter were generally high, reaching 27.9 ‰ in January.

B. pH, nutrients.

Seasonal variations in pH ranged from 6.93 (July) to 7.96 (January) (Fig. 6b). A second minimum was noted in December during the low salinity winter runoff period. The pH in Snag and Pile creeks was 0.1 to 0.2 lower than from the surrounding waters (Fig. 6b, Appendix III), with little variation between the creeks.

Figure 6 a, b, c. Air temperature, water temperature, pH, precipitation, and salinity June 1974 - August 1975 (data appear in Appendix II).

Fig. 6a

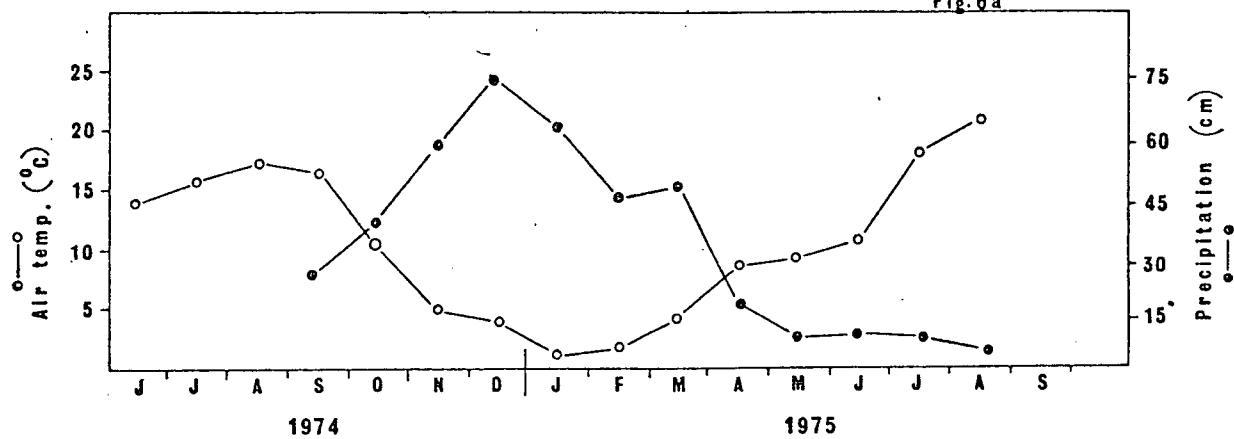


Fig. 6b

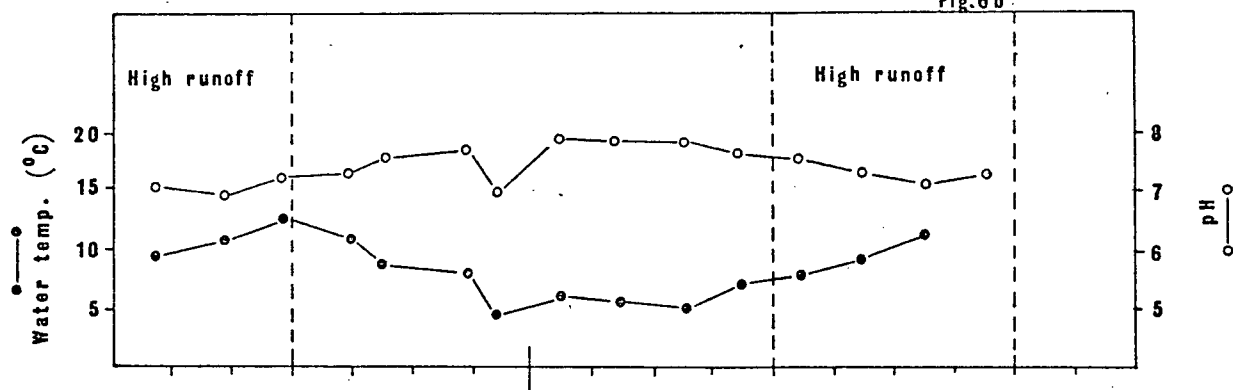
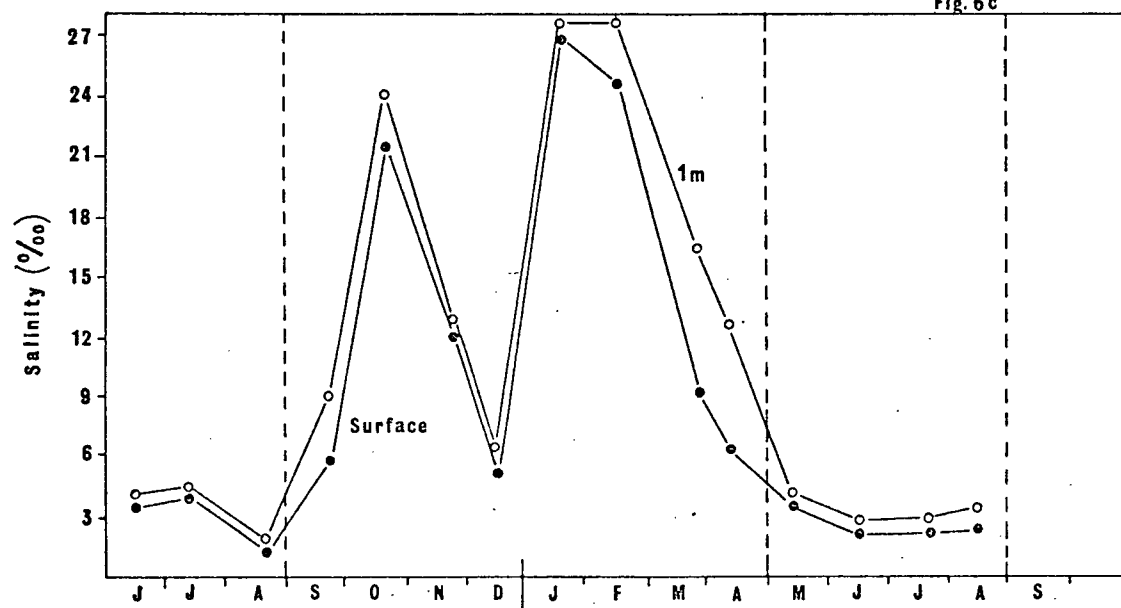


Fig. 6c



Nitrate, ammonia and ortho-phosphate concentrations in surface waters adjacent to the delta varied considerably. Nitrate reached a high in January, with low values occurring in summer and early fall (Table 3). Phosphate, less than one tenth the maximum concentration of nitrate, was also highest in January, whereas ammonia, with a slightly higher concentration, was at its maximum during May.

Nutrient concentrations were generally higher in Pile and Snag creeks compared to surrounding waters, with seasonal patterns appearing similar (Appendix III, Table 3). Nutrient concentrations in the creeks at mid-ebb tide were usually higher than at other tide times. Nitrate and phosphate concentrations in Pile creek, draining the mid-intertidal marsh, were higher than those recorded for Snag creek, draining the upper intertidal marsh. Ammonia concentrations were approximately twice as high in Snag creek.

C. Sediment and organic deposition patterns.

Maximum sedimentation occurred during the high runoff period (May-August), with an average of 0.95 ± 0.09 cm deposited during the maximum runoff in June and July. Sedimentation from October to March was low, totalling 0.15 cm. Over the 15 mo study period, 2.05 cm were deposited with an average annual estimated at 1.50 ± 0.03 cm.

Table 3. Nutrient concentrations ($\mu\text{g-at}\cdot\text{l}^{-1}$) in surface waters surrounding the delta (samples taken at high tide).

Date	NO_3^-	NH_4^+	PO_4^{3-}
1974			
8 August	0.00	0.60	1.86
6 September	0.00	0.00	0.00
22 December	0.79	1.30	0.30
1975			
22 January	29.72	0.00	2.09
19 March	15.83	0.00	1.10
30 April	- ^a	1.14	0.87
14 May	6.14	2.90	0.00
11 June	3.70	0.00	0.02
20 June	2.19	2.56	0.02
9 July	3.10	0.36	0.02

^a sample missing

Sedimentation and sediment organic content varied spatially and temporally over the delta (Fig. 7).

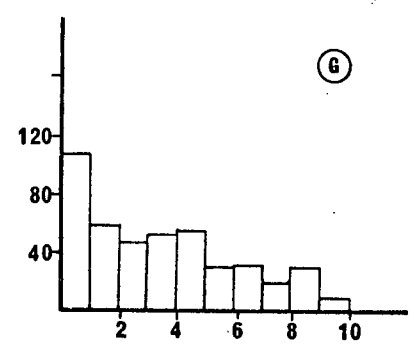
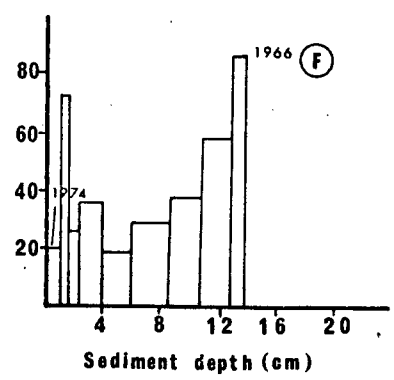
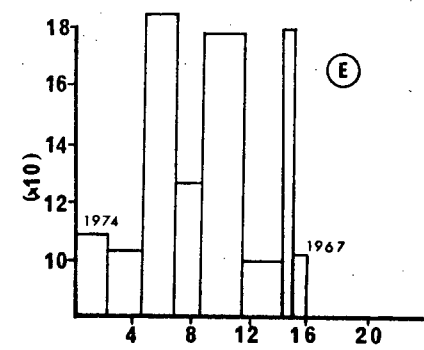
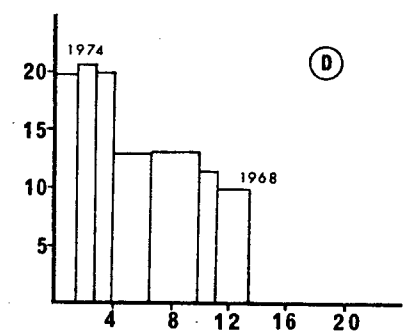
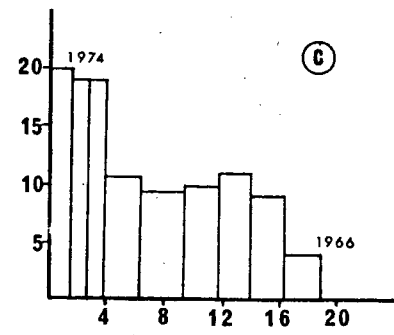
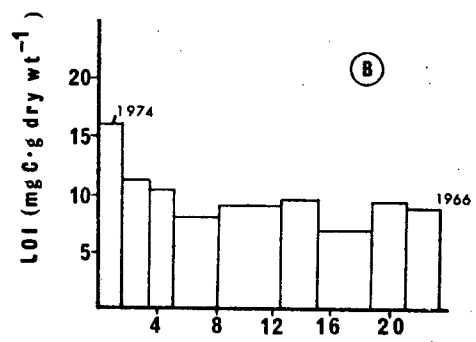
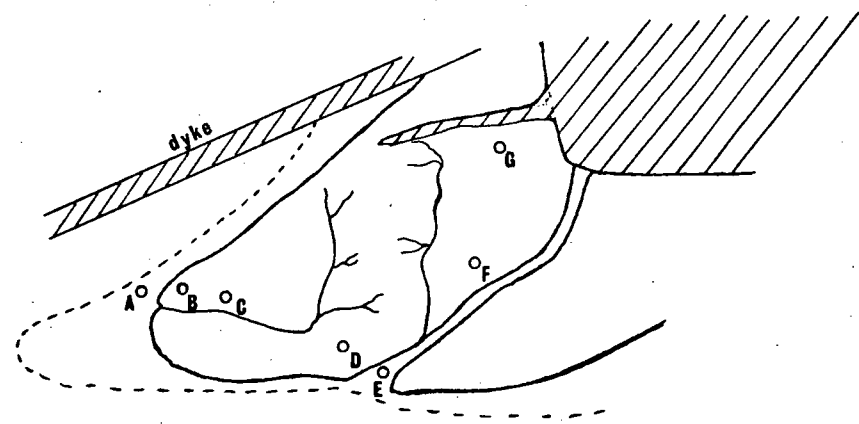
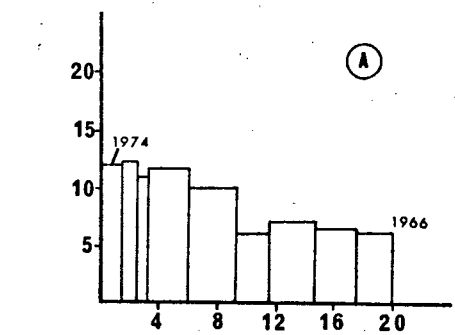
Deposition of sediment was generally greatest in 1969 and 1970 prior to dyke construction and redirection of the river, averaging 3.2 ± 0.3 cm, decreasing towards the upper intertidal zone. Rates of sedimentation noted from 1972 to 1974 were approximately half those noted for the 1970 to 1971 period when river dredging and land fill operations were in progress. Total sedimentation from 1969 to 1974 was greatest at the delta front in Areas A, B, and C, averaging 20 ± 1.3 cm. Lowest sedimentation was recorded in Area D, with an average of 12.5 cm during the same period.

The organic content (mg C) of sediments in Areas A through D generally decreased with depth (Fig. 7). Area A (low intertidal) with coarse sand had the lowest organic content. Areas B, C, and D (mid-intertidal) were similar in terms of organic content but were about 4 mg C·g dry wt sediment⁻¹ higher than comparable depths in the low intertidal zone. Area E, a creek bottom in the low intertidal zone, had the highest organic content on the delta.

D. Tidal creek flow rates.

Pile creek discharged ca. 703×10^3 l over an ebb tide whereas Snag creek was higher at ca. 810×10^3 l. These values apply only to a complete drainage of the creeks and an adjustment, using tide tables to account

Figure 7. Seasonal patterns of sedimentation and sediment organic content as determined from cores taken on the delta at locations indicated (site descriptions and data appear in Appendix IV).



for incomplete drainage, is needed to arrive at more realistic monthly discharge values.

II. Biological Factors

A. Species composition and distribution.

Benthic algae present belonged to seven classes, showing zonation and substrate-habitat specificity within the intertidal region (Table 4). The rhodophytes and dinoflagellates were restricted to the low intertidal while phaeophytes were distributed over the low and mid-intertidal zones at the periphery of the marshland. Chlorophytes and cyanophytes occurred in both the mid- and upper intertidal regions. The chlorophytes were the most common and widely distributed macroalgae on the delta with *Enteromorpha minima* and *Monostroma oxyspermum* present all year. Cyanophytes, with the exception of *Rivularia biasoletti* which persisted at the periphery of the delta, occurred in multispecific microalgal associations in small "dead zones" and open areas within the marshland. The cyanophytes were also found in association with xanthophyte mats in the upper intertidal.

Macroalgae listed in Table 4 were found as monospecific growths with some associated microalgal epiphytes (Fig. 8 a, b). Microalgal associations consisting of diatoms and/or filamentous chlorophytes were distributed over the delta. Each association had a characteristic appearance in the field (Fig. 8 c, d)

Table 4. Major algal species with their preferred substrate and location on the delta.

Species	Substrate	Intertidal location	Area
Chlorophyceae			
<i>Cladophora</i> sp.	vascular plants	upper	tidal pools
<i>Enteromorpha minima</i> (Nag.) ex Kütz.	logs and pilings	mid-upper	periphery of delta
<i>E. prolifera</i> (Müll.) J. Ag.	sedge	mid	front of delta
<i>Monostroma oxyspermum</i> (Kütz.) Doty	vascular plants	mid-upper	tidal pools and mud bank at periphery of delta
<i>Rhizoclonium implexum</i> (Dill.) Kütz.	soft mud	upper	adjacent to tidal creeks
<i>Spirogyra</i> sp.	vascular plants	upper	tidal pools
<i>Ulothrix flacca</i> (Dill.) Thur.	sedge	mid-upper	marshland
Xanthophyceae			
<i>Vaucheria dichotoma</i> (L.) Ag.	sediment	upper	open areas in sedge marsh
<i>V. intermedia</i>			
<i>Vaucheria</i> spp.			

...Continued

Table 4. Continued.

Species	Substrate	Intertidal location	Area
Phaeophyceae			
<i>Fucus distichus</i> subsp. <i>edentatus</i> (De La Py.) Powell	logs	low	sand flats
<i>Laminaria</i> sp.	sediment	low	sand flats
<i>Pylaiella littoralis</i> (Lyng.) Kjell.	sedge	low-mid	delta periphery and front
Rhodophyceae			
<i>Antithamnion pacificum</i> (Harv.) Kylin	logs	low	sand flats at delta front
Dinophyceae			
<i>Amphidinium</i> sp.	] sediment	low	creek banks and sand flats
<i>Gymnodinium</i> sp.			
<i>Peridinium</i> sp.			
Cyanophyceae			
<i>Rivularia biasoletiana</i> Menegh.	sediment	mid-upper	bank at periphery of the delta
...Continued			

Table 4. Continued.

Species	Substrate	Intertidal location	Area
<i>Calothrix scopulorum</i> Ag.	sediment	mid-upper	open areas in sedge marsh
<i>Calothrix</i> spp.			
<i>Lyngbya aestuarii</i> (Merr.) Lyngb.			
<i>Oscillatoria brevis</i> (Kutz.) Gom.			
<i>O. tenuis</i> Ag.			
<i>Phormidium</i> sp.			
<i>Spirulina subsalsa</i> Qerst.			
Bacillariophyceae (major species only, others appear in Appendix V)			
<i>Melosira moniliformis</i> (Mull.) Ag.	sedge	mid	marsh
<i>M. nummuloides</i> Ag.	sedge	mid	marsh
<i>Navicula cancellata</i> Cl.	sediment-consolidated mud	low	near tidal creek mouths
<i>N. grevillei</i> (Ag.) Cl.	sediment-consolidated mud	low	bottom of tidal creeks
<i>Nitzschia closterium</i> (Ehrbg.) W. Sm.	sediment-unconsolidated mud	low	banks of tidal creeks
<i>Pleurosigma aestuarii</i> Cl.			

Figure 8 a,b. Macroalgae showing gross appearance of *Pylaiella littoralis* (A) and *Enteromorpha minima* (B).

8 c,d. Microalgal associations showing gross appearance of Association D (C) and F (D).



and was associated with a specific substrate and habitat (Table 5). With the exception of Associations E and G, distribution of microalgal associations was greatly restricted. Complete listings of the species compositions for each association appear in Appendix V.

Enteromorpha minima is the same species reported by Prange (1976) as *Blidingia minima* var. *subsalsa* (Kjell) Scagel. Some controversy exists as to whether the latter is a valid genus. Chapman and Chapman (1973) stated that there is no justification for the retention, as characters used to identify it also occur in the genus *Enteromorpha* (i.e. prostrate disc giving rise to erect plants, small cell size). Recently, sexual reproduction, hitherto given as lacking in *Blidingia*, has been identified (Tatewaki 1972, Prange 1976) and is similar to most species of *Enteromorpha*. Based on these features, the earlier classification of *Enteromorpha* is used in this thesis.

Seasonal changes in distribution and species composition of benthic algae were apparent (Table 6, Fig. 9, Appendix IV). Macroalgae such as *Enteromorpha minima*, *Monostroma oxyspermum*, *Vaucheria dichotoma*, and *Fucus distichus* subsp. *edentatus*, as well as Associations E and F were always present. The remainder were found for only a few months and indicated a particular set of physical, chemical and/or biological conditions. It is primarily these algae which produce the seasonal distribution patterns noted in Figure 9, along with biomass.

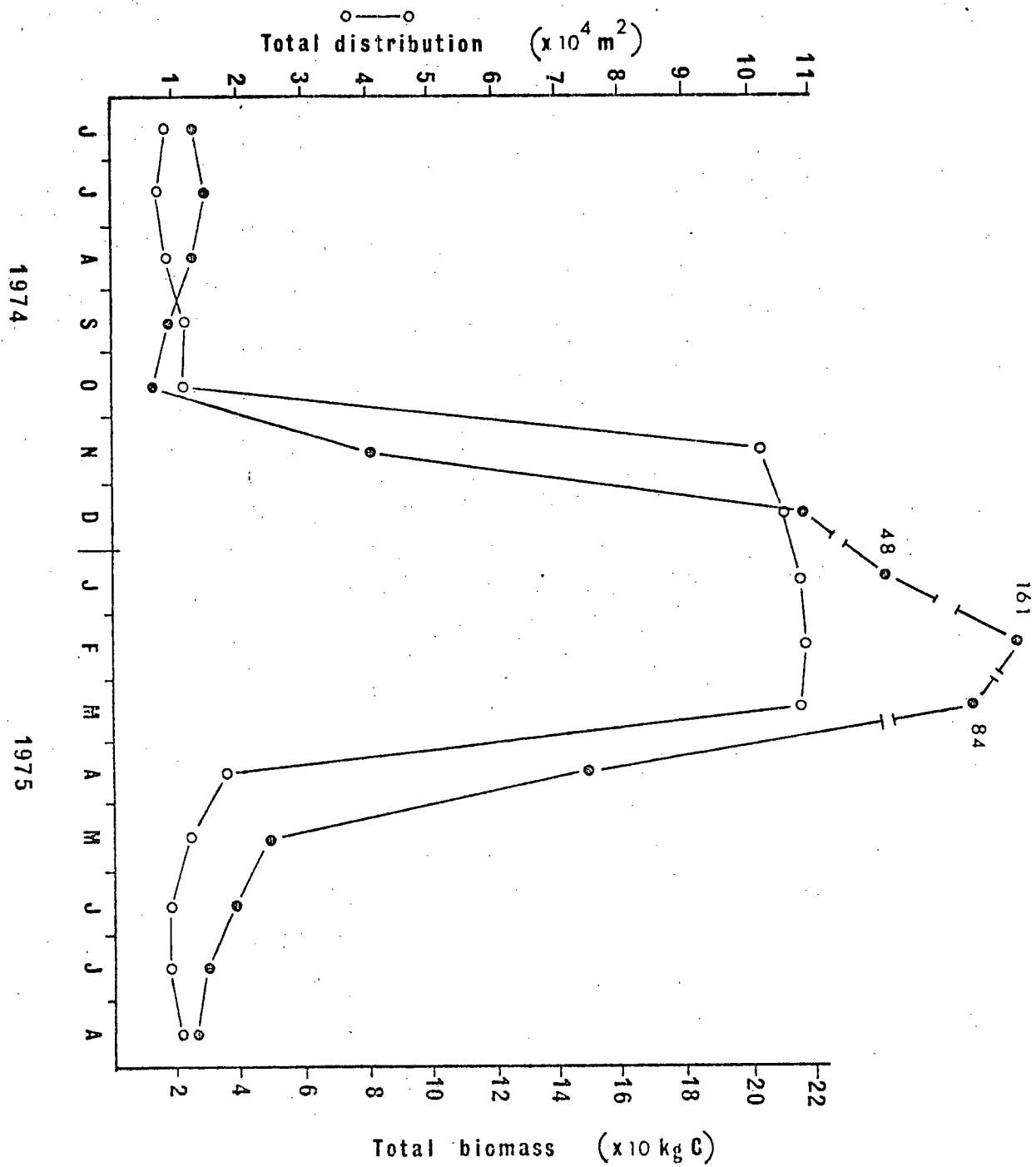
Table 5. Appearance, composition, and distribution of multispecific microalgal associations.

Association	Growth form (size)	Major species	Substrate	Intertidal location
A	dense brown filamentous clumps (≤ 5.0 cm long)	<i>Melosira moniliformis</i> <i>M. nummuloides</i>	sand-mud associated with sedge	mid
B	unconsolidated green mat (ca. 2.0 mm thick)	<i>Navicula cancellata</i>	consolidated mud in open areas adjacent to Pile Creek	low-mid
C	red-brown filamentous clumps (≤ 5.0 cm long)	<i>Navicula grevillei</i> <i>M. nummuloides</i>	coarse sand on Pile Creek bottom	low
D	light brown filamentous clumps (≤ 8.0 cm long)	<i>N. grevillei</i> <i>Melosira</i> spp.	consolidated mud, shallow pools	mid
E	brown layer, extensive (ca. 1.0 mm thick)	<i>Navicula</i> spp.	unconsolidated mud	low-mid
F	green felt-like mat (<0.5 cm thick)	<i>Vaucheria dichotoma</i> <i>Vaucheria</i> spp.	consolidated mud, sand	upper
G	green filaments with epiphytes (ca. 2.0 mm thick)	<i>Ulothrix flacca</i>	on dead vascular plants	mid-upper

Table 6. Seasonal occurrence of macroalgae and microalgal associations.

	1974					1975										
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Macroalgae																
<i>Cladophora</i> sp.	x	x	x	x								x	x	x	x	
<i>Enteromorpha minima</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Enteromorpha prolifera</i>	x	x	x	x					x	x	x	x	x	x	x	
<i>Monostroma oxyspermum</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Rhizoclonium implexum</i>	x	x	x	x	x			x	x	x	x	x	x	x	x	
<i>Spirogyra</i> sp.	x	x	x	x	x								x	x	x	
<i>Rivularia biassolettiana</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Pylaiella littoralis</i>	x						x	x	x	x	x	x	x			
<i>Fucus distichus</i> ssp. <i>edentatus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
Microalgae																
Association A	x	x	x									x	x	x	x	
B								x	x	x	x	x				
C								x	x	x	x	x	x			
D									x	x	x	x				
E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
F	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
G						x	x	x	x	x						
Total present	12	11	11	10	8	7	11	12	13	13	12	12	12	11	11	

Figure 9. Total distribution area and algal biomass.

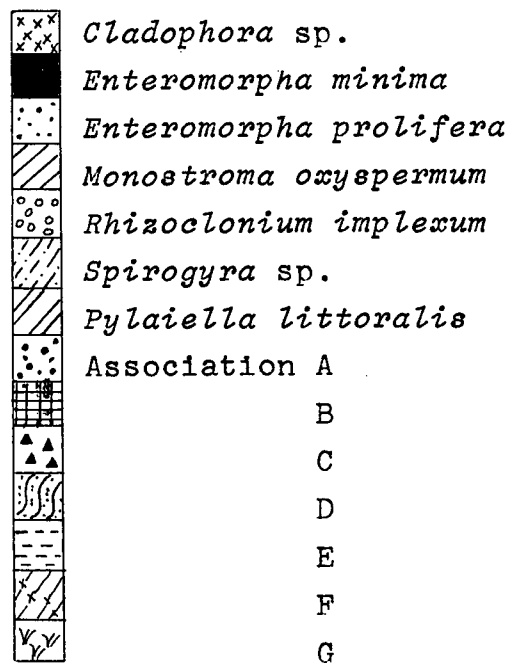


Growth present in the fall, characterized by September, covered *ca.* $10 \times 10^3 \text{ m}^2$ (Fig. 9), with Association E on the sand flats accounting for 80%. Algae were restricted to the periphery of the delta, tidal pools and open areas adjacent to the tidal creeks (Fig. 10 a). Winter (December) showed a reduction in the number of chlorophyte species and an increase in microalgal associations over that for the fall (Table 6). Distribution was *ca.* $110 \times 10^3 \text{ m}^2$ (Fig. 9) with Association G, dominated by the chlorophyte *Ulothrix flacca*, responsible for 90% of the coverage (Fig. 10 b). The spring (March) distribution pattern was similar, with Associations E and G dominant (Fig. 10 c). Species diversity was highest at this time with reappearance of chlorophytes and continuation of microalgal associations (Table 6). Summer growth, characterized by June, was again restricted to the periphery of the delta, tidal pools and creek areas as in the fall (Fig. 10 d). Chlorophytes dominated over microalgal associations (Table 6), with total distribution amounting to *ca.* $8 \times 10^3 \text{ m}^2$ (Fig. 9).

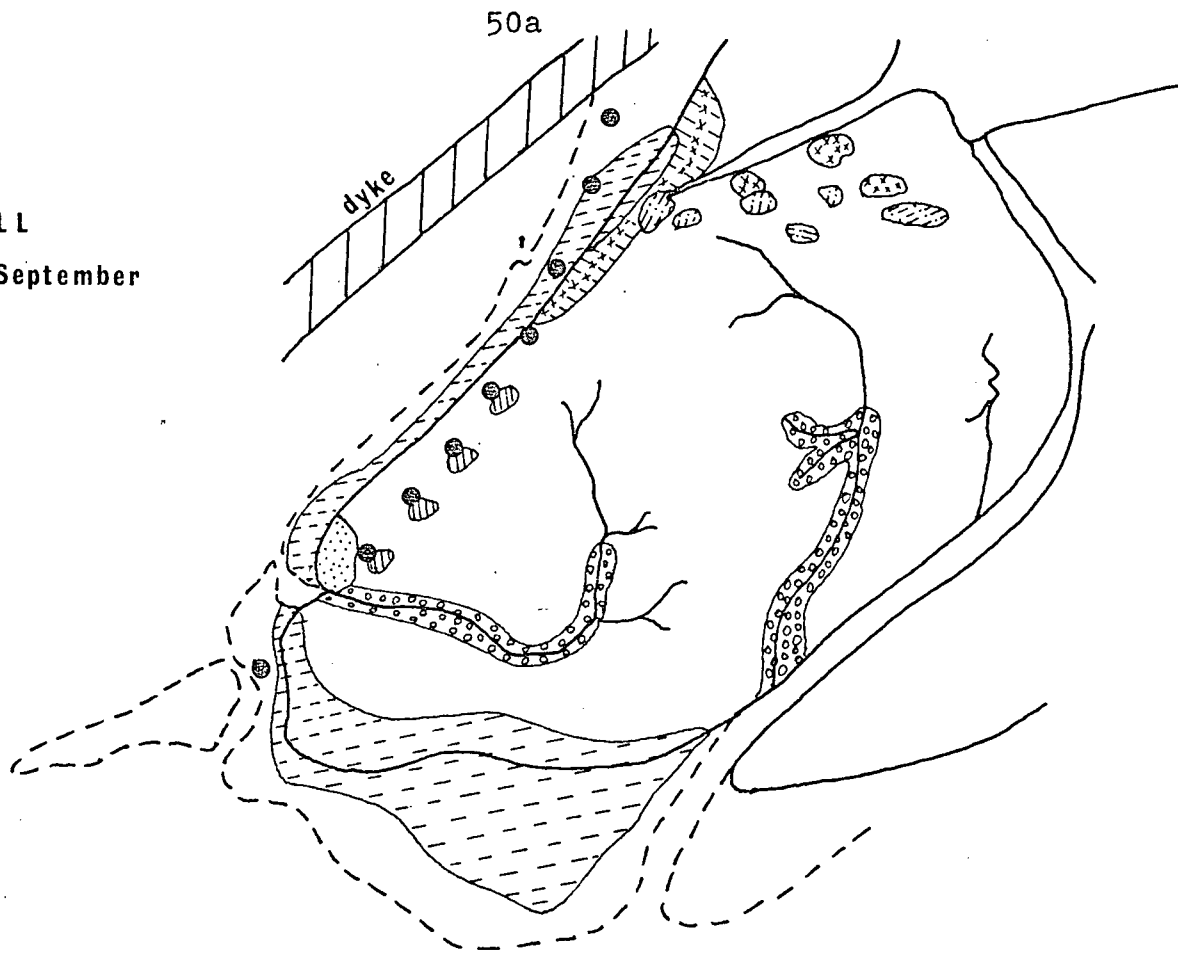
B. Biomass and production.

Standing crop biomass considered on a square meter basis indicated *Pylaiella littoralis* as the dominant contributor, followed by *Enteromorpha minima* and the chlorophyte-dominated Association G (Table 7). Association E, dominated by diatoms, had the lowest biomass

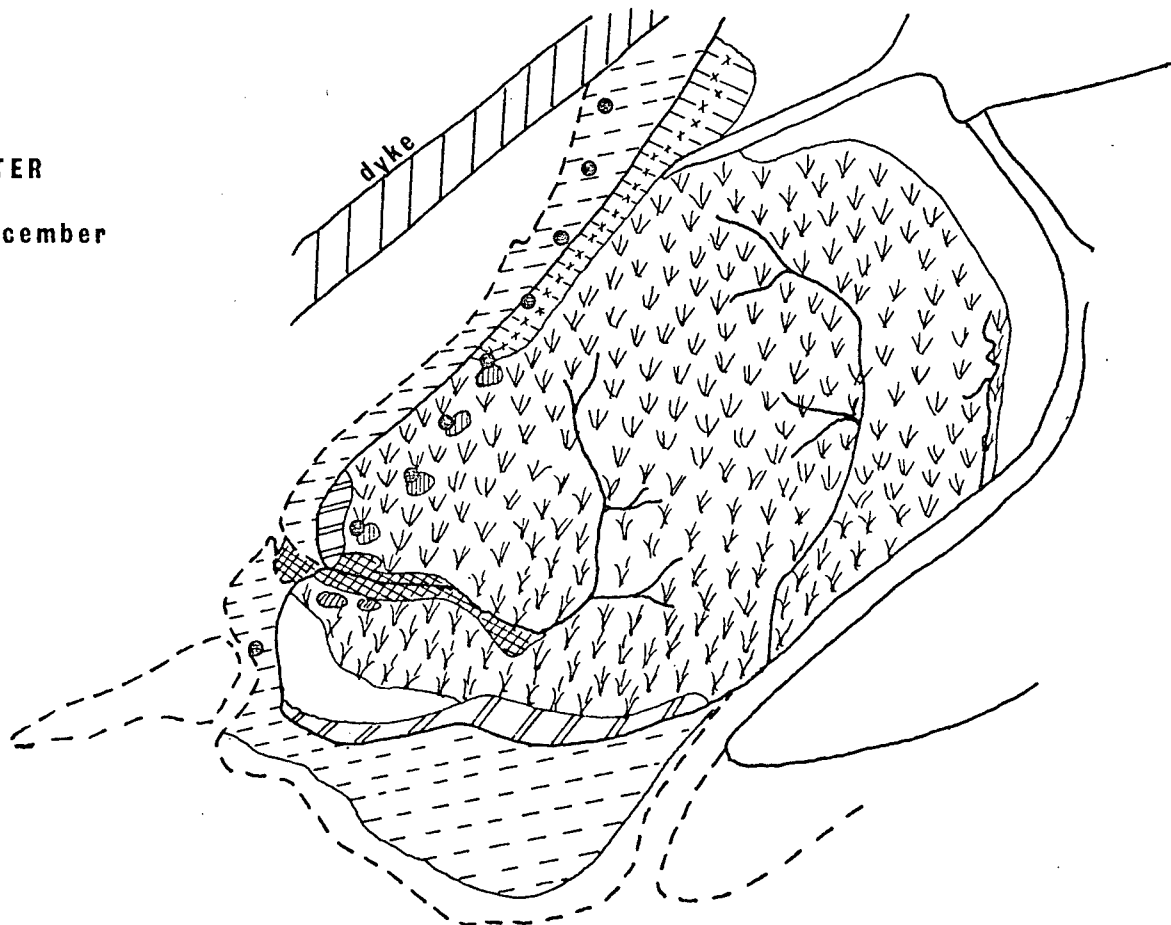
Figure 10. Distribution of benthic algae on the delta
in A) fall (September), B) Winter (December),
C) spring (March), and D) summer (June).



FALL
September

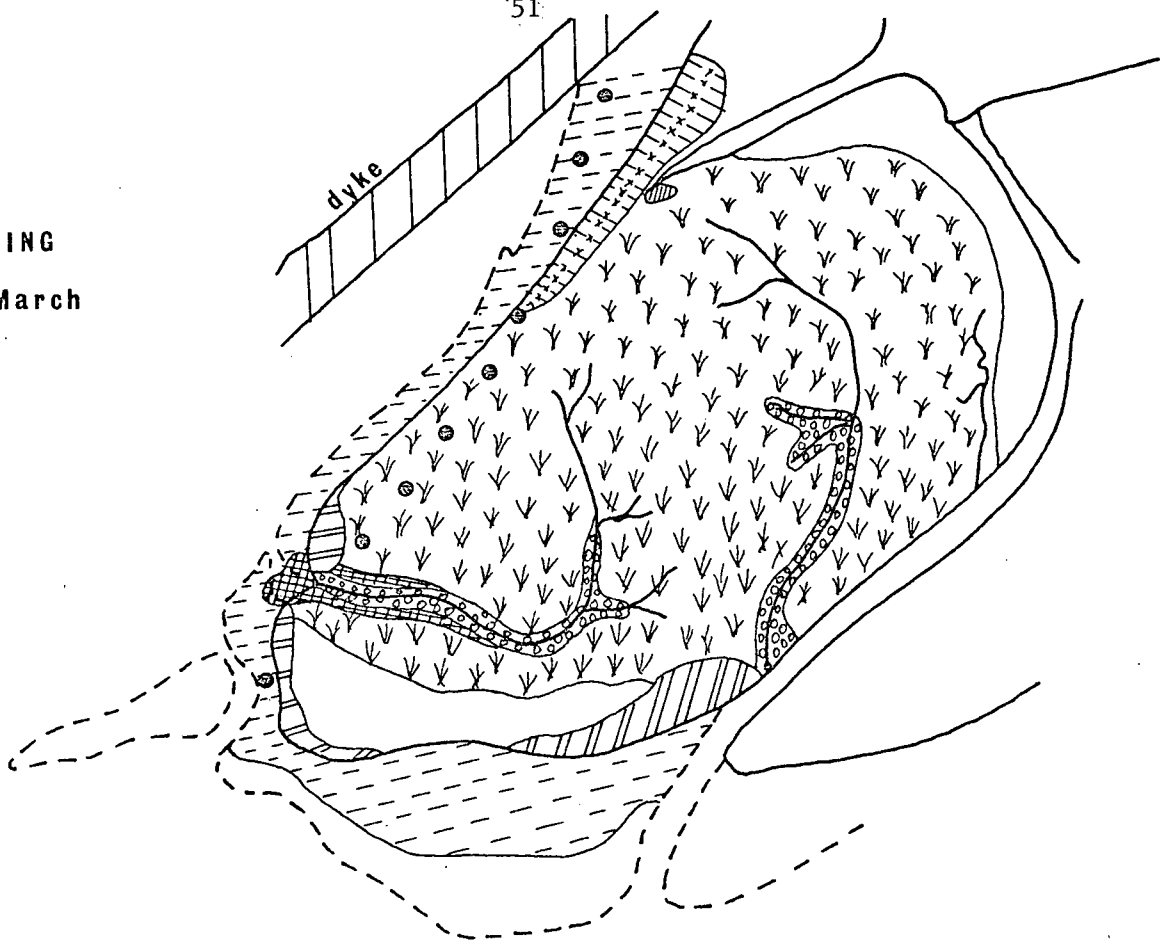


WINTER
December



SPRING

March



SUMMER

June

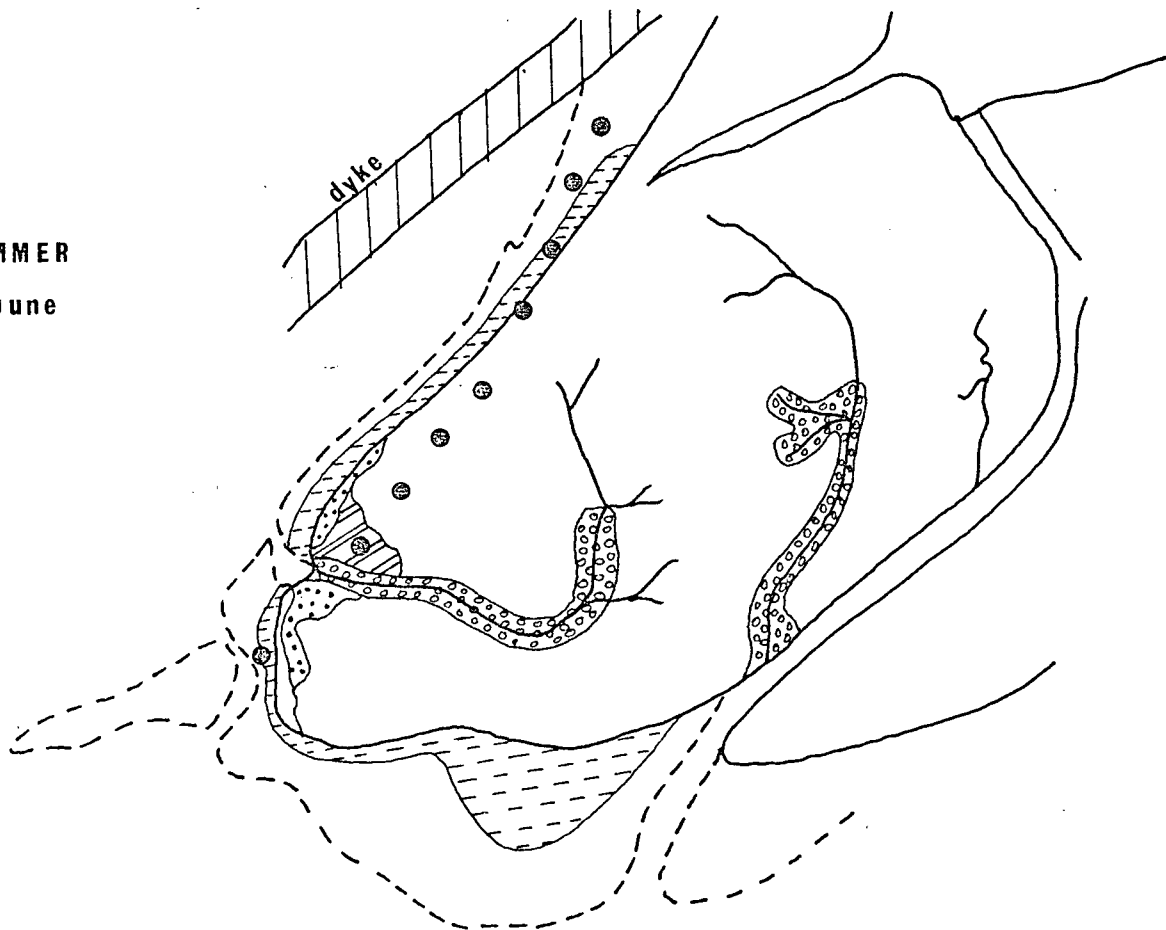


Table 7. Maximum biomass values for macroalgae and microalgal associations.

	Maximum biomass gC.m ⁻²
<i>Pylaiella littoralis</i>	69.65
<i>Enteromorpha minima</i>	24.83
Association G	17.42
<i>Enteromorpha prolifera</i>	17.31
<i>Spirogyra</i> sp.	12.00
<i>Cladophora</i> sp.	11.92
<i>Monostroma oxyspermum</i>	9.04
Association A	8.12
Association D	7.96
Association F	5.72
<i>Rhizoclonium implexum</i>	4.06
Association C	3.92
Association B	3.92
Association E	2.17

value at *ca.* $2.17 \text{ g C} \cdot \text{m}^{-2}$. Biomass determinations for each sampling appear in Appendix VI.

Total algal standing crop on the delta ranged from *ca.* 17 kg C in October to *ca.* 1600 kg C in February (Fig. 9). Monthly biomass estimates for each macroalga and microalgal association in terms of its total distribution appear in Appendix VII. Association G was the greatest contributor to standing crop biomass, especially in February. Other important algae were *Pylaiella littoralis* and Association E, both reaching maximum values in April. These algae were significant in that they made up over 50% of the standing crop biomass for these periods. *Cladophora* sp., *Monostroma oxyspermum*, and Associations B and C made minimal contributions, averaging less than 10% of the total monthly biomass (Appendix VII).

The order of dominant net primary producers was different to that noted for standing crop biomass (Tables 7, 8). The most productive macroalgae were *Spirogyra* sp. and *Monostroma oxyspermum*. Net production maxima for microalgal associations were lower, on the average, than those for macroalgae by 50% or more (Table 8). Association A was the most productive and Association D the least. Primary production over the year for macro- and microalgae at 1 m averaged about half that noted at the surface (Appendix VIII). However, at the time of maximum river flow, productivity at 1 m dropped to between 5 and 20% of surface production.

Table 8. Net production maxima and minima recorded.

		Production (gC·m ⁻² ·day ⁻¹)			
		Maxima		Minima	
		surface	1 m	surface	1 m
Macroalgae					
<i>Spirogyra</i> sp.		2.67	0.68	0.30	0.12
	21 Jun		13 Aug	30 Oct	30 Oct
<i>Monostroma oxyspermum</i>		2.55	0.98	0.35	0.14
	19 Mar		20 Feb	2 Sep	5 Jul
<i>Pylaiella littoralis</i>		2.03	0.67	0.23	0.04
	19 Mar		19 Mar	20 Jun	21 Jun
<i>Enteromorpha minima</i>		1.93	0.65	0.13	0.00
	6 Jun		6 Jun	22 Jan	18 Dec
<i>Cladophora</i> sp.		1.01	0.44	0.54	0.14
	19 Jul		27 Aug	12 Jun	12 Jun
<i>Enteromorpha prolifera</i>		0.94	0.28	0.17	0.07
	29 Jul		16 Apr	20 Feb	20 Feb
<i>Rhizoclonium implexum</i>		0.88	0.33	0.12	0.06
	16 Jul		27 Aug	30 Oct	30 Oct
Microalgae					
Association A		1.43	0.38	0.41	0.04
	29 Jul		14 May	19 Jul	19 Jul
F		1.08	0.36	0.12	0.02
	21 Jun		14 May	18 Dec	18 Dec
D		0.72	0.36	0.25	0.15
	20 Feb		22 Jan	16 Apr	15 Mar
E		0.58	0.35	0.02	0.05
	20 Jun		14 May	18 Dec	29 Jul
C		0.45	0.31	0.14	0.07
	22 Jan		22 Jan	14 May	14 May
G		0.35	0.20	0.10	0.05
	22 Nov		22 Nov	19 Mar	18 Dec
B		0.20	0.09	0.10	0.02
	22 Jan		22 Jan	19 Mar	19 Mar

The reduction in daily net primary production associated with increased water depth (Table 8, Appendix VIII) indicated the need for a correction factor to get a more accurate estimate of monthly net production. Application of the time an alga is exposed (15 cm below surface) and covered (1 m), as determined from tide tables (Appendix IX), to production data provides better estimates of monthly net production than averaging values from the surface and 1 m. Values thus arrived at were corrected for distribution (coverage) area of a producer and expressed as $\text{g C} \cdot \text{distribution area}^{-1} \cdot \text{mo}^{-1}$ (Table 9). These data give better estimates of the contribution and importance of a macroalga or microalgal association to the delta.

The algae making the greatest contribution to total net production were microalgal Associations G and E, of which the former was by far the dominant (Table 9). During its winter growth period, Association G averaged *ca.* 74% of the total monthly production. *Pylaiella littoralis* was the highest macroalgal contributor, accounting for *ca.* 18% of the total monthly production in April. Associations B and C, the lowest contributors to production, accounted for 1% of total monthly production (Table 9).

November-March had the highest net production over the study, with values at other times one quarter to one half (Table 9).

Table 9. Monthly ^{14}C net production estimates ($\text{gC} \times 10^3$) for macroalgae and microalgal associations per coverage area, corrected for coverage-exposure time.

	<i>Cladophora</i> sp.	<i>Enteromorpha</i> <i>minima</i>	<i>Enteromorpha</i> <i>prolifera</i>	<i>Monostroma</i> <i>oxypermum</i>	<i>Spirogyra</i> sp.	<i>Rhizoclonium</i> <i>implexum</i>	<i>Pylaiella</i> <i>littoralis</i>
1974							
June	3.16	7.65	4.14	6.08	20.00 ^a	10.09	4.74
July	9.90	8.90	6.16	4.37	23.60	15.35	-
August	7.32	5.12	1.71	1.16	19.07	10.23	-
September	1.55	2.45	0.54	1.32	8.63	4.09	-
October	-	2.31	-	2.33	2.40	1.55	-
November	-	1.21	-	0.92	-	-	-
December	-	0.33	-	1.12	-	-	0.93
1975							
January	-	0.22	-	1.59	-	0.62	1.34
February	-	0.76	0.12	2.91	-	1.22	10.07
March	-	1.17	0.39	7.74	-	4.71	37.69
April	-	1.67	0.67	7.25	-	5.10	33.18
May	2.73	2.37	1.63	7.25	-	7.29	30.32
June	2.25	2.05	2.63	6.61	24.60	8.25	4.58
July	7.89	5.26	4.38	4.75	25.42	13.64	-
August	4.83	3.34	1.50	2.17	22.48	10.90	-
Total	39.62	44.81	23.81	57.58	146.17	92.85	122.85

^a assume 20.00 g C minimum net production

...Continued

Table 9. Continued.

	Association							Total
	A	B	C	D	E	F	G	
1974								
June	17.18	-	-	-	37.15	18.00	-	128.19
July	3.10	-	-	-	37.13	15.58	-	124.17
August	-	-	-	-	41.85	7.06	-	93.52
September	-	-	-	-	67.12	4.65	-	90.35
October	-	-	-	-	62.39	2.30	-	73.28
November	-	-	-	-	34.01	13.42	381.60	431.16
December	-	0.30	0.08	-	31.47	1.58	223.26	254.07
1975								
January	-	0.80	0.15	5.58	97.59	1.98	209.70	319.57
February	-	0.87	0.10	10.11	127.63	3.28	315.90	472.98
March	-	0.53	0.11	12.40	107.42	7.58	289.80	469.54
April	-	0.22	0.06	33.98	121.80	7.34	-	181.22
May	17.55	-	0.04	-	58.99	12.09	-	140.26
June	16.90	-	-	-	67.20	13.73	-	148.80
July	11.32	-	-	-	24.78	12.21	-	109.65
August	-	-	-	-	34.16	6.05	-	85.23
Total	66.05	2.72	0.50	32.07	950.69	124.55	1420.26	

Three subgroupings of benthic algae can be established with reference to the time of distribution and production maxima, indicating optimal conditions (Table 10). Algae most sensitive to high light, temperature and dessication (low LTD group) are primarily phaeophytes and chrysophytes (diatoms). *Pylaiella littoralis*, diatom-dominated Associations B, C, D, and E, along with chlorophyte-dominated Association G are in this category. Less sensitive species are in the high LTD category and include the xanthophyte *Vaucheria* (Association F) and other chlorophyte species except *Monostroma oxyspermum*, which is placed in a separate group as a medium LTD species.

C. Comparison of ^{14}C and dissolved oxygen primary production estimates.

Comparison of ^{14}C net primary production estimates with those from the oxygen method show the former to be higher by an average of 8.8% (Table 11).

The ^{14}C values of net primary production as percent of O_2 gross primary production varied with each alga tested (Table 11). Chlorophytes had somewhat higher values than did the diatom associations, ranging from 64.7 - 86.1%, with an average of 76%. Estimates for associations were 70 - 82%, with an average of 75%, whereas *Pylaiella littoralis* was lower at 68.5%.

Table 10. Net primary production of macroalgae and microalgal associations on the delta ($\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$).

Species	Maxima	Month
Low LTD group		
<i>Pylaiella littoralis</i>	2.03	March
Association D	0.72	February
Association C	0.45	January
Association G	0.33	November
Association B	0.20	January
Medium LTD group		
<i>Monostroma oxyspermum</i>	2.55	March
High LTD group		
<i>Spirogyra</i> sp.	2.67	June
<i>Enteromorpha minima</i>	1.93	June
Association A	1.43	July
Association F	1.08	June
<i>Cladophora</i> sp.	1.01	July
<i>Enteromorpha prolifera</i>	0.94	July
<i>Rhizoclonium implexum</i>	0.88	July
Association E	00.58	June

Table 11. ^{14}C production^a as percent oxygen production
(averages of 10 determinations).

	percent O_2 gross production ^b	percent above O_2 net production ^c
Macroalgae		
<i>Cladophora</i> sp.	78.0	6.7
<i>Enteromorpha minima</i>	75.4	9.1
<i>Enteromorpha prolifera</i>	73.8	7.3
<i>Monostroma oxyspermum</i>	86.1	10.2
<i>Spirogyra</i> sp.	64.7	7.4
<i>Rhizoclonium implexum</i>	78.2	10.7
<i>Pylaiella littoralis</i>	68.5	11.3
Microalgae		
Association A	75.6	9.7
B	74.1	5.8
C	71.4	7.6
D	78.0	8.4
E	73.0	10.9
F	70.0	5.1
G	82.2	12.4
		Mean 8.8

^a corrected for organic exudation

^b $\frac{^{14}\text{C net production}}{\text{O}_2 \text{ gross production}}$

^c $\frac{^{14}\text{C net production}}{\text{O}_2 \text{ net production}}$

D. Dissolved organic material (DOM) exuded during production.

Dissolved organic material exuded by benthic algae amounted to between 0 and 30% of total net production (Table 12). Chlorophytes had the lowest values and *Pylaiella littoralis* and Association B the highest exudation. All microalgal associations had reasonably high rates. The time of exudation maxima varied, with June or July the most common (Table 12).

E. Addition and removal of particulate organic matter (POM).

Particulate organic matter ($> 0.45 \mu$ diameter) deposited on and removed from the delta over a tidal cycle consisted of phytoplankton, benthic macroalgae and microalgae and detrital material.

Addition. Species composition of the added organic matter changed seasonally. Planktonic diatoms originating from Howe Sound (Stockner and Cliff 1976) and the Squamish River were noted at each sampling. The marine *Thalassiosira pacifica* and *Skeletonema costatum* dominated in March and April as did *Chaetoceros* sp. and three species of dinoflagellates. Benthic diatoms, dominated by *Navicula cancellata*, apparently lifted from the delta and returned on the succeeding ebb tide, were most abundant from December to June. Benthic macroalgae, also lifted from the delta, were most prevalent from

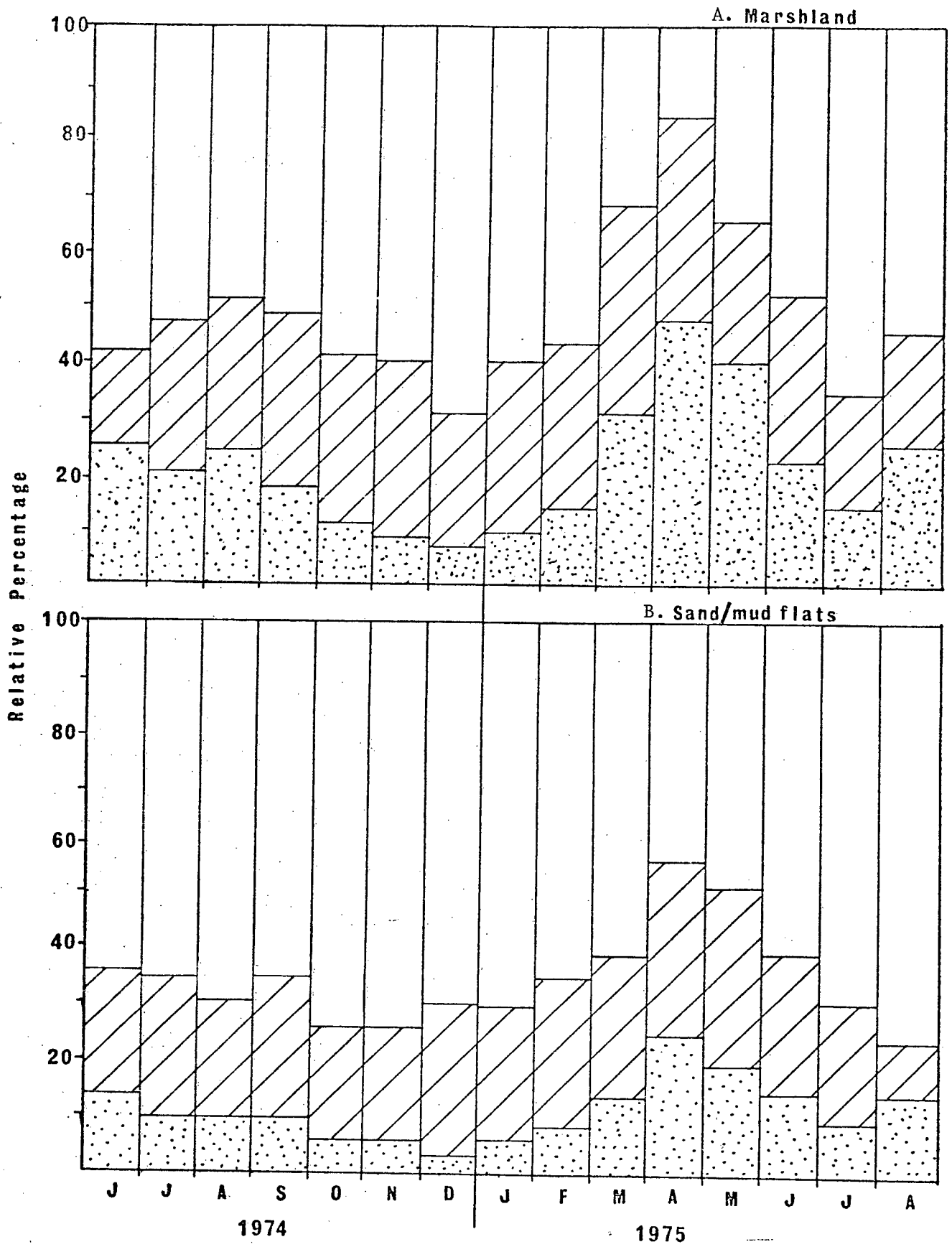
Table 12. Organic exudation as percent total net primary production measured by the ^{14}C method.

	Depth (m)	Exudation Range	Ave.	Time of maximum
Macroalgae				
<i>Cladophora</i> sp.	0 ^a	4-10	7	June
	1	2-9	6	July
<i>Enteromorpha minima</i>	0	4-10	7	June
	1	4-9	5	November
<i>Enteromorpha prolifera</i>	0	4-19	7	July
	1	3-12	6	August
<i>Monostroma oxyspermum</i>	0	4-8	6	July
	1	4-13	9	June
<i>Spirogyra</i> sp.	0	9-20	13	June
	1	5-16	15	October
<i>Rhizoclonium implexum</i>	0	0-16	8	July
	1	3-11	8	July
<i>Pylaiella littoralis</i>	0	14-30	22	June
	1	3-13	7	June
Microalgae				
Association A	0	10-28	19	July
	1	4-20	7	July
B	0	10-30	20	December
	1	0-20	16	December
C	0	4-18	13	January
	1	0-9	8	December
D	0	7-16	13	April
	1	5-6	6	February
E	0	8-25	15	June
	1	4-20	11	July
F	0	5-24	12	June
	1	0-17	10	July
G	0	5-22	10	February
	1	5-7	6	February

^a15 cm below water surface

Figure 11. Particulate organic matter added to the
delta expressed as percent detritus  ,
microalgae  , and macroalgae  .
(average of four stations)

A. Marshland
B. Sand/mud flats



October to April, with *Rhizoclonium implexum* and *Pylaiella littoralis* the main species.

Spatial and temporal variations in deposition of POM existed between the sand/mud flats and the marshland (Fig. 11). On the marshland, macroalgae were lowest in October-January, with values four times higher in April and May. Microalgae accounted for *ca.* 20% of the total organic deposition, rising to 40% in March. The percent addition of detrital material was greatest during the summer and fall, averaging about 50% (Fig. 11).

The composition of POM added to sand/mud flats in the low intertidal proved somewhat more variable than the marshland (Fig. 11). Macroalgae contributed least (*ca.* 11%), being greatest in April. Microalgae averaged 23%. Detrital material washed from the marshland, as judged from species composition, and deposited on the sand/mud flats made up *ca.* 60% of the total organic matter deposited. Addition of organic matter ($\text{g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) was generally 50% higher in the marshland (Table 13).

Removal. Seasonal variations in POM leaving the delta via tidal creeks were different for Snag and Pile creeks (Fig. 12). In Pile creek, *Pylaiella littoralis* (April-May), *Rhizoclonium implexum* (June) and *Enteromorpha prolifera* (August-September) were recorded as abundant. The lowest macroalgal composition was in November (8%) and the highest in April (50%) (Fig. 12). The species noted for Pile were also common in Snag creek but in lower amounts, making up a maximum of *ca.*

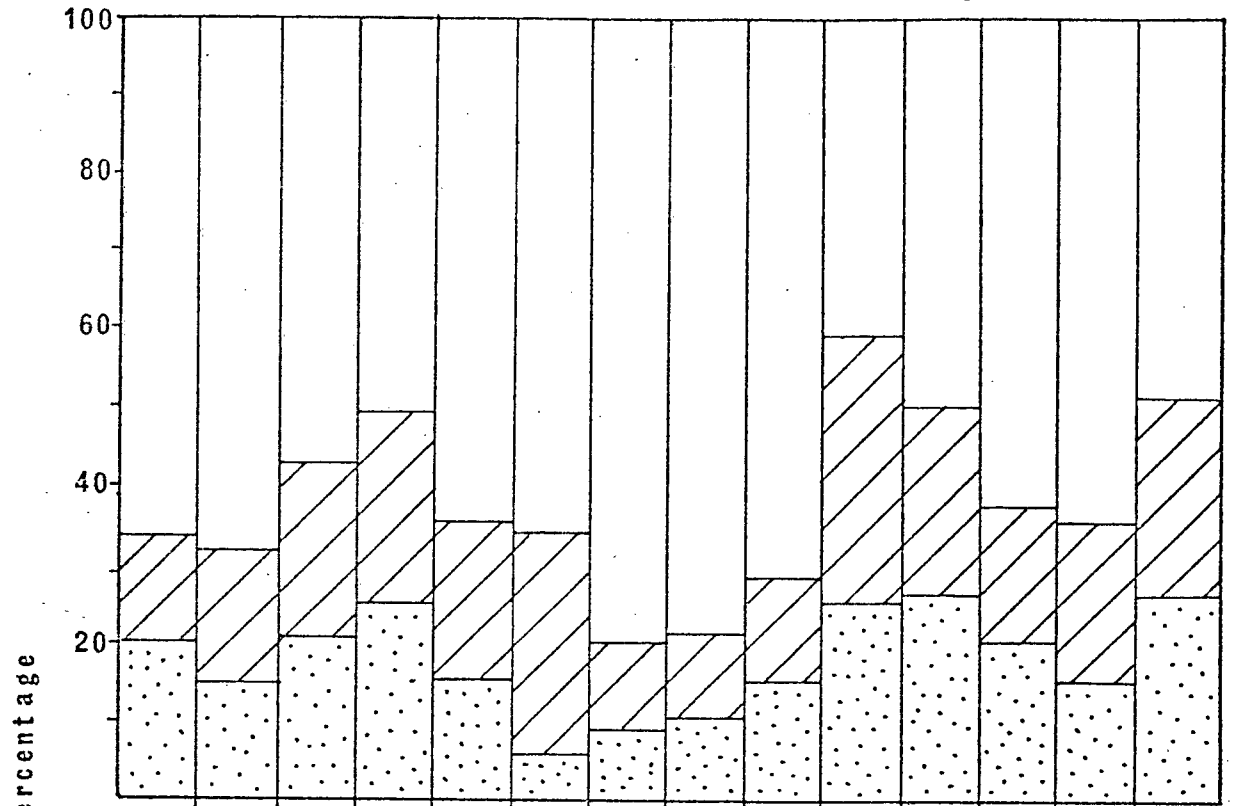
Table 13. Addition of particulate organic matter to the delta ($\text{mg C}\cdot\text{m}^{-2}$) (mean of 4 sampling sites in each area, sampling period over 1 tidal cycle).

Month	Marshland	Sand/mud flats
1974		
June	76	31
July	92	40
August	112	60
September	64	29
October	42	27
November	32	18
December	4	2
1975		
January	10	5
February	30	18
March	120	34
April	150	40
May	139	37
June	92	38
July	89	34
August	104	30

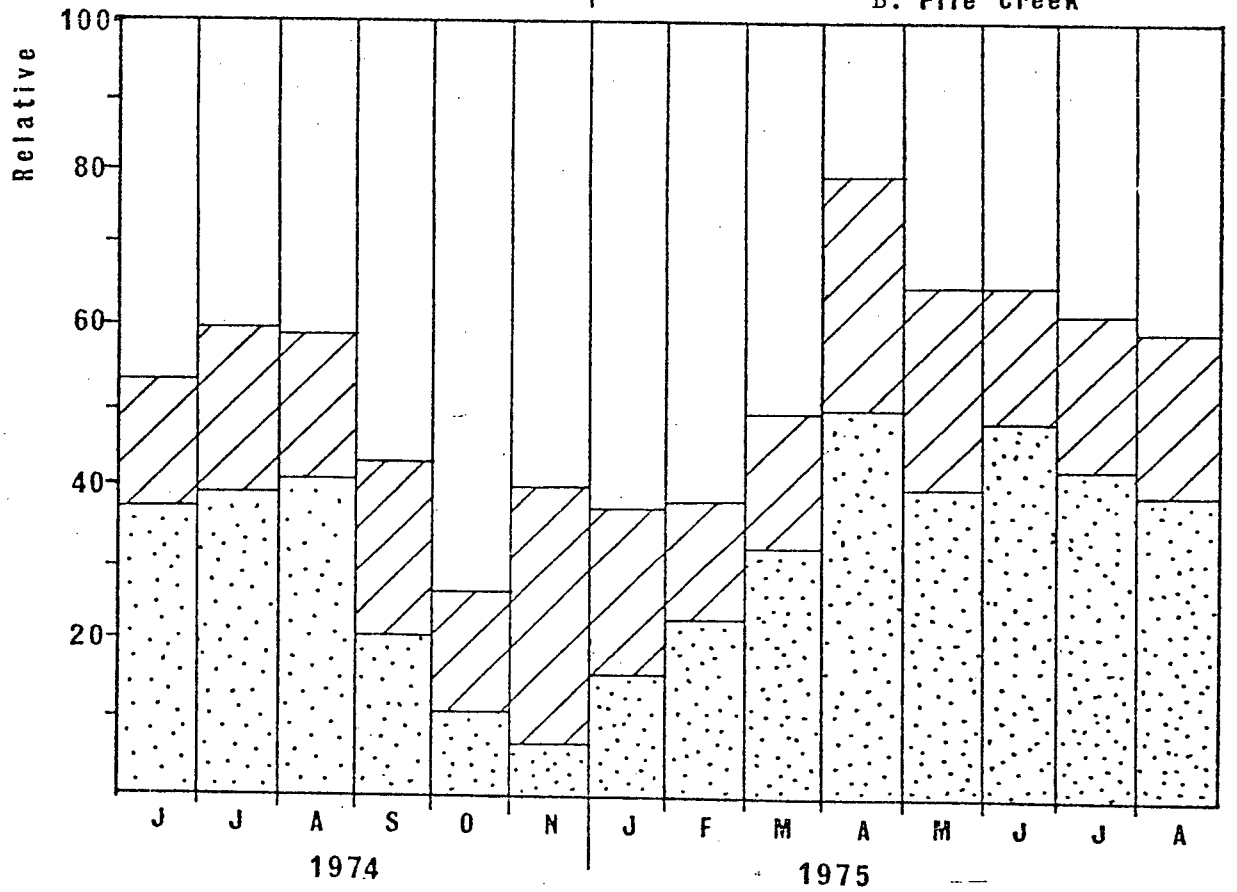
Figure 12. Particulate organic matter removed through Snag and Pile creeks as percent detritus  , microalgae  , and macroalgae  . (composite of data from high and low creek levels).

A.) Snag creek
B.) Pile creek

A. Snag creek



B. Pile creek



25%. Microalgae (diatoms) recorded from both creeks in high numbers were *Melosira* spp. and *Navicula* spp. The removal of microalgae showed basically the same seasonal patterns as macroalgae with November and April being the high periods in both creeks. Detrital material in Snag creek was higher than that recorded from Pile creek, reaching *ca.* 80% in January.

The particulate organic content of waters draining the creeks was higher (greater than 60%) when the water level was just below the delta surface compared to when it reached the creek bottoms (Table 14).

Estimates of POM and nutrient removal from Pile creek may represent overestimates corrected to some extent by removing background concentrations. Since the area east of the creek at the delta front (Fig. 2) is at a lower elevation, water not draining off the delta is brought in and included in that sampled. However, placement of the sampling station at the delta front rather than farther up the creek where elevations were equal on both sides was considered best as the latter would result in a considerable underestimate by only monitoring a part of the delta surface.

The species composition of identifiable organic matter removed from the delta surface in flood tide was directly related to location of sampling site and time of year. Algae most readily removed were filamentous forms (*Pylaiella littoralis*, *Enteromorpha prolifera*, *Ulothrix flacca*) along with diatom dominated microalgal

Table 14. Particulate organic matter removed from the delta by Snag and Pile Creeks ($\text{mgC}\cdot\text{l}^{-1}$) at high and low water levels^a.

	Snag Creek			Pile Creek		
	High	Low	Ave.	High	Low	Ave.
1974						
June	21.9	15.3	18.6	24.2	12.7	18.4
July	20.2	15.4	17.8	21.1	11.4	16.3
August	20.0	15.2	17.6	17.4	13.1	15.3
September	17.1	8.7	12.9	15.2	14.1	14.7
October	16.5	7.2	11.9	17.1	9.7	13.4
November	11.7	8.7	10.2	18.2	9.5	13.9
December	6.9	4.9	5.9	8.9	5.7	7.3
1975						
January	11.4	5.7	8.6	13.9	4.1	9.0
February	23.7	15.8	19.8	19.4	12.0	15.7
March	24.7	17.0	20.9	25.4	17.9	21.7
April	19.1	10.1	14.6	17.1	8.7	12.9
May	15.3	12.0	13.7	21.9	12.0	16.9
June	20.4	17.2	18.8	22.7	15.2	18.9
July	20.0	14.7	17.4	27.2	14.9	21.1
August	19.9	14.9	17.4	17.2	10.8	14.0

^ahigh water level ca. 15 cm below delta surface; low water level near creek bottom.

associations. The greatest abundance of each was recorded at the end of its growth period.

The amount removed was also dependent upon site and time of year (Table 15). Removal rates from sand/mud flats were lowest in July 1974. Sedge-free areas in the mid- and upper intertidal had removal rates considerably higher than the sand/mud flats. Values varied with the mid-intertidal removal rates more than twice the upper intertidal at certain times of the year, reaching highs in March (Table 15). The marshland had generally higher values with maximum removal in March, falling to a low in November.

F. Caloric equivalents.

Caloric equivalents ($\text{kcal} \cdot \text{g organic}^{-1}$) for macroalgae were generally lower than those of the diatom dominated microalgal associations (Table 16). Associations dominated by *Vaucheria* (F) and *Ulothrix* (G) also had low values. The caloric content of sediments varied considerably as a function of sediment type, location within the intertidal zone and the species of vascular plant in the area (Table 16). Sediment Area F had the greatest caloric content and Area G the least. Detrital material from the delta averaged a caloric content similar to some diatom associations. Material removed from and added to the delta also had high caloric values in the spring and summer period. Fall-winter values were lower by more than $1 \text{ kcal} \cdot \text{g organic}^{-1}$:

Table 15. Particulate organic matter ($\text{mgC} \cdot \text{m}^{-2} \cdot \text{flood tide}^{-1}$) removed from the major habitat types on the delta.

	Sand/mud flats	Marshland (sedge-free)		Marshland (<i>Carex</i> meadow)
		mid	upper	
1974				
June	27.5	163.5	98.0	268.4
July	18.5	201.5	113.0	261.7
August	24.5	191.0	115.0	268.6
September	23.5	184.0	113.0	204.0
October	28.0	153.0	118.5	199.6
November	26.5	136.0	114.5	194.4
December	22.5	216.0	121.5	253.4
1975				
January	35.0	296.0	127.0	305.3
February	-a	-a	-a	-a
March	53.0	362.0	168.5	337.4
April	51.0	218.0	98.0	239.0
May	37.5	178.5	105.5	230.4
June	27.5	288.5	108.5	266.0
July	22.0	206.0	98.5	259.9
August	20.0	216.5	109.5	251.4

^a data missing

Table 16. Caloric equivalents for algae, sediments, detritus, and POM.

Material	No.	%LOI	kcal. g dry wt ⁻¹	kcal. g organic ⁻¹
<i>Cladophora</i> sp.	5	52.9	2.24	4.32 $\pm$ 0.18
<i>Enteromorpha minima</i>	10	74.2	3.05	4.84 $\pm$ 0.09
<i>Enteromorpha prolifera</i>	5	63.1	3.01	4.49 $\pm$ 0.05
<i>Monostroma oxyspermum</i>	10	89.9	3.06	4.29 $\pm$ 0.04
<i>Spirogyra</i> sp.	5	91.2	3.64	3.99 $\pm$ 0.10
<i>Rhizoclonium implexum</i>	10	74.8	3.49	4.65 $\pm$ 0.23
<i>Pylaiella littoralis</i>	10	73.0	3.41	4.67 $\pm$ 0.07
Association A	5	53.1	2.61	4.92 $\pm$ 0.19
B	5	50.2	2.57	5.12 $\pm$ 0.23
C	5	59.1	2.98	5.04 $\pm$ 0.17
D	5	60.2	3.09	5.13 $\pm$ 0.10
E	5	41.9	2.62	6.25 $\pm$ 0.05
F	3	75.9	3.02	3.98 $\pm$ 0.09
G	3	80.1	3.13	3.91 $\pm$ 0.09
Sediment Area				
A	5	11.2	0.51	4.55 $\pm$ 0.05
B	6	17.7	0.91	5.14 $\pm$ 0.21
C	5	15.3	0.79	5.16 $\pm$ 0.14
D	6	42.5	1.79	4.21 $\pm$ 0.18
E	6	46.9	2.39	5.09 $\pm$ 0.20
F	4	18.9	1.08	5.71 $\pm$ 0.12
G	5	49.1	1.93	3.91 $\pm$ 0.10
Detritus	8	50.8	3.07	6.04 $\pm$ 0.39
Removed organic matter				
March-August	5	48.0	3.28	6.83 $\pm$ 0.37
September-February	5	59.3	3.00	5.05 $\pm$ 0.27
Added organic matter				
March-August	5	45.0	2.95	6.56 $\pm$ 0.29
September-February	5	51.0	2.72	5.33 $\pm$ 0.14
<i>Carex lyngbyei</i>				
Intact	3	85.5	3.49	4.08 $\pm$ 0.10
Decomposed	3	71.4	2.95	4.13 $\pm$ 0.09

G. Benthic algae, vascular plant, detritus utilization
by amphipods.

Within the 30 x 30 m² grid sampled at low tide amphipods were noted in 46% of the examination points, and of these, macroalgae were used as cover 90% of the time. Analysis of data collected showed a very statistically significant relationship between amphipods and *Pylaiella littoralis*, a filamentous brown alga (Table 17). Relationship of *Enteromorpha minima* and amphipods was also significant but to a much lower degree, whereas the association with *Monostroma oxyspermum* was not significant.

Adult and juvenile amphipods tested in the laboratory preferred filamentous algae for cover, with *P. littoralis* ranking highest, as in the field (Table 18). Adult amphipods chose *E. minima* and *M. oxyspermum* more often than did the juveniles who preferred diatom associations and detritus. *Carex* shoots were chosen least by both groups.

Careful examination in the field indicated that active feeding occurred by both adult and juvenile amphipods associated with *P. littoralis* and *E. minima* when submerged at low tide in pools. Laboratory studies on feeding showed the same preference for *P. littoralis* by adults and juveniles (Table 18). As with cover, adults selected *E. minima* and *M. oxyspermum* more often than the juveniles who chose the microalgal association

Table 17. Results of analysis using a 2 x 2 contingency table showing relationship of macroalgae and amphipods in a 30 x 30 m² grid on the marshland at low tide. (Tabulated $\chi^2 = 3.84$ at $P_{0.05}$).

Associated algae	χ^2 computed
<i>Pyraliella littoralis</i>	43.79*
<i>Enteromorpha minima</i>	4.46*
<i>Monostroma oxyspermum</i>	2.66

* indicates significance

Table 18. Cover and feeding preference shown by amphipods tested in the laboratory (total of 300 adult or juvenile amphipods - 15 trials of 20 each).

Source	Cover		Feeding	
	Adult	Juvenile	Adult	Juvenile
<i>Pylaiella littoralis</i>	138	156	122	145
<i>Enteromorpha minima</i>	102	69	91	31
<i>Monostroma oxyspermum</i>	24	12	31	16
Association A	6	14	10	25
Detritus	25	44	46	79
<i>Carex lyngbyei</i>	5	5	0	4
(partly decayed brown shoots)				

and detritus. Again, sedge shoots were not used as a food source except by juveniles when greatly decayed.

Analyses of gut contents from amphipods in controlled feeding experiments showed a characteristic color and in some cases it was possible to locate intact fragments of algae. However, it was impossible to relate gut contents from amphipods collected in the field to a particular food source even though they were found feeding on it at the time of collection. The fatty acid analysis technique did give some indication of food utilization in the field.

The algae and detritus tested had characteristic fatty acids, as determined by the time in sec to a peak (Table 19). The number of fatty acid peaks which appear to be unique to any species varies and certainly can be identified in the fatty acid spectrum of amphipods fed on a specific alga. In each of the macroalgae, two fatty acids could be traced. In addition, fatty acid peaks of the detrital material could be located in amphipods using this as a food source.

Analysis of amphipods collected while actively feeding in the field indicated two fatty acid peaks which could be traced back to *Enteromorpha minima*, *Pyraliella littoralis* and detrital material. The peaks attributed to detritus were somewhat higher and of

Table 19. Fatty acid analysis of selected food sources and amphipods fed on them.

Food source	Time to peak (s)	Amphipods using food source, time to peak (s)
<i>Monostroma oxyspermum</i>	177* 820* 973*	173* 214 252 817*
<i>Pylaiella littoralis</i>	230* 460*	183 237* 459* 627
<i>Enteromorpha minima</i>	123 130 147 388* 525*	135 151 386* 522*
Association A	161* 590*	nil
Field detritus	136* 171* 410* 466* 490* 550*	119 134* 142* 174* 408* 493* 590
Fatty acid peak from amphipods feeding in the field		170*D ^a 234*P 384*E 468*P 493*D 527*E 553*D 813*M

* characteristic fatty acid peak for a food source
(+ 5 s difference)

^a letters indicate peaks in field fed amphipods which correspond to those found in detritus (D), *Enteromorpha* (E), *Pylaiella* (P), and *Monostroma* (M).

longer duration in comparison to those of intact algae. Thus, it appears that detritus may be the favored food source for amphipods.

III. Statistical Analysis of Factors Influencing Primary Production

Results of a previous study using simple linear regression suggest salinity, temperature and light significant in limiting primary production at Squamish. (Pomeroy and Stockner 1976). Extending this, stepwise multiple regression (TRIP) was run to test the combined effect of these three factors plus nutrients on net production to point out the most likely factors influencing each algae. This approach is necessary as fluctuations in production cannot be attributed to a single factor or cause.

For macroalgae, light and temperature strongly influence net production (Table 20). Phosphate and salinity are important to a lesser degree. Correlations are positive with the exception of salinity which is negative for *Spirogyra* sp., a freshwater alga.

Microalgal associations, aside from E and F, were present for a short time. This resulted in sample sizes not large enough to provide good analyses at the probability level used ($p=0.05$). However, examination of the correlation matrix indicates that either temperature or light may influence net production of these.

Table 20. Statistical analysis of primary production data using stepwise multiple regression ($p = 0.05$). Dependent variable = net production, independent variables = salinity, light, temperature, nitrate, phosphate, and ammonia.

	Factor	Individual F prob	Combined F prob	RSQ
<i>Cladophora</i> sp.	light	0.0002		
	PO ₄	0.0095	0.0004	0.7620
<i>Enteromorpha minima</i>	light	0.0005		
	temperature	0.0027	0.0009	0.7993
<i>E. prolifera</i>	light	0.0004	0.0004	0.6629
<i>Monostroma oxyspermum</i>	light	0.0360		
	temperature	0.0019	0.0067	0.4658
<i>Rhizoclonium implexum</i>	light	0.0002		
	PO ₄	0.0078	0.0006	0.5112
<i>Spirogyra</i> sp.	salinity	0.0075		
	light	0.0000	0.0000	0.8842
Association E	light	0.0009		
	temperature	0.0085	0.0007	0.6943
Association F	salinity	0.0042		
	temperature	0.0079	0.0014	0.4699

DISCUSSION

Consideration must be given to structural and functional aspects in attempting to understand any ecosystem. Analysis of ecosystem structure or organization (spatial distribution of components, their abundance or coverage area, species composition plus controlling physical, chemical and biological factors) provides a basis for interpreting the more dynamic or functional side of an ecosystem. Function is best revealed through the flow of energy and materials and is characteristic of a particular ecosystem.

The following discussion represents a structure-function analysis of the autotrophic components (vascular plants and benthic algae) of the Squamish delta. Operation of this level of the ecosystem and its response to environmental change are significant and have considerable influence over heterotrophic components. It is a necessary first step in the understanding of overall ecosystem function.

I. Ecosystem Structure

Ecosystem structure in an estuary is regulated by primary factors which govern entry of a species and by secondary factors which determine establishment and spatial-temporal patterns of distribution. Factors affecting these are also significant in controlling primary production as will be discussed. Structure of

the benthic algal community will be considered first, followed by that of the vascular plants.

Osmoregulatory capability (degree of euryhalinity) is the primary factor controlling entry of an alga into the Squamish estuary. A notable feature of algal flora on the delta is lack of species richness, with primarily chlorophytes and diatoms present. This is in contrast to other coastal intertidal habitats such as rocky marine shores (Littler and Murray 1974) and coastal plain estuaries (Foreman 1975) with a greater abundance of phaeophytes and rhodophytes. Impoverishment and species variation reflects the inability of many common intertidal marine species to enter and survive in areas of reduced salinity. The gradual drop in marine species through regions of less saline waters has been commonly noted (Doty and Newhouse 1954, Zaneveld 1969, Remane and Schleiper 1971). At Squamish this results in a "typical" estuarine algal community structure consisting of a mixture of low salinity tolerant species coming from the sea (*Fucus*, *Laminaria*, *Pylaiella*), several algae common and sometimes restricted to estuaries (*Enteromorpha*, *Rhizoclonium*, *Vaucheria* and diatoms), plus a very few freshwater species (*Spirogyra*, *Cladophora*).

The establishment of an alga physiologically able to enter the Squamish estuary is dependent upon the interaction of secondary factors—physical, chemical and

biological in nature- which vary over the year. The result is seasonal species patterns and altered ecosystem structure.

Algal substrate and habitat preference, evident at Squamish (Tables 4,5) is important in determining spatial-temporal distribution patterns. The effect of substrate on algal colonization has been investigated using a number of artificial substrates including plastic (Risk 1973, Harlin 1973) and concrete (Foster 1975). The general conclusion is that finer textured surfaces are less favorable for algal settlement. Such a pattern helps explain the distribution of algae at Squamish, with many growing on surfaces relatively rough in texture. Substrate specificity may also be a reflection of a chemical leaching from the surface, either stimulating or inhibiting growth of an alga (e.g. *Enteromorpha minima* on wood).

Theoretical patterns of distribution and ecosystem structure based solely on substrate preference do not coincide with observed patterns on the Squamish delta. Modifying this is the problem of habitat preference. For example, *Pylaiella littoralis* was epiphytic on *Carex lyngbyei* at the periphery of the delta but not in the central portions. *E. minima* was found on wood surfaces only in the lower intertidal and *Monostroma oxyspermum* was located in tide pools only in the upper intertidal. Factors including salinity-osmoregulation,

temperature, light intensity and quality, desiccation and competition operate at Squamish to produce observed ecosystem structure.

Interspecific competition , chemical and physical, is an important factor regulating structure of the autotrophic components at Squamish. The most dramatic, significant example is seen with respect to *Carex lyngbyei*, the dominant vascular plant on the delta. As vegetation height increases, the amount of light reaching the sediment is drastically reduced (Table 2). This reduction results in two things. First, an enhancement of distribution and, along with it, production for species of algae with low light preference (Table 20). Second, in species requiring more light for optimum photosynthesis, the result is reduced production, restricted distribution to areas of light penetration (pools, open areas) and suitable substrate. Complete removal of the species could occur when light falls below the critical level. Data on primary production (Appendix VIII), distribution (Appendix VII) and biomass (Appendices VI, VII) indicate suppression of algal colonization and growth is in part controlled by the presence of vascular plants. Increased colonization and distribution is seen only as a result of *Carex* acting as a substrate for *Pylaiella littoralis* and Association G, both of which favor low light. The increase is significant for production and energy flow as will be discussed.

In addition to a competitive response between vascular plants and benthic algae, there is competition between species of macroalgae and/or microalgal associations. Very limited growth of *Enteromorpha minima* occurs mixed in with large stands of *Fucus* on the preferred substrate of both (wood). Within a meter, there are luxuriant stands of *E. minima* under the same conditions of substrate, salinity, light and temperature. *Fucus*, either by its extensive, robust growth form which results in shading, or by means of a large amount of organic exudate (Sieburth 1969), excludes *E. minima*. Hruby (1976) working with *Laminaria* sp. and *Iridea* sp., notes a similar situation in which the zonation line between the two varies, dependent upon growth of the larger species. Light reduction is suggested as significant in inter-species competition, lending support to findings of the current study.

Competition of a chemical nature may also be active in determining algal distribution and production patterns. The possible effect of exudation from *Fucus* has been mentioned but no supportive data are known. However, Berglund (1969) mentions a substance exuded by *Enteromorpha* sp., which greatly stimulates its own growth but not that of other species. This could explain the large unialgal growths of *E. minima* and *E. prolifera* observed at Squamish. Once the alga becomes established in the absence of a dominant light

reducing species, it could grow undisturbed by competitors. Converse to this, exudation of growth antagonists or inhibitors is noted for other marine algae and could contribute to the formation of unialgal patches (Conover and Sieburth 1964, Sieburth 1968, Russel and Fielding 1974, Fletcher 1975). Growth stimulators may also exist. Much work remains to be done in this area but since a tidal marsh environment is under stress, a condition favoring release of exudates, these may be important in controlling ecosystem structure.

Light, in view of its significance for photosynthesis, is an obvious factor controlling distribution and primary production. In the presence of a suitable substrate, the lower limit of growth for an alga at Squamish is primarily under the influence of reduced light intensity and changed spectral quality experienced with depth. The often turbid nature of estuaries, especially the fjord-type typified by Squamish, increase the attenuation rate rapidly (Fig. 4) and results in a compression of vertical zonation with depth in a relatively short distance (Druehl 1967). The appearance at Squamish of brown algae higher up on the shore relative to other coastal intertidal habitats is suggestive of this compression. In addition, to light, salinity may affect the lower limit of distribution during freshet when strong low salinity lens is present. The result would be loss of species with low osmoregulatory capabilities.

The upper limit of an alga is variable and controlled by several factors. High light intensity, known to be damaging to attached marine algae (Hellebust 1974) may be a limitation to species normally found in the lower intertidal region which, due to vertical compression, experience longer periods of high light on exposure. Being less well adapted, they cannot survive even if able to colonize. Chlorophytes common to the upper intertidal seem better adapted to tolerate increased light (Biebl 1956), often having higher optimal light requirements for net photosynthesis (Mathieson and Burns 1971). This is reflected in the wide distribution of *Monostroma oxyspermum*, *Rhizoclonium implexum*, *Cladophora* sp. and *Spirogyra* sp. on the upper regions of the delta.

Primary production of these species is positively correlated with light intensity (Table 20). Rapid light attenuation on immersion during the high runoff period of summer restricts algae to a higher position in the intertidal where all but the most light tolerant are selected against on emersion. The increased light regime and vertical compression selects for algae of the upper intertidal. This is evident comparing species composition between the study area and the extreme eastern part of the estuary where effects of river freshet are least, resulting in low light attenuation and reduced vertical compression. The lower limit of growth for a

given alga appears greater in the region of reduced light attenuation. Several brown algae are abundant with a concomitant decrease in chlorophyte diversity. Similar seasonal salinity patterns for this eastern region and the study area (Levings *et al.* 1976) reduce the possibility of salinity influencing species distribution between the two regions.

Accompanying increased summer light intensities are conditions of increased temperature to which an alga must also adapt (i.e. eurythermal). In determining the effects of temperature on distribution and production, consideration must be given to emersion and immersion temperatures. Water temperatures remain moderate over a tidal cycle throughout the year (Fig. 6) and statistical analyses show this change significant in limiting production of algae tolerant of high temperature and desiccation (Table 10, 20). However, an even greater influence exerted by temperature is the extremes of water to air temperature on emersion (Fig. 6). Algae experience daytime emersion during summer and night-time during the winter, exposing them to great temperature extremes throughout. Spatial-temporal distribution and production patterns are explained partially by the degree to which a species is eurythermal. Studies by Healey (1972), Yokohama (1972), and Mathieson and Norall (1975) suggest an adaptive shift in the production-temperature relations for several algae present

throughout the year, with lower optimal temperatures for net production in winter compared to summer. Algae present for a part of the year may have a limited tolerance to temperature changes. Duration of exposure to a higher or lower temperature rather than the amount of change may be important, as exposure time increases with height in the intertidal.

Resistance to desiccation shown by an alga is another factor determining the structure of the benthic algal community at Squamish. Emersion-immersion time and duration, air temperature and drying effects of winds, frequent during the summer, all affect rate of desiccation. Algae such as *Cladophora* sp., *Monostroma oxyspermum* and *Spirogyra* sp. have little apparent resistance, being restricted to tide pools on emersion. Others such as *Enteromorpha minima*, *E. prolifera* and *Pylaiella littoralis* withstand desiccation very well. Intermediate between these two groups are diatom dominated associations requiring some moisture, either in the form of gradual runoff or tide pools.

Desiccation for a portion of the time appears to be of benefit to some algae. Johnson *et al.* (1974) and Brinkhuis *et al.* (1976) report that for intertidal species tested, especially those in the mid-upper regions, production on emersion often exceeds that on immersion by 1.6 - 6.6 times. Species from the lower intertidal have equal or lower emersion production rates compared

to immersion, being adversely affected by increased light and desiccation (Brown and Johnson, 1964, Imada *et al.* 1970). *Enteromorpha*, along with other high LTD tolerant chlorophytes (Table 10), may have the capacity for greater emersion production. Similarly, species favoring low light, such as *Pylaiella littoralis* (Table 10), may benefit from emersion during the winter when light is reduced. Thus, it is suggested that desiccation may affect benthic algal distribution and production in a negative or positive fashion, depending upon species, location in the intertidal and season. Vertical compression results in a selection for mid-upper intertidal high light tolerant species in the summer. Increased production on desiccation may lead to maximum benthic algal production in an estuary.

Euryhalinity (osmoregulatory capability), in addition to governing the entry of an alga into an area can also act as a controlling factor in seasonal and spatial patterns of distribution and production. The water column over the delta remains relatively homogeneous over a tidal cycle ($\pm 3^{\circ}/\infty$) for most of the year. The majority of wide and rapid salinity changes occur on exposure to either conditions of rain, evaporation in shallow tidal pools or desiccation. Certain species show this limitation clearly, with *Spirogyra* sp. the most notable. Its presence in tidal pools is negatively correlated with salinity (Table 20), disappearing on

increased salinity after freshet. *Cladophora* sp. shows the same seasonal patterns but appears less sensitive to salinity (slightly more euryhaline).

Van der Werff (1960) suggests that salinity governs the distribution and production of benthic diatoms in estuaries. However, more recently Williams (1964) and Admiraal (1977) have provided contradictory data. Admiraal states that benthic diatoms actually have a very high tolerance to salinity change, showing a drop in net production of only 30% going from 4 to 60 ‰ salinity. This supports data from Squamish showing the high salinity tolerance of estuarine benthic diatoms (Table 6, Appendix VIII). Salinity does appear to affect the species diversity of an association, with lower salinity producing greater diversity. Sullivan (1977) reports a similar situation for edaphic (benthic) diatom associations in New Jersey salt marshes.

In order to persist over an extended period, an alga must be able to adapt to rapid changes as well as to continually increasing and decreasing salinity of the surrounding waters. Algae colonizing the delta can be classified into two groups based on salinity. Some can tolerate salinity ranges (0 - 30 ‰ -- strongly euryhaline) whereas others are more restricted, (either 0 - 15 or 15 - 30 ‰ -- weakly euryhaline). The majority of macroalgae and microalgal associations are strongly euryhaline. Thus, with the exceptions of *Spirogyra* sp.

and *Cladophora* sp., salinity does not appear to be a major factor controlling distribution and production of algae on the portion of the Squamish delta studied.

In contrast to the complex interactions of factors controlling structure of the benthic algal community, is the apparent simplicity of factors for the vascular plants. Macrovegetation on the Squamish delta, dominated by *Carex lyngbyei*, has been investigated by Lim and Levings (1973) and Levings and Moody (1976). Zonation from low to high intertidal of low sedge to high sedge to grasses and clover was noted. This is considered a response to total immersion, light availability, and salinity. Since *C. lyngbyei* originated in a freshwater habitat (Stebbins 1950), low salinity concurrent with its growth period and the lack of substrate-habitat preference are viewed as major factors permitting entry and establishment over virtually the entire delta surface. High light intensity and daytime emersion favor growth of emergent vegetation. Rapid growth and the dense nature of *C. lyngbyei* remove the low light species through light limitation, as was the case for benthic algae.

C. lyngbyei is well adapted to existence on a tidal marsh such as Squamish and exerts a strong influence on ecosystem structure and function, as will be discussed.

In summary, structure of the autotrophic component of the tidal marsh ecosystem at Squamish can be described

in terms of species composition, spatial arrangements, dispersions and abundance. Species composition is initially governed by osmoregulatory capabilities of an alga. Species succession throughout the year is seen as primarily a response to light intensity, with sedge growth having a strong influence. Desiccation, with the concomitant effects of temperature and salinity, is also considered a significant factor. Spatial arrangement and dispersion are controlled by substrate-habitat preference and degree of habitat specificity. Producers showing strong specificity tend to be aggregated (e.g. *Spirogyra* sp., Association B), whereas those with weaker specificity appear randomly distributed (e.g. Associations E and G, *Monostroma oxyspermum*). Interspecific competition is yet another factor affecting spatial arrangement.

The abundance of each primary producer is an important aspect of ecosystem structure, organization, and function. Measured as standing crop biomass, abundance reflects the amount of preferred substrate-habitat available, the adaptability of the producer to the environment (i.e. net productivity) and the growth form (micro- vs macroalgae). *Carex lyngbyei* is the major contributor of biomass. Associations G and E and *Pylaiella littoralis* are next highest in abundance (Appendix VI). The value of abundant preferred substrate and the character of weak habitat specificity are

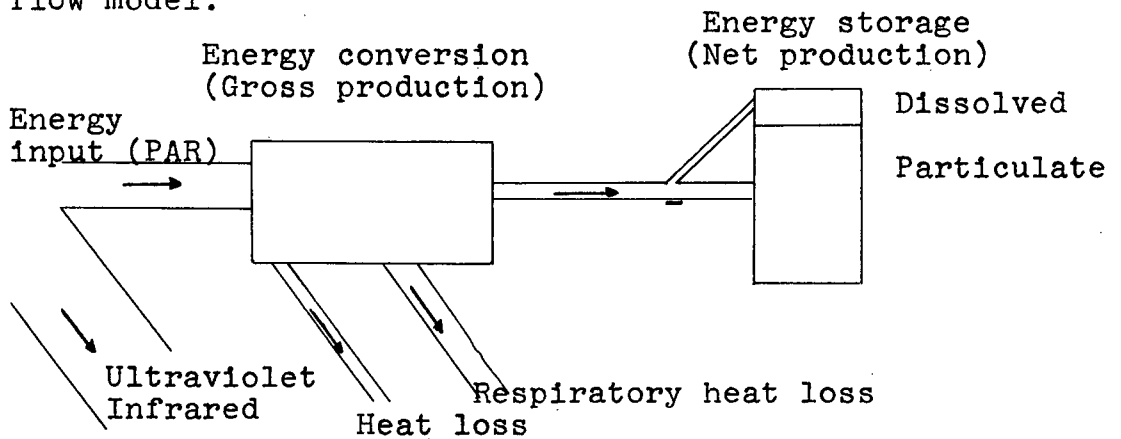
reasons for their dominance, since all have wide distribution (Fig. 10). On a square meter basis, Associations E and G have the lowest biomass on the delta (Table 7).

II. Ecosystem Function

Structural analysis of an ecosystem is of limited value in understanding ecosystem operation. It is an indication of what is present, how it is distributed, and an estimate of the amount present. Possible factors controlling structure may also be derived, as done in this thesis. Comparisons of different ecosystems are possible using such data. However, neither the function in or importance of a particular component to the ecosystem nor operation of the ecosystem as a unit are revealed.

Ecosystem processes and interrelations (functions) are best described in terms of energy rather than straight organic matter (Lieth 1968). Energy provides a more comparative basis, removing variations in organic and carbon content of different organisms. The study of ecological energetics (energy flow) deals with the input of energy (primarily solar) and the pathways and efficiencies with which it is converted by autotrophs (primary producers) and utilized by heterotrophs (decomposers and consumers). The magnitude and efficiency of solar energy conversion, its manner of storage as

chemical energy and subsequent utilization are characteristic of a particular ecosystem (i.e. give it functional identity). However, even though the autotrophic and heterotrophic components may differ, the initial pathways of energy transfer are basically the same and can be presented as a universal energy flow model.



The flow pattern may represent two approaches to the study of energetics. By representing a single producer, such as *Enteromorpha minima*, an emphasis is placed on food chain or population analysis. The importance and use of each producer is determined and compared with that of others. This results in specific information on mechanisms influencing energy flow. Examining energy flow on a community (vascular plant or benthic algal) or ecosystem basis provides for a broader view. Having determined specific and general pathways, it is possible to predict the sources and effects of energy

loss from an ecosystem and potential consequences of structural alteration.

Energy flow reported over a year provides a well defined measure. Most communities and species have natural periodicities related to changing physical-chemical factors, making a measurement over this time period desirable and the common practice in establishing energy pathways. Within the long term variation, short term or seasonal patterns exist, in which significant producers change. Determination of this is valuable. A producer may be a preferred food source for a particular consumer in addition to contributing to the general energy pool of the ecosystem. Brinkhuis (1976a, b) notes the value of measurements over the entire year for persistent species and over the growth period for seasonal species in determining the function of a species within an ecosystem.

Data from the first four months research are not included in formulation of energy pathways. This allows for a period of methodology development and improvement. Thus, the one year period from September 1974 through August 1975 is selected.

The study of energy flow is in its infancy compared to other areas of ecology and is unfortunately based on numerous assumptions. Unless all energy sources, methods and rates of storage, conversion, input, utilization and losses for either a single producer or the

ecosystem as a unit can be determined independently, many assumptions and estimates must be made in deriving energy pathways. Ecosystem structure provides some information with respect to these areas, as will be discussed.

A. Energy sources, conversion, input and storage.

Energy sources. Three energy sources exist at Squamish. The first, and that common to other ecosystems, is radiant energy. Two basic components of the radiation energy environment, solar and longwave thermal radiation flux, are important. To consider one in the absence of the other provides only a partial understanding of total radiation change at the earth's surface. However, Odum (1971) points out that even though the "total radiation flux determines the 'conditions of existence' to which an organism must adapt, it is the integrated solar radiation...which is of greatest interest in terms of productivity and nutrient cycling within the ecosystem."

Solar radiation reaches the biosphere at a constant rate of $2 \text{ g cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$, becoming attenuated exponentially due to scattering and absorption by cloud cover and water vapor in the atmosphere (Odum 1971). At most, 67% may reach sea level on a clear summer day, with attenuation occurring to varying degrees as a function of wavelength and frequency (Gates 1965). Reifsnyder and Lull (1965) estimate that on a clear day sea level

radiation is composed of *ca.* 10% ultraviolet (<400 nm), 45% visible (400-700 nm), and 45% infrared (>700 nm). However, under conditions of dense cloud cover, dust and vapor, further attenuation and alteration of spectral distribution occurs permitting primarily visible radiation to pass through the atmosphere. Attenuation becomes especially significant at Squamish where cloud cover and industrial haze are common.

Visible radiation (photosynthetically available radiation--PAR) is that portion of total solar radiation actually available to and usable by primary producers. Phillipson (1966) estimates annual PAR input for areas at decreasing latitudes with Britain (*ca.* 55° N) receiving $2.5 \times 10^5 \text{ kcal} \cdot \text{m}^{-2}$, Michigan (*ca.* 44° N) 4.7×10^5 and Georgia (*ca.* 32° N) $6.0 \times 10^5 \text{ kcal} \cdot \text{m}^{-2}$. Reifsnyder and Lull (1965) give a theoretical maximum annual PAR for the northwestern United States (*ca.* 47° N) of $6.95 \times 10^5 \text{ kcal} \cdot \text{m}^{-2}$, assuming a horizontal surface. Estimated annual PAR input for Squamish of $4.15 \times 10^5 \text{ kcal} \cdot \text{m}^{-2}$ (Table 1) falls well below this and slightly below that for Michigan. The discrepancy from the theoretical PAR can be attributed to steep mountains surrounding Squamish and to the frequent presence of an industrial haze layer. Both tend to decrease intensity and duration of radiation. Solar radiation represents the single most important source of energy to an ecosystem.

A second source of energy for producers on the Squamish delta is that of tidal action. The mean tidal

amplitude of *ca.* 4 m, supplemented by current and winds, provides a considerable energy subsidy. This tends to reduce the cost of internal self-maintenance of primary producers, maximizing the energy going into production (storage) and minimizing that to respiration. The principle of an estuary as an energy subsidized system has been well documented (Odum 1971, Odum and Fanning 1973, Nixon and Oviatt 1973; Odum 1974, Steever *et al.* 1976) and the benefits are clear. However, past a certain tidal amplitude, differing between systems, physical stress (mechanical damage) outweighs the benefits. This negative effect is not evident at Squamish, as suggested by high production of vascular plants during the summer and algal epiphytes during the winter. Maintenance of positive production over the delta throughout the year does not indicate excessive tidal fluctuation. A

A third source of energy affecting the Squamish delta is addition (import) of particulate and dissolved organic matter. This originates from Howe Sound (plankton), the landward portion of the Central Basin (benthic algae, detritus) and from *Fucus* beds seaward of the study area. Energy from addition is unlike the previous two sources in that it does not require conversion, being immediately available to consumers. Along with tidal energy, it acts as a bonus to the delta ecosystem, enhancing available energy in the primary trophic level.

Although added organics account for only *ca.* 5% of total available energy, their presence is considered significant to the system, acting as a substrate for heterotrophic uptake, growth stimulators and/or inhibitors and as food for grazing and detrital organisms.

Energy conversion, input and storage. Energy enters the Squamish ecosystem primarily by photosynthetic conversion (i.e. gross primary production).

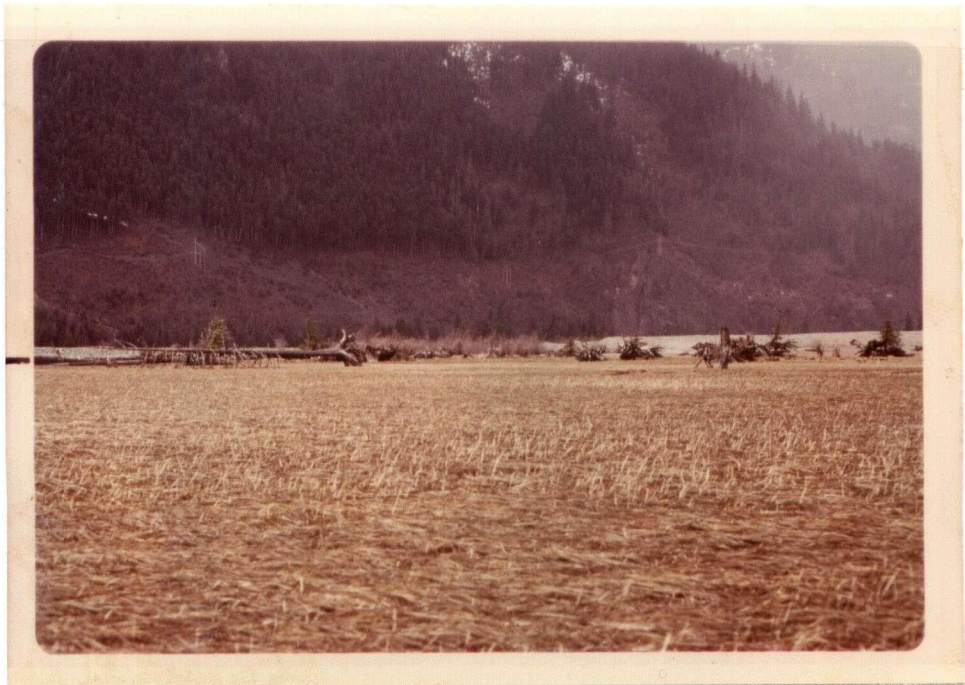
1) Vascular plants. *Carex lyngbyei*, which occupies *ca.* 80% of the intertidal marshland at Squamish, is the major site of energy conversion and storage on the delta. Due to its dominance, a discussion of energy flow through *Carex lyngbyei* is assumed to represent that for the vascular plant community on the delta.

Levings and Moody (1976) present growth and biomass data upon which production and energy flow are based in this thesis. In early March the tidal marsh is a flat mat of decaying vegetation remaining from the previous year (Fig. 13), with some new shoots becoming apparent. The decaying mat disappears by May and in mid June die-back of fresh growth becomes apparent (Levings and Moody 1976). Maximum growth is reached in July (Fig. 13) and minimum in August at the end of the growing season (Appendix XI). Decomposition proceeds over winter and into spring and summer of the following year.

Net production (above and below ground) was estimated to be *ca.* $2067 \text{ g organic} \cdot \text{m}^{-2} \cdot \text{season}^{-1}$ (Appendix XI).

Figure 13. *Carex lyngbyei* meadow in early March, showing mat of decayed vegetation, and in late July at the time of maximum growth.

Early March



Late July



Assuming organic matter to be 50% C, total net primary production amounts to about $1034 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. This value likely represents an underestimate. Basing net production on standing crop biomass often fails to account for turnover of live material between sampling periods (Kirby and Gosselink 1976, Turner 1976). Unmeasured herbivory, tissue decay and erosion, exudation, tidal amplitude (energy subsidy), current action and winds, along with favorability of the growing season all affect turnover rate (Vollenweider 1974). Turnover rate appears faster in high energy, subsidized environments such as tidal marshes. Hatcher and Mann (1975) estimate an average loss of 28.5% of end of year standing biomass for salt marshes. Nixon and Oviatt (1973) indicate a loss of 10 - 15% for similar marshes. Thus, assuming loss of above ground organic matter to be a minimum of 10%, a total production estimate of $2177 \text{ g organic} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ is arrived at, based on above and below ground estimates.

Caloric content determined for *Carex lyngbyei* ($4.08 \text{ kcal} \cdot \text{g organic}^{-1}$) compares favorably with values reported by Straskraba (1968) and Grabowske (1973) for other *Carex* species. Below ground energy content (i.e. rhizomes) was assumed to be the same as above ground (Dykyjova and Pribil 1975). Thus, energy available to the delta ecosystem as end of year standing crop of $\text{ca. } 8880 \text{ kcal} \cdot \text{m}^{-2}$ is separated into $4707 \text{ kcal} \cdot \text{m}^{-2}$ above

ground and 4173 kcal m^{-2} below ground. Utilization is essentially restricted to the area of production.

Assuming a respiration rate of 50% for *Carex lyngbyei* with its freshwater origin (Stebbins 1950), under brackish conditions, the above values must be doubled to obtain estimates of gross production. This amounts to *ca.* $97 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, approaching the upper limit of energy input ($100 \text{ kcal} \cdot \text{m}^{-2}$) noted by Odum (1971). If the respiration estimate were lowered to 30% (an average for macroalgal respiration), the delta would still rank high in terms of energy input (*ca.* $67 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), indicating its great productive capacity.

Energy conversion by *Carex lyngbyei* is very efficient. Average photosynthetic efficiency (net production/PAR) of 3.04% calculated over the growing season is high compared to most terrestrial systems at 1-3% (McNaughton and Wolf 1973). Peak photosynthetic efficiencies of 4.95% in June compare with the maximum of 5% noted by Phillipson (1966). Abundant moisture, nutrients and the influence of tidal energy subsidy lead to efficient use of solar energy.

The majority of energy conversion and storage carried on by vascular plants remains as POM, with only a small fraction leached as organic exudates (DOM) (Tukey 1970, Wetzel and Manny 1972, Turner 1974, Gallagher *et al.* 1976). Assuming 3-4% of converted energy goes to DOM, and a caloric content equal to that for POM, an

estimated $236 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ DOM is exuded above ground during the growth period of *Carex lyngbyei*. Although this represents a very low portion of production, it is significant in terms of the total amount added over the large growth area.

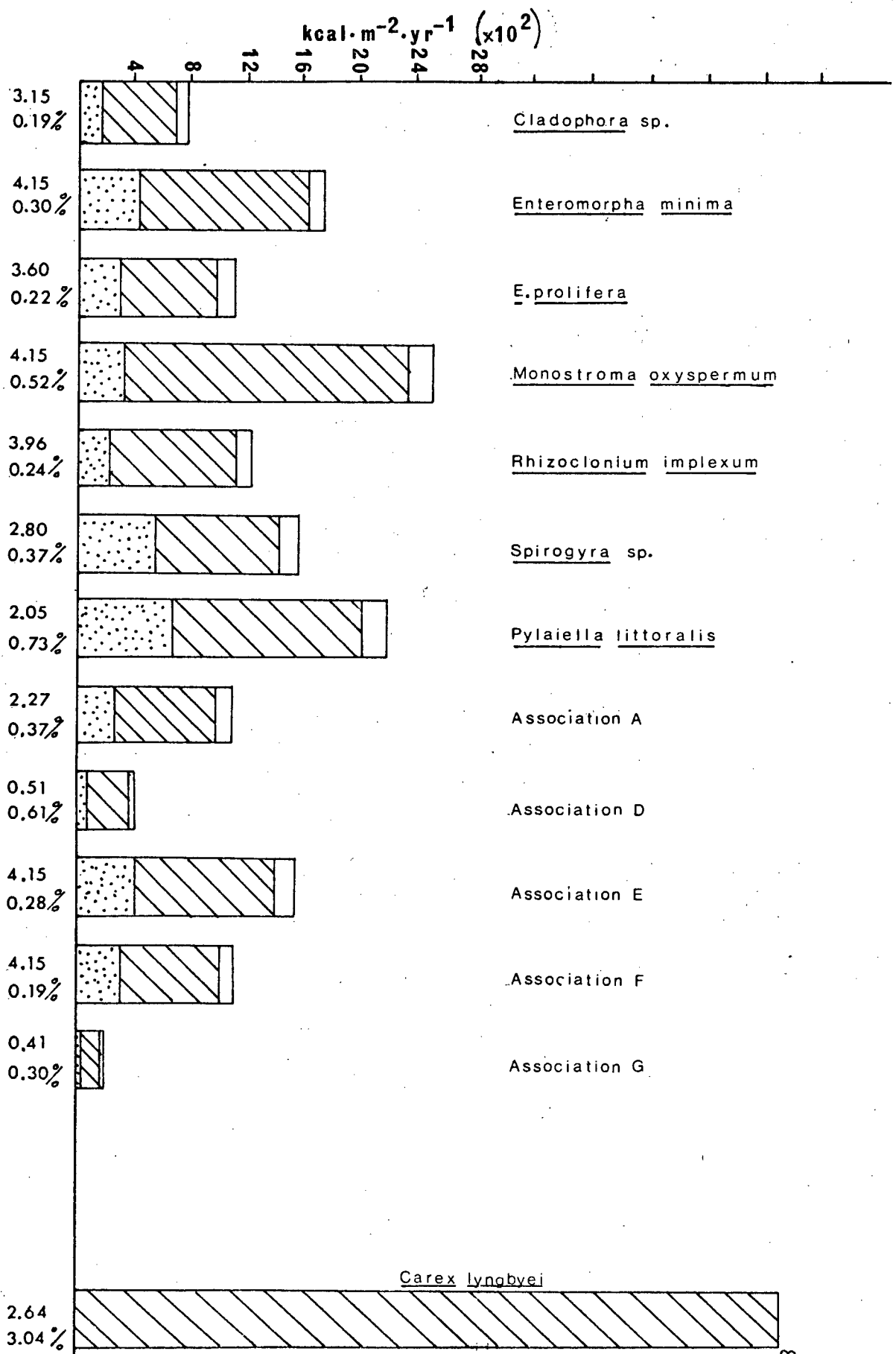
2) Benthic algae. Fourteen major benthic algal species and/or associations with differing seasonal patterns, productivity and ecology dominate the algal flora of Squamish. The capacity of each for energy conversion and storage and their contribution to available energy on the delta attributable to benthic algae are discussed.

To facilitate examination of energy flow through a square meter of each producer, energy conversion (gross production) is separated into respiration and available stored energy (DOM,POM) Fig. 14).

Monostroma oxyspermum and *Pylaiella littoralis* are the potentially most valuable species (Fig. 14). These are both low LTD forms with high production maxima (Table 10). Two high LTD species, *Enteromorpha minima* and *Spirogyra* sp. (Table 10) also appear as major sources of energy input and storage. (Fig. 14). The conclusion drawn is that species, either persistent or seasonal, are present throughout the year with a high potential input of available energy. This is based on high storage rate (net production) and reasonably high photosynthetic efficiencies (Fig.14) and caloric content

Figure 14. Energy input (gross production) for each major producer separated into dissolved organic , particulate organic , and respiration  .

The numbers under each producer refer to available PAR ($\text{kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \times 10^5$) over the growth period and to photosynthetic efficiency (%), respectively. (Minor Associations  and B not included in graph).



8880 kcal

(Table 16). The high ranking of Association E, a persistent diatom-dominated grouping of low productivity, is primarily due to the high caloric content (*ca.* 1.5 times that of the noted macroalgae). The importance of basing ecosystem function on energy relations is emphasized. The very minor energy contribution by a m^2 of Association G should be noted at this point for future reference. Low productivity (Table 10), biomass (energy storage) and caloric content (Table 16) dictate its apparent minor role.

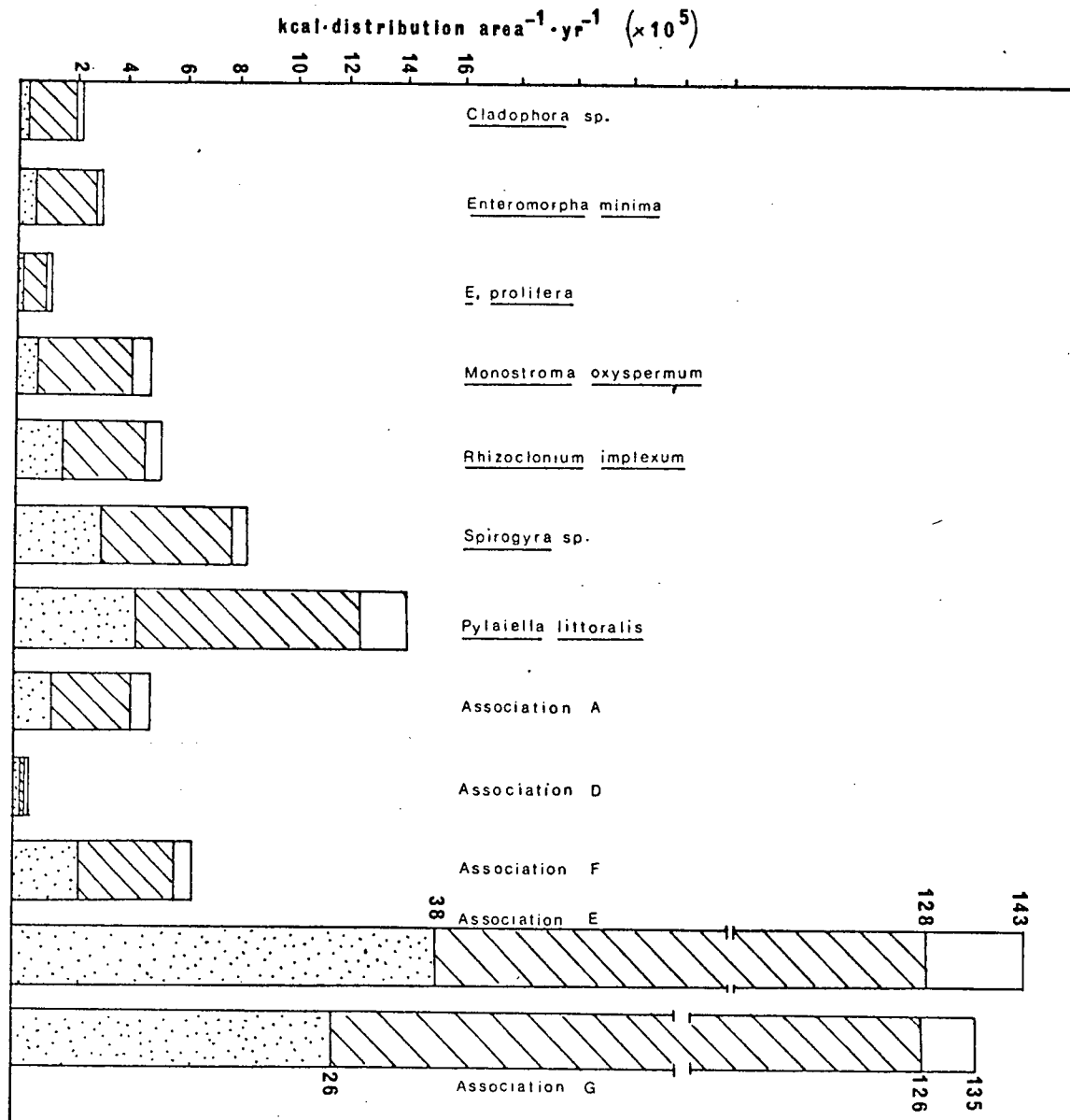
In summary, the high rates of energy conversion and storage by the above noted algal producers is attributable to: 1) being highly adapted to and tolerant of the estuarine environment (persistent species-strongly eurythermal and euryhaline) or being "bloom" species taking advantage of optimum conditions as suggested by King and Schramm (1976) (seasonal species-weakly eurythermal and euryhaline); or 2) being of thallose or filamentous morphology; or 3) having a high photosynthetic efficiency relative to other algae, resulting in higher net production (energy storage); or 4) in the case of Association E, having a very high caloric content in the presence of low net production and photosynthetic efficiency. These factors determine potential importance of a producer to energy flow on the Squamish delta.

Figure 14 clearly shows how *Carex lyngbyei* dominates the energy environment at Squamish. Available energy from a square meter is at least 4.5 times that contributed by the most productive alga.

The effect of ecosystem structure on the magnitude of energy conversion and storage by various benthic algae is evident in Figure 15 which considers the distributional area of each producer. Microalgal Associations E and G make the greatest contribution to available energy rather than macroalgae as considered on a square meter basis. The high energy input of Association G (primarily *Ulothrix*), which had the lowest input per square meter, is attributed to growth during a period of optimum physical-chemical conditions (low LTD), concurrent with the presence of uniform substrate (*Carex*) covering some $90 \times 10^3 \text{ m}^2$. Energy available for use over the year of $111 \times 10^5 \text{ kcal}$ represented ca. 43% of the total attributed to benthic algae. Annual available energy for Association E of ca. $104 \times 10^5 \text{ kcal}$ over an area of $10 \times 10^3 \text{ m}^2$ amounted to 41% of the total. This highly productive nature of sand/mud flat diatom associations has been noted (Pomeroy 1959, Williams 1962, Gallagher and Daiber 1974) and will be discussed further. Associations E and G accounted for 84% of total available energy originating from benthic algae.

It is thus not simply the productive capacity ($\text{kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) of an alga which determines its importance to

Figure 15. Energy input (gross production) for each major producer, separated into dissolved organic  , particulate organic  , and respiration  . (Minor Associations B and C not included.)



the delta ecosystem but also its ability to colonize extensive rather than restricted habitats (i.e. having wider tolerance to light, salinity, desiccation and temperature). Highly productive species with narrow tolerance ranges covering small areas are generally of less importance (Fig. 15).

Benthic algae release a large portion (up to 30%) of daily net production as DOM. Determinations made in this study are considered as minimum values. Only the effect of increased light was considered. Other stress factors shown to enhance DOM release include temperature, salinity, desiccation and subsequent re-immersion (Sieburth 1969, Penhale and Smith 1977). All these operate at Squamish, as discussed, which could lead to even higher exudation by chlorophytes (Table 12) compared to other benthic algae, suggesting the former are more tolerant of the stresses of a tidal marsh existence.

Pro-rating total net production for each month indicates seasonal shifts in the distribution of available energy among producers (Appendix XII). In the fall and winter distribution is primarily in Associations E and G (up to 90%), whereas in spring and summer, distribution is wider, with more emphasis placed on macro-algae, especially chlorophytes.

In a similar fashion, pro-rating over the year of each producer identifies the season of maximum energy

conversion and storage (Appendix XIII). Time of the peak for each varies, approximately coinciding with its classification in the high, medium and low LTD groups (Table 10).

Data from prorating indicate that seasonal distribution of energy input is such that maximum periods are staggered, resulting in continual energy storage in the system. However, variations in the magnitude of this storage varies, causing distinct seasonal patterns.

3) Seasonal variation in energy conversion and storage. Characteristic energy flow patterns exist in fall, winter, spring, and summer for the benthic algal community. These are based on variations in 1) sources of energy (solar, tidal); 2) ecosystem structure (species composition and distribution); and 3) production potential (energy conversion and storage) (Fig. 16).

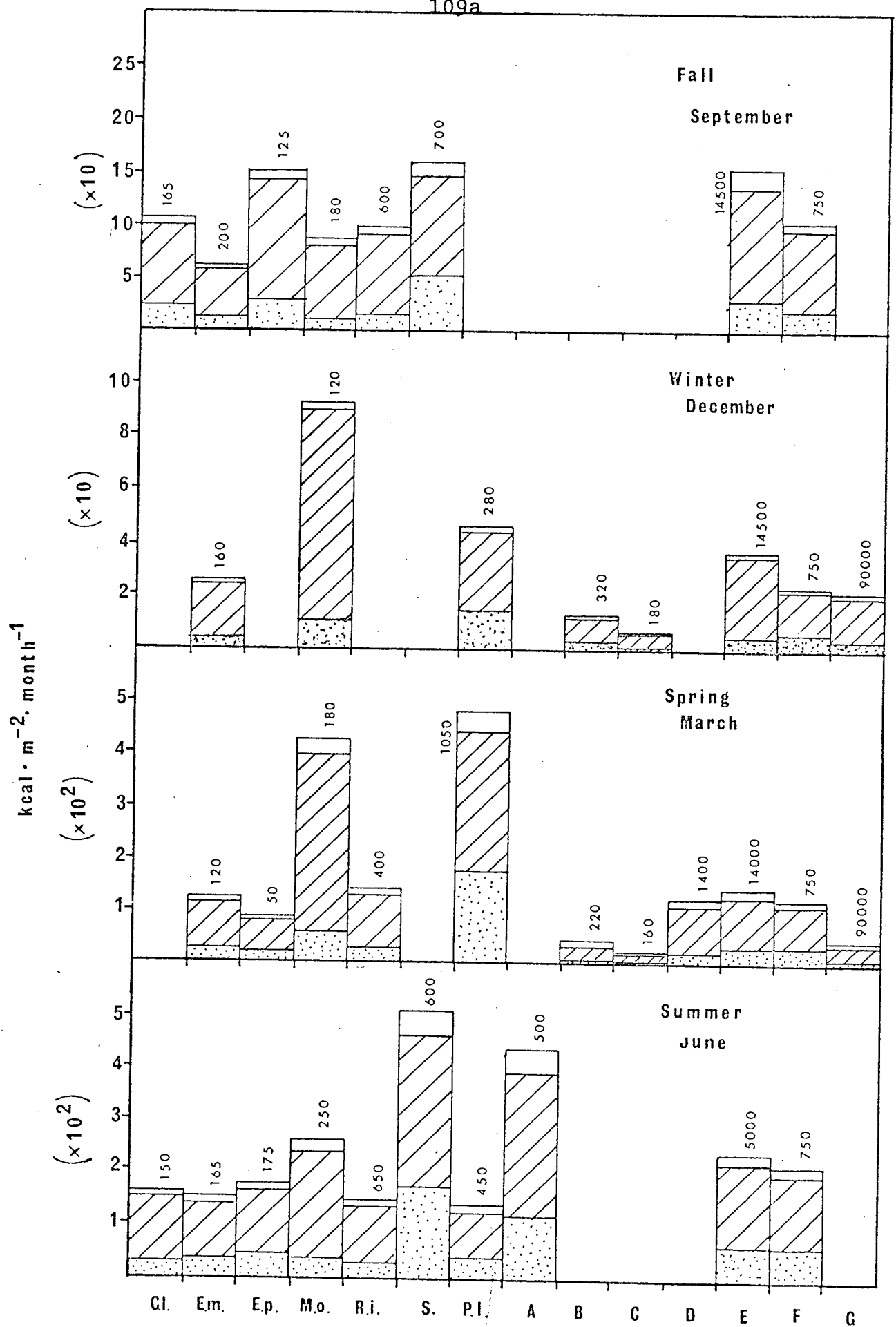
Variations in algal producers over the year (chlorophytes - summer, fall; diatoms and phaeophytes - winter, spring) have been discussed and attributed to light, temperature, salinity and competition. The increased energy input of persistent producers such as *Monostroma oxyspermum* and *Enteromorpha minima* in spring and summer reflects the presence of more favorable growth conditions just as with seasonal species.

Taking distributional area of benthic algae into account, energy input and storage shows very definite increases from summer through to the following spring

Figure 16. Energy flow ($\text{kcal} \cdot \text{m}^{-2} \cdot \text{mo}^{-1}$) through major benthic algal producers in fall (September), winter (December), spring (March) and summer (June). Numbers above each bar refer to distributional area in square meters.

Cl -- *Cladophora* sp.
 Em -- *Enteromorpha minima*
 Ep -- *E. prolifera*
 Mo -- *Monostroma oxyspermum*
 Ri -- *Rhizoclonium implexum*
 S -- *Spirogyra* sp.
 Pl -- *Pylaiella littoralis*

 A -- Association A
 B -- Association B
 C -- Association C
 D -- Association D
 E -- Association E
 F -- Association F
 G -- Association G



(Table 21). This is logical in view of past discussions of ecosystem structure and the controlling effect of *Carex lyngbyei* on the extent of the benthic algal community. It tends to restrict distribution and total energy input during summer via shading and promote during winter and spring by acting as a substrate. Low respiratory costs of winter (17%) compared with spring (35%) indicate reduced stress and less energy diverted to metabolic processes. Whittaker (1975) suggests that, on the average, energy input is *ca.* 1.5 times energy storage for aquatic systems. At Squamish, this value is 1.6 during the winter and 1.38 for the year. This is a slightly higher rate of energy storage on the Squamish delta compared to other systems and is credited to the delta being an energy subsidized ecosystem.

B. Annual energy flux and general ecosystem function.

Energy conversion and storage by the major autotrophic components (vascular plants and benthic algae) on the Squamish delta have been considered, along with controlling physical-chemical factors. Combining this with data on energy loss (organic removal), utilization (grazing and detrital feeding), and retention (incorporation into sediments), it is possible to discuss pathways of energy flux for the primary level of the Squamish delta ecosystem.

Table 21. Total energy input (gross production), storage (net production as DOM, POM), and losses (respiration) for benthic algal producers in fall, winter, spring and summer as $\text{kcal} \times 10^3 \cdot \text{mo}^{-1} \cdot \text{study area}^{-1}$.

	Fall (September)		Winter (December)		Spring (March)		Summer (June)	
	$\text{kcal} \cdot 10^3$	%	$\text{kcal} \cdot 10^3$	%	$\text{kcal} \cdot 10^3$	%	$\text{kcal} \cdot 10^3$	%
Gross Production (energy input)	2453.9		2905.3		6588.0		2144.4	
Respiration (energy loss)	629.9	26	493.6	17	2304.7	35	543.9	28
Net Production (energy storage)								
DOM	190.7	8	387.0	13	436.0	7	190.7	9
POM	1637.3	66	2024.7	70	3847.3	58	1359.8	63

Two habitats can be identified on the Squamish delta based on differences in structure and energetics. The sand/mud flats habitat of the lower intertidal is simple with respect to structure and energy flux (movement), whereas the *Carex* marshland in the mid-upper intertidal is much larger and more complex. Energy flux through a square meter of each is discussed.

Sand/mud flat habitat. Energetics of this area are based on a single producer, the diatom dominated Association E. Approximately 41% of total energy input and storage resulting from the activity of benthic algae comes from continued production of this association throughout the year (Table 22). Available energy ($850 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) from net production and organic addition amounts to ca. 78% of total energy input. Over half of the available energy is removed, either as DOM or POM to the surrounding estuary and waters of Howe Sound. Approximately 17% is retained and incorporated into the substrate where it either acts as a food source for micro-organisms or is permanently lost in the sediment.

A turnover time of four days for Association E, the most rapid on the delta, plus low retention of energy suggest the sand/mud flat habitat to be very efficient in terms of energy cycling. Net phyto-production for the year (gross primary production + organic addition) - (respiration + organic removal)

Table 22. Annual energy flux for sand/mud flats (area = 15875 m²) and sedge marshlands (area = 111125 m²).

	Sand flats kcal·m ⁻² ·yr ⁻¹	Marshland above ground below ground kcal·m ⁻² ·yr ⁻¹	
A. Input			
Gross primary production			
benthic algae	910	178	-
vascular plants	-	9416	8347
Added organic matter	<u>185</u>	<u>543</u>	<u>-</u>
	1095	10137	8347
		total = 18484	
B. Losses			
Respiration			
benthic algae	245	36	-
vascular plants ^a	-	4708	4173
Losses to turnover			
vascular plants	-	471	-
Removed particulate organic matter	170	2350	-
Exuded organic matter	86	154 ^d	-
Unmeasured ^b grazing ^c and undetected removal	404	1480	-
C. Incorporation in sediment	<u>190</u>	<u>930</u>	<u>4173</u>
	1095	10137	8347
		total = 18484	

^a assume respiration of *Carex* = 50%

^b obtained by difference (Input - other expenditures)

^c assume ca. 5% going to grazing

^d including 3% of vascular plant net production as DOM of 141 kcal

amounts to $+239 \text{ kcal} \cdot \text{m}^{-2}$ or 22% storage of total energy input on the delta. This is a measure of the net change (storage or loss) in the amount of carbon held by a system and is valuable in appraising function (Woodwell *et al.* 1973). In this case, it is further indication of a strongly exporting habitat.

Carex marshland. The *Carex* marsh habitat is separated into above and below ground components as dictated by structure, energy input, storage and utilization.

Above ground energy input is distributed between *Carex* (93%), benthic algae (2%), and added organics (5%), together contributing *ca.* 10 times the energy per square meter of the sand/mud flats (Table 22). The greater addition of organic matter over that of the flats is due to the "trapping" nature of the *Carex*, causing particles to settle out.

Available energy (net production and added organics) amounts to *ca.* 54% of input, a drop of 27% over that found on the flats but a substantial increase in terms of actual energy ($5474 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). Higher rates of respiration plus a turnover time averaging 19 days (Appendix X) are responsible for the drop in energy storage efficiency. However, of this stored energy, an estimated 67% is removed from the delta to surrounding waters, or *ca.* eight times that contributed by the sand/mud flats. The importance of the marshland is emphasized.

Calculation of net phyto-production gives a value of $+1338 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ or 12% of total energy input. This indicates that the marsh is even more highly exporting in nature than the sand/mud flats in terms of percent and actual contributions.

In contrast, the below ground portion of the marsh appears as a virtually isolated system with no addition (import) and little removal of material except sedge rhizomes at the periphery of the delta (Table 22).

Combining data from the sand/mud flat habitat and the *Carex* marsh, it is clear that Squamish is a vascular plant dominated system, with only *ca.* 3% of energy input due to benthic algae. The sand/mud flat habitat plays a very minor role in total energy flux, adding a maximum of 1.4% of the energy.

The estimated value of 3% is considered to be an underestimate due to methodology used in this study (i.e. incubation of samples in water). Johnson *et al.* (1974) indicate production of benthic algae from the mid-upper intertidal to be 1.6 - 6.6 times greater in air than in water. However, desiccation reduces the degree of production in air. Algae at Squamish experience considerable desiccation at low tide during the summer due to wind and high temperatures. Therefore, assuming an increase of four times water production, in air, and exposure of the algae at low tide during the day for *ca.* 50% of their growth period, net primary

production for benthic algae could amount to *ca.* 7% rather than 3%. This estimate of net production, taking air into account is considered realistic in view of the fact that not all algae show increased production in air. Species from the lower intertidal areas (i.e. *Pylaiella littoralis* and some microalgal associations) often show reduced rates of production (Johnson *et al.* 1974).

Increasing energy input attributable to benthic algae to 7% approximates an estimate of 8% made for benthic algae on the Nanaimo estuary (Sibert and Naiman, unpublished data). However, this value must also be increased to account for production on exposure, increasing it to *ca.* 15%. On both the Nanaimo and Squamish estuaries intertidal microalgae play a larger role than do macroalgae, a fact which may reflect greater available habitat and growth efficiency.

Few studies exist comparing energetics of benthic algae and vascular plants on deltas. Teal (1962), preparing an energy budget for a salt marsh in Georgia, estimated that of total available energy, benthic algae (primarily sand/mud flat diatoms) accounted for 25%. More recently, Gallagher and Daiber (1973, 1974) report an estimate of 25 - 30% for benthic algae relative to *Spartina* for a Delaware salt marsh. The projected value of 7% estimated for the Squamish delta is much lower in comparison. This may be due to: 1) an overestimate of gross production by *Carex* (i.e. assuming 50%

respiration), 2) a variation in algal species and restricted distribution of highly productive diatom associations due to shading by sedge and covering by sediment during freshet, and 3) a more northerly location, resulting in reduced solar energy and conversion rates.

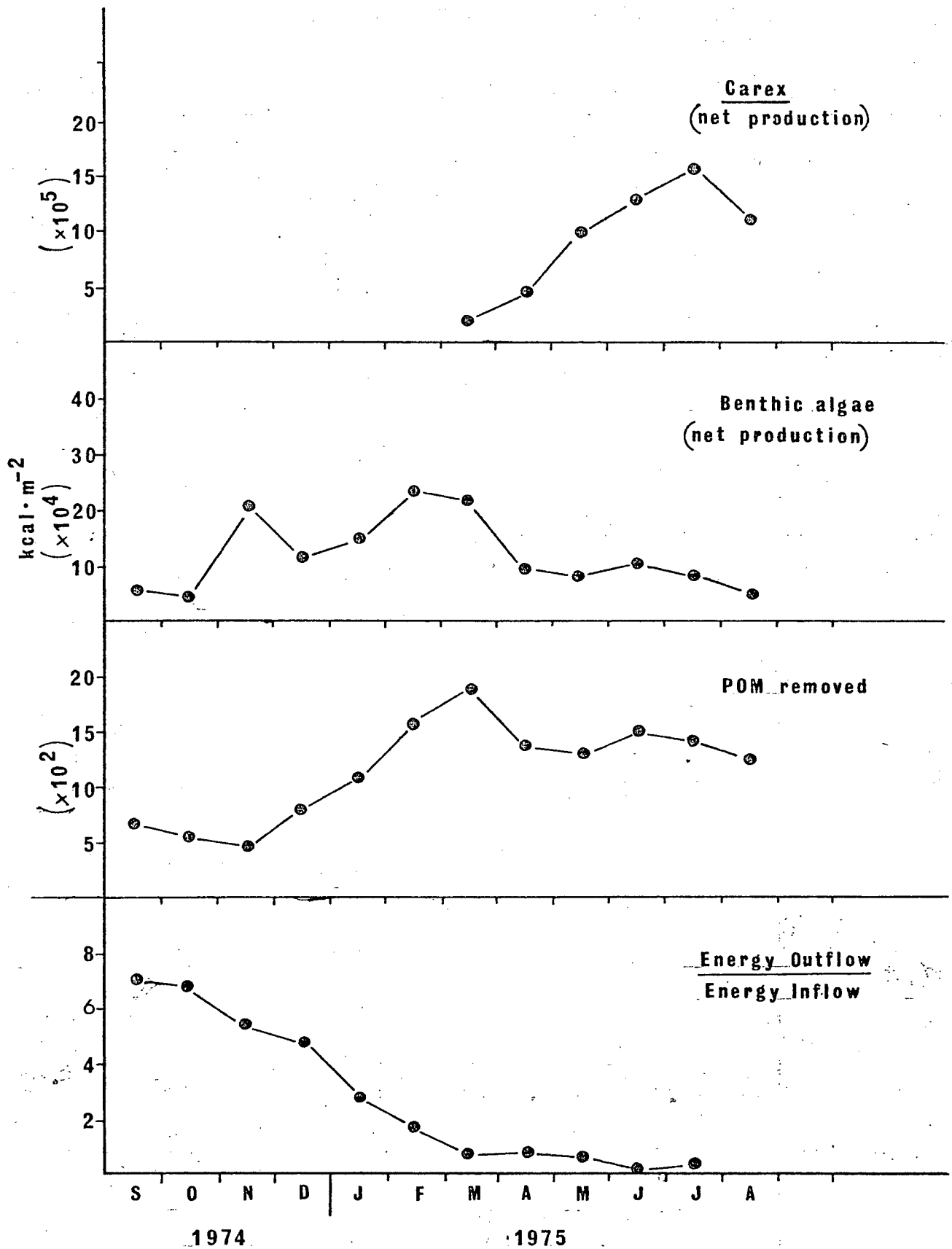
In a tidal marsh system dominated by *Carex lyngbyei* it is the manner in which energy is put into the system by benthic algae rather than the absolute amount that is the important feature (i.e. flux rather than standing crop biomass). Benthic algae act as continually present, readily available sources of energy directly utilizable by at least one major consumer on the delta (amphipods). Alternatively, on rapid breakdown, algae contribute energy to the general detrital pathway. There is little lag between the time of conversion and utilization of stored energy. *C. lyngbyei* displays a definite time lag between production, decomposition, and utilization. Thus, the marsh may be regarded as a large energy regulator with high energy storage and timed release throughout the year.

Energy flow and ecosystem function at Squamish are cyclic in nature, as summarized in Figure 17. Some of the important features will be discussed. The bulk of energy conversion and storage, above and below ground, occurs by *C. lyngbyei* in spring and summer. During this period little consumption of living material occurs,

aside from that going to as yet unidentified invertebrates and insects (5%, C. D. Levings, personal communication). *Anisogammarus confervicolus*, an important consumer on the delta (Anonymous 1972), is not able to utilize *Carex lyngbyei* unless first decomposed (Table 17, Chang 1975). Low level release of DOM (4%) over the large growth area could have a considerable impact on ecosystem function by acting as an energy source for bacteria, which are utilized by filter and detrital feeders. Turner (1974) and Gallagher *et al.* (1976) indicate the importance of this pathway in estuaries dominated by *Spartina alterniflora*, suggesting that much of the DOM is metabolized within the marsh ecosystem. Contrary to this, Penhale and Smith (1977), working with *Zostera*, believe that the majority of DOM is flushed out of the estuary by tidal action. Low levels of DOM in waters adjacent to the delta and in upper Howe Sound suggest rapid uptake and *in situ* utilization, as indicated by Gallagher *et al.* (1976) for salt marshes. More study is needed in this area of energy storage and utilization.

Energy input by benthic algae is low during spring and summer, being restricted by the presence of vascular plant growth, high light, temperature and low salinity (Fig. 17). Its importance at this time, as throughout the year, is as a readily available food source. Results from this study indicate preferential feeding on filamentous (*Pyraliella littoralis* and *Enteromorpha minima*)

Figure 17. Seasonal pattern of energy storage (net production) by *Carex lyngbyei* and benthic algae, energy removal as POM and the ratio of energy outflow/energy inflow.



and, to some extent, thallose (*Monostroma oxyspermum*) algae by amphipods (Table 17). Peak biomass of filamentous algae approximately coincides with that for juvenile amphipods which readily consume such species as *Pylaiella littoralis* under laboratory conditions. Chang (1975) suggests the need for algae in the diet of amphipods for maximum growth and survival. Data from feeding studies based on fatty acid analysis indicate ingestion of algae under field conditions. In addition to an energy source, benthic algae, primarily *Pylaiella littoralis* and *Enteromorpha minima*, serve as sites of cover at low tide, preventing desiccation of amphipods remaining on the marsh surface at low tide (Tables 16, 17). Associations of benthic algae and other consumers similar to that described for amphipods likely exist. Studies of this nature are required to further indicate the function of benthic algae in a *Carex* marsh ecosystem.

Removal of POM is high in spring and summer (Fig. 17), reflecting increased decomposition rates. Removal is greater by an average of 10 times on the marsh compared to the sand/mud flats (Table 15). The origin of the POM can be traced to algae present on the delta and primarily to *Carex* produced the previous year. Decomposition remains low over the winter, showing increases in spring and summer in response to higher temperatures and light and increased activity and abundance of grazer-decomposer organisms. Preliminary studies done

in this thesis on POM show the amount and composition of material removed from the delta to be a function of growth, substrate-habitat type (Table 15), current and wave action, depth of water in tidal creeks (Table 14), and type of area drained by the creeks (Fig. 12).

High variability thus exists over the delta with respect to POM removal (Dewitt and Daiber 1973, Odum *et al.* 1972, Boon 1975, Erkenbrecher and Stevenson 1975, Gardner 1975). Shisler and Jobbins (1977) note similar problems in salt marshes of the eastern United States. Teal (1962), Odum and de la Cruz (1967), Biggs and Flemer (1971), Heald (1971), Mann (1972a), Riley (1973), Schultz and Quinn (1973), Valiela and Teal (1974) and Heinle *et al.* (1977) all note the importance of POM to salt marshes and estuaries. As judged from results at Squamish on production and removal rates of POM, its importance in estuarine ecosystems dominated by *Carex* tidal marshes is as great as in salt marshes.

The majority of POM produced over the year is removed from the delta (ca. 70%) (Table 22). Kirby and Gosselink (1976) suggest a similar rate of removal for POM in a Louisiana salt marsh dominated by *Spartina alterniflora*. However, de la Cruz (1973) reports a removal rate of only 21% for a similar marsh in Georgia. Variation may be a result of the factors noted at the top of this page. The portion of POM retained on the delta at Squamish becomes incorporated into the upper layer of the marsh during heavy sedimentation at freshet

(June-July). Approximately 40-50% of what is incorporated is mobilized by micro-organisms and returned to the system to participate in estuarine processes. The remaining energy is lost in a "sediment sink" of varying depth, indicated by little change in organic content (i.e. beyond depth of reworking). Biggs and Flemer (1972) also indicate a mobilization of ca. 50%.

Addition of POM to the delta is also highest in spring and summer (Fig. 17) and variable from sand/mud flats to *Carex* marsh (Fig. 11). A greater proportion of macroalgae are added to the marsh in response to the filtering nature of *Carex*. It is acting as a trap for energy (organic matter) entering from external sources and a retention mechanism for energy stored and broken down on the delta. In this way, energy is available for the marsh ecosystem and not totally removed by the twice daily tidal flushing. Retention of a larger proportion of detritus on the sand/mud flats reflects a reduced ability to trap large particles (i.e. macroalgae). The nature of the substrate, large sand to mud, favors settlement and incorporation of detritus.

The ratio of energy removal/energy storage (net production + organic addition) is a good indication of energy flux throughout the year (Fig. 17). A ratio < 1.0 reflects accumulation of energy, whereas >1.0 reflects removal in excess of storage. Based on this ratio, spring and summer are times of high energy accum-

ulation whereas fall and winter are times when the estuarine ecosystem is drawing heavily on stored energy (Fig. 17).

The only source of energy input via primary production to the delta during fall and winter are benthic algae (Fig. 17). Total conversion and energy storage reaches its peak during the winter when the competitive action of *Carex* is at a minimum and low LTD tolerant algae (Table 10) can colonize and add to energy storage. POM removal is low during the fall, an indication that much of the *Carex* from the previous year has been removed, leaving minimal amounts on the delta.

Increase in POM removal over the winter parallels increased algal growth and may be reflecting the onset of breakdown of the present year's crop of *Carex* (Levings and Moody 1976) by decomposers favoring lower temperatures. Amplifying removal rate are increased wave and current action in winter.

The below ground portion of the marsh was described structurally and from an energy flux standpoint as a separate unit contributing little to energy flux in the estuarine ecosystem. However, seasonal changes exist in energy stored in the rhizomes. Bernard (1974) and Bernard and MacDonald (1974) note a negative production (i.e. utilization of stored energy) in winter through to the next growing season for species of *Carex* occurring in wetland situations. This is also considered to be the case for *Carex* at Squamish. Breakdown of rhizomes

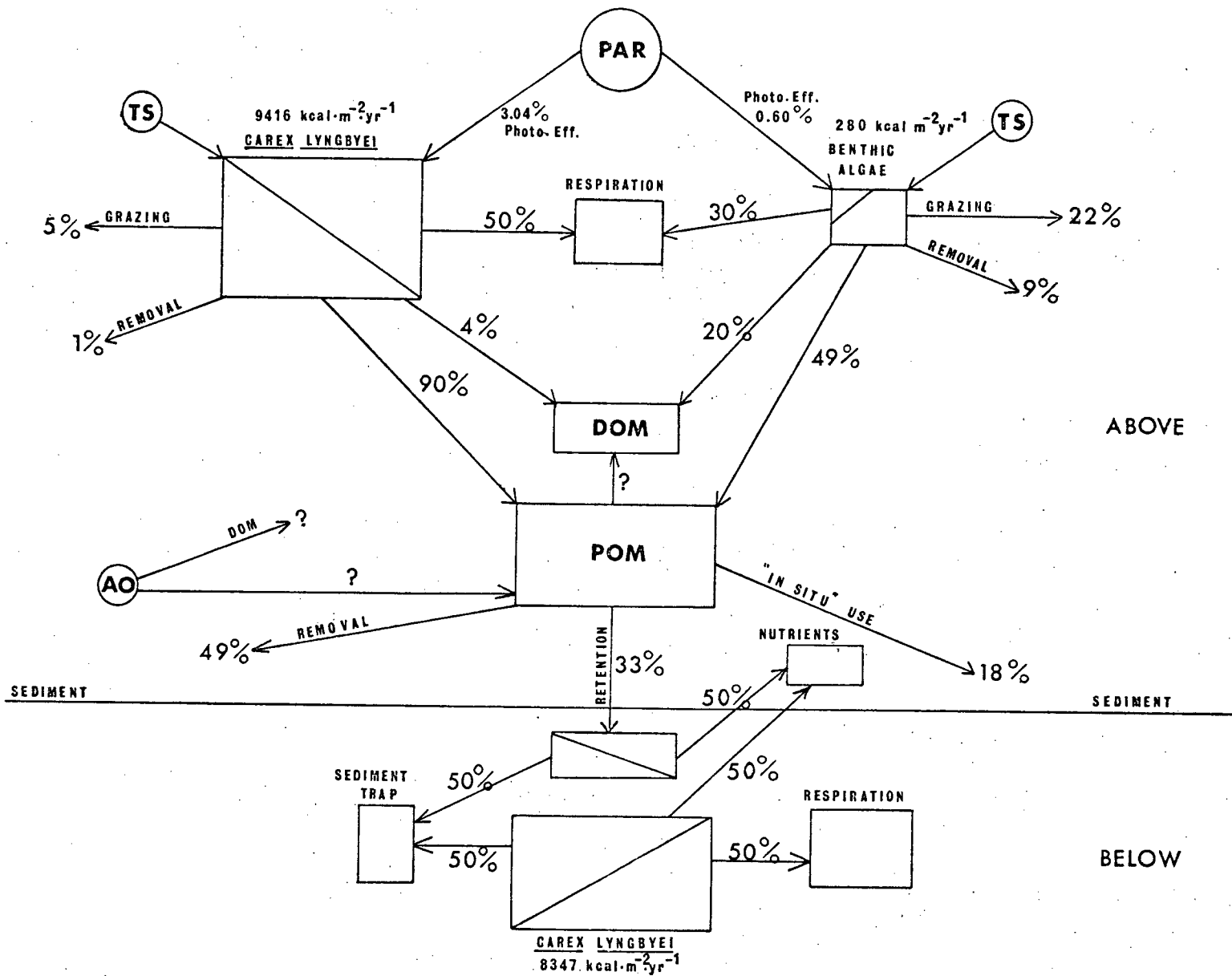
below ground provides energy for organisms which rework the sediment, releasing nutrients and organic material to the surface. In light of these features, the below ground portion of the marsh is seen as important in above ground ecosystem structure and function.

III. The Squamish River Delta as a Productive, Energy Rich Ecosystem

The Squamish River delta is a very dynamic system, annually converting, storing and contributing large amounts of energy to the surrounding estuary. Primary pathways of energy flux are summarized in Figure 18 for ease of understanding.

It is clear that the delta is a detrital-based system, with most of the energy input and storage attributable to vascular plants growing on the tidal marsh (Fig. 18, Table 22). Smalley (1959), Odum (1963), Odum and de la Cruz (1963), and Pomeroy *et al* (1969) note similar findings in Georgia salt marshes. In these marshes, 70 - 90% of available energy going to detritus originates from species of *Juncus* and *Spartina*. Zieman (1975) reports 90% of production from turtlegrass beds in Florida enters the detrital chain. These data are comparable to those from Squamish, which indicates ca. 90% input of vascular plant production to the detrital chain.

Figure 18. Proposed energy flux through *Carex lyngbyei* (above and below ground) and benthic algae. Relative percentages derived from Table 22 represent flux in a "characteristic" square meter of delta surface. Energy remaining after respiratory costs are removed is partitioned into grazing, DOM and POM, representing a total 100% of available energy. POM is similarly partitioned. (TS = tidal energy subsidy, AO = added organic matter, PAR = photosynthetically available radiation).



Benthic algae with their low energy input and storage (3%) primarily function as: 1) an energy source for specialized consumers, 2) a possible requirement in the diet of certain invertebrates (e.g. amphipods (Chang 1975)) and 3) an auxiliary source of detritus, being most abundant when breakdown of *Carex* is thought to be lowest.

Large amounts of DOM, from sources indicated in Figure 18, supply ample substrate for heterotrophic activity, promoting vascular plant breakdown. Pomeroy *et al.* (1975) provide an excellent discussion and indicate the importance of DOM to microbial activity in estuaries. The proportion resulting from benthic algal exudation is minimal and may function more in inter-species competition with other algae or in determining species composition of associated consumers.

Particulate organic matter, which forms the base of the detrital food chain, originates primarily from vascular plants (Fig. 18). It is estimated that *ca.* 49% of energy available as POM is removed from the delta to function in the detrital food chain of the surrounding estuarine ecosystem. This value compares very well with the estimate of 45% by Teal (1962) for a Georgia salt marsh.

Approximately 18% of available energy is utilized by detritivores on the delta as it is produced. This estimate of "*in situ*" utilization is lower than those

given by Teal (1962) for a Georgia salt marsh and Thayer *et al.* (1975) for an eelgrass (*Zostera marina*) bed in North Carolina. Both studies indicate 55% utilization by consumers. The greater use may reflect the presence of more consumers (micro- and macrofauna) and the breakdown of *Zostera* and *Spartina* to a more usable form compared to *Carex*.

Due to heavy sedimentation at Squamish, it is estimated that *ca.* 33% of available energy (POM) is retained on the delta and becomes incorporated into the sediment (Fig. 18). Mobilization by decomposers occurs slowly, returning *ca.* 50% to the system as nutrients, etc. An equal amount remains trapped in the sediment along with *ca.* 50% of the energy stored in *Carex* rhizomes. The remaining 50% in *Carex* is returned to the system via the action of decomposers (Fig. 18).

Some data exist in the literature with which to compare Squamish in terms of primary production. The *Carex* tidal marsh, which dominates total energy flow on the delta, is among the most productive of those reported in the literature (Levings and Moody 1976) (Table 23). An average of *ca.* $550 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Appendix XI) exceeds estimates for wetlands in the interior of British Columbia. Higher production rates are attributed to abundant nutrients (Bernard 1973), retained and rapidly recycled (Odum 1971); daytime emersion during productive parts of the year; low salinity, reducing metabolic stress; and the benefits of a tidal energy subsidy.

Table. 23. Comparison of net production (energy storage) as $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for *Carex lyngbyei* and vascular plants of other marsh areas.

Location	Habitat	Net Production (energy storage) $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$	Reference
Squamish River Delta British Columbia	<i>Carex lyngbyei</i> tidal marsh	550	Levings and Moody 1976
Fraser Delta British Columbia	<i>C. lyngbyei</i> tidal marsh	450	Yamanaka 1975
Western New York USA	<i>C. lacustris</i> wet-land	735	Bernard and MacDonald 1974
San Francisco Bay California	<i>Spartina foliosa</i> salt marsh	135 - 345	Mahall and Park 1976
New England, Mary- land, Virginia	<i>S. alterniflora</i> salt marsh	215 - 690	Nixon and Oviatt 1973b Keefe and Boynton 1973
Sapelo Island Georgia	<i>S. alterniflora</i> salt marsh	1600	Teal 1962
Bridgewater Bay Southern England	<i>S. alterniflora</i> salt marsh	380	Ranwell 1961
Puget Sound Washington	<i>Zostera marina</i> marine	518	Phillips 1974

The estimated net production of *Carex lyngbyei* is similar to values given in the literature for *Spartina* spp. on salt marshes of the United States. The latter are among the most naturally productive ecosystems (Odum 1971).

Comparative data for benthic algal production in tidal and salt marsh estuarine ecosystems are not that abundant in the literature. Estimates relating to diatom-dominated microalgal associations are best documented (Table 24). Net production estimates determined for Squamish appear somewhat lower than those for other estuarine and marine intertidal situations. This is a reflection of a more northerly location, with reduced photosynthetically available radiation, and likely variations in species composition of the microalgal associations.

Taken as a unit, the Squamish River delta ranks among the most highly productive naturally occurring ecosystems. This may be attributed to: 1) presence of a tidal energy subsidy, reducing energy going to metabolic processes; 2) extreme nature of the environment, which selects for species well adapted to year round existence or opportunistic species with high productivity for a short period; and 3) continual input of energy into the system by benthic algae. Schelske and Odum (1961) note similar reasons behind the high productivity of Georgia salt marshes.

Table 24. Comparisons of net production (energy storage) as $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for diatom-dominated microalgal associations in estuarine and marine habitats.

Location	Habitat	Net Production (energy storage) $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$	Reference
Squamish River Delta British Columbia	sand/mud flat <i>Carex</i> tidal marsh	114 150 ^a	estimated from Appendix VIII this study
Deleware, USA	salt marsh	60 ^b	Gallagher and Daiber 1974
Duplin River marsh Georgia, USA	<i>Spartina alter- niflora</i> dominated salt marsh	190 ^c	Pomeroy 1959
Great Sippewissett Marsh, Falmouth, Massachusetts, USA	salt marsh	274 ^d	Van Raalte <i>et al.</i> 1968
Washington, USA	intertidal marine sand flats	143 - 226	Pamatmat 1968
Denmark	intertidal marine sediments	115-178	Grontved 1960

^a average over a square meter of marsh surface

^b assume respiration = 25% gross production

^c assume respiration = 10% gross production

^d maximum value based on estimate of $75 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$

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Appendix I. Light attenuation in the water column adjacent to the delta, as % incident radiation.

Date	Depth		
	0m ^a	1m	2m
1974			
20 June	40	9	1
5 July	60	10	1
19 July	65	10	2
11 August	70	15	5
27 August	75	20	8
2 September	75	22	10
13 September	80	25	15
17 October	90	30	18
30 October	90	37	23
22 November	90	35	25
18 December	90	38	24
1975			
22 January	90	36	22
20 February	90	54	28
19 March	92	38	20
16 April	80	26	10
14 May	86	30	13
12 June	70	8	1
16 July	65	10	1
29 July	55	8	2
13 August	70	20	10

a

15 cm below water surface

Appendix II. Salinity, temperature and incident radiation (PAR).

Date	Depth (m)	Salinity ^a °/oo	Temperature		air	Light (PAR)
			water ^a	tide pool ^b		
1974						
21 June	0 ^c	3.5				
	1	4.0	9.0	17.9	14.0	192.4
19 July	0	4.3	10.2			
	1	4.8	10.6	17.4	15.1	174.0
20 August	0	1.2	12.0			
	1	1.7	-	17.9	17.8	140.0
18 September	0	5.8	10.7			
	1	9.0	-	15.4	15.6	125.4
17 October	0	22.2	8.6			
	1	24.5	8.8	-	10.1	109.8
17 November	0	11.5	8.5			
	1	12.0	10.5	-	4.5	32.8
17 December	0	5.1	4.0			
	1	5.8	4.7	-	3.4	25.9
1975						
21 January	0	27.3	5.8			
	1	27.5	6.0	-	0.1	19.8
19 February	0	25.6	5.2			
	1	27.5	5.7	-	0.6	32.7

.....Continued

Date	Depth (m)	Salinity ^a ‰	Temperature			Light (PAR)
			water ^a	tide pool ^b	air	
19 March	0	9.0	-	8.0	4.1	39.0
	1	16.0	-			
18 April	0	6.2	7.9	12.0	7.6	117.0
	1	12.6	9.0			
15 May	0	4.0	8.6	14.7	10.9	180.0
	1	6.0	-			
20 June	0	2.5	9.1	18.2	13.8	289.0
	1	3.0	-			
16 July	0	1.8	10.0	17.4	17.5	271.2
	1	2.9	10.8			
13 August	0	2.0	11.4	19.3	20.5	175.0
	1	3.1	11.8			

^a from Levings et al (1976)

^b determined with a standard mercury thermometer

^c 15 cm below water surface

Appendix III. Nutrient concentrations in tidal creeks (see Fig. 3 for sampling locations) ($\mu\text{g-at}\cdot\text{l}^{-1}$).

Date	Creek ^a Level	NO ₃ ⁻		NH ₄ ⁺		PO ₄ ⁻³		pH
		Pile	Snag	Pile	Snag	Pile	Snag	
1974								
19 July	H	2.41	1.83	4.14	7.19	1.32	1.19	6.98
	M	2.77	2.17	3.10	9.41	0.99	0.79	6.90
	L	2.01	1.92	4.92	6.03	1.17	1.02	6.94
2 September	H	0.50	0.21	3.40	5.71	2.30	1.72	7.08
	M	1.12	0.74	3.90	6.33	2.49	1.98	7.12
	L	0.74	0.37	2.49	5.46	1.90	1.32	7.10
1975								
22 January	H	31.40	-	1.74	-	4.39	-	7.66
	M	39.90	27.29	3.12	3.98	4.90	3.17	7.55
	L	33.71	21.07	2.94	3.14	4.19	2.88	7.58
19 April	H	3.93	4.39	1.39	2.75	0.94	1.19	7.67
	M	4.80	5.12	2.43	3.91	1.32	1.98	7.62
	L	4.17	4.72	2.01	3.49	0.89	0.94	7.69
12 June	H	1.92	1.35	6.21	9.42	9.72	1.12	7.15
	M	4.71	2.99	7.49	12.31	0.91	1.40	7.16
	L	3.12	2.42	5.12	9.99	0.61	1.19	7.19

^a H=just below delta surface
M=mid creek level
L=creek bottom

Appendix IV. Annual sedimentation rates and sediment organic content (LOI) determined from cores taken in 1974 from locations indicated below.

A. Spatial variation in mean sedimentation rates.

Area	Core numbers	Mean sedimentation·yr ⁻¹ (cm)	Area description
A	1-4	2.25	sand flat, low intertidal
B	5-8	2.56	<i>Eleocharis palustris</i> , consolidated mud, mid-intertidal
C	9-12	2.06	<i>Carex lyngbyei</i> tall growth (0.5-1.5 m) consolidated mud, mid-intertidal
D	13-16	1.79	<i>C. lyngbyei</i> short growth (<0.5 m), consolidated mud, mid-intertidal
E	17-20	2.03	creek bottom, unconsolidated mud, low intertidal
F	21-24	1.58	dead zone, strongly decomposing, unconsolidated mud, upper intertidal
G	25-28	- ^a	<i>Potentilla pacifica</i> zone, compact humid sediment, upper intertidal

^a years not identified, sectioned in cm intervals

Appendix IV B. Year of deposition, depth, and LOI.

Core	Year deposited	Depth interval (cm)	LOI ^a (mg C·g dry wt. ⁻¹)	Percent LOI
Area A	1974	1.50	11.6	2.4
	73	1.00	11.7	2.4
	72	1.00	10.7	1.8
	71	2.50	10.9	2.3
	70	3.50	10.0	1.4
	69	2.50	5.5	1.1
	68	3.00	6.2	1.3
	67	2.75	6.0	1.2
	66	2.50	5.8	1.2
		<u>20.25</u>		
Area B	1974	1.75	15.8	3.1
	73	1.50	11.1	2.2
	72	1.50	10.7	2.1
	71	2.75	7.6	1.7
	70	4.50	8.4	1.9
	69	3.00	9.5	1.9
	68	3.50	6.7	1.3
	67	3.00	8.7	1.7
	66	1.50	8.3	1.7
		<u>23.00</u>		
Area C	1974	1.50	20.1	4.0
	73	1.25	18.2	3.6
	72	1.25	18.2	3.6
	71	2.50	10.8	2.1
	70	3.50	9.6	1.9
	69	2.00	9.9	2.0
	68	2.00	10.5	2.2
	67	2.00	8.0	1.5
	66	2.50	3.0	0.6
		<u>18.50</u>		
Area D	1974	1.50	19.2	38.6
	73	1.00	20.4	40.9
	72	1.25	19.8	38.8
	71	2.75	12.7	25.3
	70	2.50	12.7	25.7
	69	1.50	11.1	22.4
	68	2.00	9.9	19.4
		<u>12.50</u>		

.....Continued

Core	Year deposited	Depth interval (cm)	LOI ^a (mg C·g dry wt. ⁻¹)	Percent LOI
Area E	1974	2.20	115.0	22.9
	73	2.00	111.0	22.2
	72	2.50	187.1	37.4
	71	2.00	124.5	25.0
	70	3.00	177.5	35.4
	69	3.50	98.5	19.7
	68	1.00	175.6	35.1
	67	1.00	103.1	20.6
		<u>16.20</u>		
Area F	1974	0.50	41.7	8.3
	73	1.00	74.7	14.9
	72	1.00	24.3	4.9
	71	1.50	37.0	7.5
	70	2.00	19.1	3.8
	69	2.50	25.0	5.1
	68	2.00	28.0	5.8
	67	2.00	57.3	11.3
	66	1.75	86.9	17.3
		<u>14.25</u>		
Area G ^b	1974	1.0	104.9	20.9
		1.0	58.5	11.7
		1.0	43.4	8.6
		1.0	51.5	10.3
		1.0	56.0	11.2
		1.0	35.6	7.1
		1.0	35.7	7.1
		1.0	30.5	6.1
		1.0	34.8	6.8
		1.0	22.8	4.6
		<u>10.0</u>		

^a mean of 6 samples from each layer

^b annual layers not detected

Appendix V. Seasonal changes in species composition of microalgal associations.
Numbers represent relative percent composition.

Association A

	Jun 74	Jul 74	May 75	Jun 75	Jul 75
<i>Melosira moniliformis</i>	60	0	80	50	0
<i>M. nummuloides</i>		0			0
<i>Synedra</i> spp.	10	10	0	15	10
<i>Thalassionema</i> sp.		10	5		15
<i>Navicula grevillei</i>	10	20	10	5	20
<i>Rhizoclonium implexum</i>	20	60	5	30	50

Association B

	Dec 74	Jan 75	Feb 75	Mar 75	Apr 75
<i>Navicula cancellata</i>	80	90	90	90	90
<i>Pleurosigma</i> sp.	10	5	5	5	5
<i>Hantzschia</i> sp.	10	5	5	5	5
<i>Nitzschia</i> sp.					

Association C

	Dec 74	Jan 75	Feb 75	Mar 75	Apr 75	May 75
<i>Navicula grevillei</i>	75	80	80	70	40	30
<i>Melosira nummuloides</i>	] 10	5	5	20	40	20
<i>M. moniliformis</i>						
<i>Thalassionema</i> sp.	] 5	5	5	5	5	20
<i>Synedra</i> spp.						
<i>Nitzschia</i> sp.						
<i>Gomphonema</i> sp.	] 10	10	10	5	15	30
<i>Achnanthes</i> sp.						
<i>Ulothrix flacca</i>						

....Continued

Appendix V. Continued.

Association D

	Jan 75	Feb 75	Mar 75	Apr 75
<i>Navicula grevillei</i>	] 30	30	40	40
<i>Navicula</i> spp.				
<i>Melosira moniliformis</i>	] 0	35	40	30
<i>M. nummuloides</i>				
<i>Thalassionema</i> sp.	] 40	30	20	30
<i>Synedra</i> sp.				
<i>Hantzschia</i> sp.	] 20	5	0	0
<i>Pleurosigma aestaurii</i>				

Association E

	1974								1975							
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
<i>Navicula cancellata</i>	60	65	60	50	40	20	5	20	20	35	50	70	75	70	75	
<i>N. grevillei</i>	5	0	0	0	0	5	5	5	5	5	5	5	5	0	0	
<i>Navicula</i> spp.	10	10	20	30	10	15	20	25	15	25	15	15	10	10	10	
<i>Melosira nummuloides</i>	] 0	0	0	0	0	0	5	10	10	0	0	0	0	0	0	
<i>M. moniliformis</i>																
<i>Melosira</i> spp.	] 10	10	10	5	5		10	20	10	5	0	0	0	0	0	
<i>Pleurosigma aestaurii</i>																
<i>Synedra tabulata</i>	] 10	10	10	5	5											
<i>Synedra</i> sp.																
<i>Pinnularia trevelyana</i>	] 10	10	10	5	5											
<i>Thalassionema</i> sp.																
<i>Nitzschia</i> sp.	] 15	15	10	5	25		50									
<i>Achnanthes</i> sp.																
<i>Hantzschia</i> sp.	] 15	15	10	5	25		55	20	40	30	30	10	10	20	15	
<i>Liomorphora</i> sp.																

....Continued

Appendix V. Continued.

Association F	1974							1975						
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Aug
<i>Vaucheria dichotoma</i>	85	80	80	80	80	70	60	50	50	60	70	80	80	80
<i>Phormidium</i> sp.	5	5	5	5	0	0	0	0	0	0	0	5	5	5
<i>Navicula</i> sp.	5	10	10	10	0	0	0	0	0	10	10	10	10	10
<i>Thalassionema</i> sp.	5	5	5	5	20	30	40	50	50	30	20	5	5	5
<i>Synedra tabulata</i>														
<i>Pinnularia</i> sp.														
<i>Nitzschia</i> sp.														
<i>Diploneis</i> sp.														
<i>Rhizoclonium implexum</i>														

Association G	Nov 74	Dec 74	Jan 75	Feb 75	Mar 75
<i>Ulothrix flacca</i>	70	70	60	70	80
<i>Synedra tabulata</i>	30	30	40	30	20
<i>Navicula grevillei</i>					
<i>Melosira</i> sp.					
<i>Licmophora</i> sp.					
<i>Achnanthes</i> sp.					
<i>Thalassionema</i> sp.	30	30	40	30	20
<i>Nitzschia</i> sp.					

Appendix VI. Distribution (coverage area) and biomass data for macroalgae and microalgal associations.

Date	<i>Cladophora</i> sp.		<i>E. minima</i>		<i>E. prolifera</i>		<i>M. oxyspermum</i>	
	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²
1974								
6 June	150	8.74	160	-	250	8.42	200	7.21
21 June	180	9.21	200	3.74	250	8.91	220	8.14
5 July	400	10.74	250	20.12	300	9.92	200	7.32
19 July	400	11.92	250	24.83	250	9.81	200	7.00
11 August	400	9.00	200	20.28	150	7.84	200	4.19
27 August	400	7.12	200	20.12	150	5.03	180	-
2 September	180	6.12	200	13.42	150	3.41	180	4.39
13 September	150	5.31	200	-	100	2.02	180	4.21
30 October	-	-	200	9.90	-	-	120	3.98
22 November	-	-	180	7.82	-	-	120	3.71
18 December	-	-	160	3.75	-	-	120	3.00
1975								
22 January	-	-	140	2.51	-	-	125	1.50
20 February	-	-	120	1.88	50	1.92	120	2.72
19 March	-	-	120	1.96	50	7.74	180	3.94
16 April	-	-	120	1.48	50	9.31	220	7.17
14 May	110	2.92	130	2.72	150	11.39	220	7.92
12 June	150	5.72	150	3.30	150	14.92	250	9.04
20 June	150	6.18	180	-	200	17.31	250	9.00
16 July	400	7.19	250	18.42	250	14.72	220	8.92
29 July	420	10.30	280	17.10	200	12.00	200	7.10
13 August	480	8.89	220	18.12	150	12.11	200	5.21
28 August	400	8.12	200	18.49	100	9.31	200	4.99

....Continued

Appendix VI. Continued.

Date	<i>R. implexum</i>		<i>Spirogyra</i> sp.		<i>P. littoralis</i>		Association A	
	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²
1974								
6 June	600	3.15	500	3.42	550	5.98	900	8.12
21 June	600	3.72	500	3.91	580	6.12	600	7.40
5 July	750	3.64	400	4.08	-	-	280	-
19 July	750	3.71	600	-	-	-	280	3.80
11 August	750	3.05	800	10.20	-	-	-	-
27 August	750	-	800	-	-	-	-	-
2 September	600	2.00	800	5.90	-	-	-	-
13 September	600	2.72	600	5.27	-	-	-	-
30 October	400	1.50	400	2.09	-	-	-	-
22 November	-	-	-	-	-	-	-	-
18 December	-	-	-	-	280	2.96	-	-
1975								
22 January	150	1.30	-	-	400	6.10	-	-
20 February	300	1.61	-	-	950	9.15	-	-
19 March	400	2.36	-	-	1050	12.80	-	-
16 April	600	3.28	-	-	1400	69.65	-	-
14 May	600	4.06	-	-	900	22.52	1000	5.32
12 June	650	-	600	3.43	500	6.88	500	7.83
20 June	650	3.10	600	-	400	5.00	500	7.60
16 July	700	3.52	500	3.94	-	-	300	3.41
29 July	700	3.41	600	4.21	-	-	400	3.98
13 August	800	3.10	850	11.72	-	-	-	-
28 August	800	2.74	900	12.00	-	-	-	-

....Continued

Appendix VI. Continued.

Date	Association B		Association C		Association D		Association E	
	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²
1974								
6 June	-	-	-	-	-	-	5000	0.75
21 June	-	-	-	-	-	-	5000	0.90
5 July	-	-	-	-	-	-	4000	0.86
19 July	-	-	-	-	-	-	4000	-
11 August	-	-	-	-	-	-	4500	0.61
27 August	-	-	-	-	-	-	4500	-
2 September	-	-	-	-	-	-	8000	0.95
13 September	-	-	-	-	-	-	8000	0.90
30 October	-	-	-	-	-	-	10000 ¹	0.99
22 November	-	-	-	-	-	-	10100	1.07
18 December	320	0.74	180	1.01	-	-	14500	1.14
1975								
22 January	320	1.24	180	2.31	800	3.83	14500	1.78
20 February	425	3.92	210	2.21	1000	7.11	14500	1.76
19 March	220	2.18	160	1.36	1400	7.96	14000	1.59
16 April	110	0.81	160	1.41	1000	3.84	14000	2.17
14 May	-	-	140	0.62	-	-	10000	1.94
12 June	-	-	-	-	-	-	5000	-
20 June	-	-	-	-	-	-	5000	0.95
16 July	-	-	-	-	-	-	4000	0.74
29 July	-	-	-	-	-	-	4000	0.78
13 August	-	-	-	-	-	-	4500	0.59
28 August	-	-	-	-	-	-	4500	0.59

....Continued

Appendix VI. Continued

Date	Association F		Association G	
	m ⁻²	gC·m ⁻²	m ⁻²	gC·m ⁻²
1974				
6 June	750	4.98	-	-
21 June	750	4.71	-	-
5 July	750	-	-	-
19 July	750	5.14	-	-
11 August	750	5.72	-	-
27 August	750	5.10	-	-
2 September	750	5.92	-	-
13 September	750	-	-	-
30 October	750	4.01	-	-
22 November	750	3.98	90000	0.75
18 December	750	1.49	90000	1.99
1975				
22 January	750	1.20	90000	4.92
20 February	750	1.94	90000	17.42
19 March	750	2.41	90000	8.72
16 April	750	2.14	-	-
14 May	750	4.12	-	-
12 June	750	5.30	-	-
20 June	750	5.40	-	-
16 July	750	5.12	-	-
29 July	750	5.43	-	-
13 August	750	4.94	-	-
28 August	750	4.34	-	-

Appendix VII. Total biomass for macroalgae and microalgal associations as kgC·distribution area⁻¹.

Date	<i>Cladophora</i> sp.	<i>Enteromorpha</i> <i>minima</i>	<i>Enteromorpha</i> <i>prolifera</i>	<i>Monostroma</i> <i>oxyspermum</i>	<i>Rhizoclonium</i> <i>implexum</i>	<i>Spirogyra</i> sp.	<i>Pylaiella</i> <i>littoralis</i>
1974							
6 June	1.31	0.60	2.11	1.44	1.89	1.71	3.29
21 June	1.66	0.75	2.22	1.79	2.23	1.96	3.55
5 July	4.30	5.03	2.93	1.46	2.73	1.63	-
19 July	4.77	6.21	2.95	1.40	2.78	4.90	-
11 August	3.60	4.06	1.18	0.84	2.29	8.16	-
27 August	2.85	4.02	0.75	0.86	1.74	1.44	-
2 September	1.10	2.68	0.51	0.79	1.20	4.72	-
13 September	0.80	2.33	0.20	0.73	1.63	2.16	-
30 October	-	1.98	-	0.48	0.60	0.84	-
22 November	-	1.41	-	0.45	-	-	-
18 December	-	0.60	-	0.36	-	-	0.83
1975							
22 January	-	0.35	-	0.19	0.20	-	2.44
20 February	-	0.23	0.10	0.33	0.48	-	8.69
19 March	-	0.24	0.39	0.71	0.84	-	13.44
16 April	-	0.18	0.41	1.58	1.97	-	97.51
14 May	0.32	0.35	1.71	1.74	2.44	-	20.29
12 June	0.86	0.50	3.24	2.26	2.23	2.06	3.44
20 June	0.93	3.30	3.46	2.25	2.02	2.01	2.00
16 July	2.88	4.61	3.68	1.96	2.46	1.97	-
29 July	4.33	4.79	2.40	1.42	2.39	2.53	-
13 August	4.27	3.99	1.82	1.04	2.48	9.96	-
28 August	3.25	3.70	0.93	1.00	2.19	10.80	-

....Continued

Appendix VII. Continued.

Date	Association						Total algal	
	A	B	C	D	E	F	G	biomass·mo ⁻¹
1974								
6 June	7.31	-	-	-	3.75	3.74	-	27.14
21 June	4.44	-	-	-	4.50	3.53	-	26.63
5 July	2.75	-	-	-	3.44	3.69	-	28.06
19 July	1.06	-	-	-	2.94	3.86	-	30.87
11 August	-	-	-	-	2.75	4.24	-	27.13
27 August	-	-	-	-	4.58	3.83	-	20.07
2 September	-	-	-	-	7.60	4.44	-	23.05
13 September	-	-	-	-	7.20	3.72	-	18.78
30 October	-	-	-	-	9.90	3.01	-	16.80
22 November	-	-	-	-	10.70	2.99	67.50	83.04
18 December	-	0.24	0.18	-	16.53	1.12	179.10	198.95
1975								
22 January	-	0.40	0.42	3.06	25.18	0.90	442.80	476.56
20 February	-	1.67	0.46	7.11	25.52	1.46	1567.80	1613.84
19 March	-	0.48	0.22	11.14	22.26	1.81	784.80	836.32
16 April	-	0.09	0.23	3.84	30.38	1.61	-	138.78
14 May	5.32	-	0.09	-	19.40	3.09	-	54.73
12 June	3.91	-	-	-	6.63	3.98	-	64.28
20 June	3.80	-	-	-	4.75	4.05	-	27.64
16 July	1.02	-	-	-	2.96	3.84	-	25.38
29 July	1.59	-	-	-	3.12	4.07	-	26.63
13 August	-	-	-	-	2.66	3.70	-	29.91
28 August	-	-	-	-	2.57	3.26	-	27.69

Appendix VIII. ^{14}C production and organic exudation data.
($\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)

Cladophora sp.

Date	Production		Exudation	
	s*	lm	s*	lm
1974				
6 June	0.72	0.22	0.05	-
21 June	0.79	0.23	0.05	0.01
5 July	0.87	0.29	0.07	0.02
19 July	1.10	0.21	-	-
11 August	0.71	0.49	0.04	0.02
27 August	0.64	0.43	0.03	0.01
2 September	0.55	0.28	0.03	0.02
13 September	0.52	0.29	0.05	0.02
1975				
14 May	0.52	0.32	0.04	0.01
12 June	0.49	0.13	0.04	0.01
20 June	0.68	0.14	0.08	0.01
16 July	0.77	0.18	0.08	-
29 July	0.90	0.18	0.07	0.02
13 August	0.68	0.29	0.05	-
28 August	0.63	0.32	0.04	0.03

Enteromorpha minima

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	1.74	0.63	0.10	0.02
21 June	-	0.51	-	0.02
5 July	1.12	0.28	0.11	0.02
19 July	0.46	0.19	0.04	0.01
11 August	0.75	0.79	0.06	0.05
28 August	0.98	0.79	0.09	0.03
2 September	0.39	0.27	0.03	0.02
13 September	0.48	0.49	0.02	0.02
30 October	0.52	-	0.03	-
22 November	0.24	0.10	0.01	0.02
18 December	-	-	-	-
1975				
22 January	0.12	0.09	0.01	-
20 February	0.47	0.30	0.03	0.02
19 March	0.51	-	0.04	-
16 April	0.69	0.52	0.05	0.03
14 May	0.74	0.51	-	-
12 June	0.98	0.36	0.08	0.02
20 June	1.09	0.15	0.09	0.01
16 July	0.94	0.39	-	-
29 July	-	-	-	-
13 August	0.66	0.31	0.05	0.02
28 August	0.41	0.39	0.03	0.02

* s = 15 cm below surface

....Continued

Appendix VIII. Continued.

Enteromorpha prolifera

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	0.46	0.10	0.04	0.01
21 June	0.76	0.11	0.07	-
5 July	0.83	0.13	0.08	0.01
19 July	0.90	0.13	0.07	0.01
11 August	0.53	0.25	0.03	0.02
27 August	0.46	0.17	0.01	0.01
2 September	0.33	0.30	0.03	0.01
13 September	0.26	0.19	0.02	0.01
1975				
20 February	0.16	0.06	0.01	0.01
19 March	0.42	0.17	0.03	0.01
16 April	0.55	0.28	0.04	-
14 May	0.45	0.24	0.03	0.01
12 June	0.54	0.25	-	0.01
20 June	0.60	-	0.06	0.03
16 July	0.70	0.17	0.07	0.01
29 July	0.86	0.21	0.09	0.01
13 August	0.42	0.15	-	0.02
28 August	0.41	0.25	0.04	0.01

Monostroma oxyspermum

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	0.92	0.10	0.08	0.01
21 June	1.22	0.16	0.09	0.02
5 July	0.74	0.11	0.05	0.02
19 July	0.99	-	0.07	-
11 August	0.34	0.12	0.02	0.01
27 August	0.47	0.20	0.03	0.01
2 September	0.33	0.17	0.02	0.01
13 September	0.48	0.25	0.03	0.01
30 October	0.54	0.30	0.05	0.02
22 November	0.67	0.25	0.04	0.02
18 December	0.97	0.39	0.05	0.03
1975				
22 January	0.84	0.42	-	-
20 February	1.99	0.91	0.10	0.07
19 March	2.43	0.90	0.12	0.08
16 April	1.74	0.90	0.09	0.07
14 May	1.43	-	0.05	-
12 June	1.24	0.22	-	-
20 June	0.91	0.14	0.07	0.02
16 July	0.90	0.17	0.08	0.02
29 July	0.54	0.15	0.05	0.02
13 August	0.52	0.20	0.04	0.02
28 August	0.37	0.17	0.03	0.01

....Continued

Appendix VIII. Continued.

Rhizoclonium implexum

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	0.59	0.12	0.06	0.01
21 June	0.67	0.16	0.09	0.01
5 July	0.74	0.16	0.10	0.02
19 July	0.69	0.15	0.07	0.01
11 August	0.51	0.19	0.04	0.01
27 August	0.75	0.31	0.04	0.02
2 September	0.32	0.16	0.01	0.02
13 September	0.23	0.09	0.02	-
30 October	0.11	0.06	0.01	-
1975				
22 January	0.42	0.23	0.02	0.02
20 February	0.49	0.21	0.00	-
19 March	0.63	0.20	-	-
16 April	0.79	0.28	0.03	0.01
14 May	0.50	0.13	0.04	0.01
12 June	0.43	0.10	0.07	0.02
20 June	0.48	0.10	0.04	-
16 July	0.75	0.19	0.13	0.02
29 July	0.76	0.16	0.11	0.02
13 August	0.58	0.18	0.04	0.01
28 August	0.69	0.17	0.05	0.01

Spirogyra sp.

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	-	-	-	-
21 June	2.13	0.43	0.54	0.16
5 July	2.04	-	0.46	-
19 July	1.49	0.32	-	0.02
11 August	1.12	0.27	0.17	0.03
27 August	1.34	0.21	0.20	-
2 September	0.93	0.27	0.09	0.02
13 September	1.14	0.25	0.11	0.04
30 October	0.26	0.10	0.04	0.02
1975				
12 June	1.74	0.37	0.30	0.06
20 June	1.39	0.24	0.22	-
16 July	1.90	0.30	0.28	0.11
29 July	1.62	0.23	0.29	0.10
13 August	1.07	0.62	0.12	0.07
28 August	0.92	0.47	0.16	0.04

....Continued

Appendix VIII. Continued.

Pylaiella littoralis

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	0.23	0.08	0.10	0.01
21 June	0.22	0.04	0.07	-
18 December	0.24	-	-	-
1975				
22 January	0.36	0.13	0.10	0.01
20 February	0.65	0.32	0.11	0.01
19 March	1.72	0.65	0.31	0.02
16 April	1.07	0.61	0.17	0.02
14 May	1.29	0.48	-	-
12 June	0.24	0.07	0.09	0.01
20 June	0.17	0.04	0.06	-

Association A

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	1.00	0.22	0.24	0.01
19 June	0.64	0.22	0.18	0.01
5 July	0.38	0.08	0.09	0.02
19 July	0.31	0.04	0.10	-
1975				
14 May	0.84	0.36	0.09	0.02
12 June	1.21	0.35	0.22	0.02
20 June	1.04	-	0.20	-
16 July	0.46	0.14	0.38	-
29 July	1.13	0.20	0.30	0.01

Association B

Date	Production		Exudation	
	s	lm	s	lm
1974				
18 December	0.08	0.04	0.04	0.01
1975				
22 January	0.16	0.08	0.04	0.01
20 February	0.12	0.05	-	-
19 March	0.09	0.02	0.01	0.00
16 April	0.11	0.05	0.02	0.01

....Continued

Appendix VIII. Continued.

Association C

Date	Production		Exudation	
	s	lm	s	lm
1974				
18 December	0.29	0.17	0.06	0.02
1975				
22 January	0.37	0.29	0.08	0.02
20 February	0.27	0.14	0.04	0.01
19 March	0.24	0.15	0.01	0.00
16 April	0.17	0.10	-	-
14 May	0.12	0.07	0.02	-

Association D

Date	Production		Exudation	
	s	lm	s	lm
1975				
22 January	0.58	0.34	0.10	0.02
20 February	0.65	0.33	0.09	0.02
19 March	0.37	0.14	0.03	0.01
16 April	0.21	-	0.04	-

Association E

Date	Production		Exudation	
	s	lm	s	lm
1974				
6 June	0.31	0.05	0.05	-
21 June	0.21	0.05	0.07	0.01
5 July	0.29	0.06	0.06	0.01
19 July	0.32	0.07	0.08	-
11 August	0.41	0.16	0.06	0.02
27 August	0.30	0.21	0.04	0.01
2 September	0.39	0.21	-	-
13 September	0.47	0.23	0.07	0.01
30 October	0.24	0.17	0.02	0.01
22 November	0.11	0.08	0.01	0.01
18 December	0.02	-	-	-
1975				
22 January	0.16	0.09	0.03	0.01
20 February	0.17	0.07	0.03	0.01
19 March	0.39	0.11	-	-
16 April	0.47	0.23	0.06	0.01
14 May	0.55	0.33	0.04	0.02
12 June	0.51	0.11	-	-
20 June	0.49	0.14	0.09	0.02
16 July	0.31	0.12	0.08	0.01
29 July	0.30	0.04	0.08	0.01
13 August	0.29	0.11	-	0.02
28 August	0.27	0.19	0.06	0.02

....Continued

Appendix VIII. Continued.

Association F

Date	Production		Exudation	
	s	lm	s	lm
1974				
5 June	0.84	0.14	0.19	-
21 June	0.91	0.13	0.17	0.02
5 July	0.62	0.17	0.14	0.02
19 July	0.76	0.15	0.13	0.02
11 August	-	-	-	-
27 August	0.59	0.23	0.05	0.01
2 September	0.40	0.23	0.02	0.02
13 September	0.48	0.25	0.02	0.02
30 October	0.23	0.11	0.02	0.01
22 November	0.14	0.09	0.02	-
18 December	0.11	0.02	0.01	0.00
1975				
22 January	-	-	-	-
20 February	0.28	0.14	0.06	0.01
19 March	-	-	-	-
16 April	0.59	0.22	0.05	0.02
14 May	0.68	0.31	0.06	0.02
12 June	0.57	0.13	0.16	0.02
20 June	0.59	0.16	0.19	0.02
11 July	0.54	0.10	0.12	0.02
29 July	0.50	0.12	0.14	0.02
13 August	0.41	0.14	0.03	0.01
28 August	-	-	-	-

Association G

Date	Production		Exudation	
	s	lm	s	lm
1974				
22 November	0.30	0.19	0.01	0.01
18 December	0.15	0.05	0.01	-
1975				
22 January	0.11	0.09	0.01	-
20 February	0.17	0.13	0.01	0.01
19 March	0.09	-	0.01	-

Appendix IX. Estimated monthly percent emersion (exposed) and immersion (covered) time for the Squamish delta as determined from tide tables.

Month	Covered %	Exposed %
1974		
June	25	75
July	25	75
August	50	50
September	75	25
October	75	25
November	84	16
December	84	16
1975		
January	84	16
February	84	16
March	50	50
April	75	25
May	50	50
June	25	75
July	25	75
August	50	50

Appendix X. Turnover times for major producers based on average biomass and primary production values.

	Time (days)		Time (days)
<i>Cladophora</i> sp.	17	Association A	8
<i>Enteromorpha minima</i>	20	Association B	21
<i>E. prolifera</i>	24	Association C	8
<i>Monostroma oxyspermum</i>	8	Association D	17
<i>Rhizoclonium implexum</i>	6	Association E	4
<i>Spirogyra</i> sp.	9	Association F	15
<i>Pylaiella littoralis</i>	40	Association G	48

Appendix XI. Annual net primary production estimates for
Carex lyngbyei based on growth increments^a.

	Biomass g organic·m ⁻²	Growth increment g organic·m ⁻²
1974		
29 March	32.8	32.8
28 April	92.8	60.0
28 May	391.0	298.2
19 June	475.6	84.6
5 July	831.4	355.8
30 July	1023.8	192.4
18 August	1095.7	71.9
18 September	466.5	negative
		1095.7

Above ground net production = 1095.7 g organic·m⁻²·season⁻¹

Below ground net production^b = 971.7 g organic·m⁻²·season⁻¹

Total net production = 2067.4 g organic·m⁻²·season⁻¹

^a after Levings and Moody (1976) using harvest method of
 Milner and Hughes (1968)

^b assuming below ground production is 47% of total net
 production (Yamanaka 1975)

Appendix XII. Net energy production for major algal producers. Pro-rated values represent percent of total for each month (calculations based on data from Table 11).

	<i>Cladophora</i> sp.	<i>Enteromorpha</i> <i>minima</i>	<i>Enteromorpha</i> <i>prolifera</i>	<i>Monostroma</i> <i>oxypernum</i>	<i>Rhizoclonium</i> <i>implexum</i>	<i>Spirogyra</i> sp.	<i>Pyraliella</i> <i>littoralis</i>	Association						
								A	B	C	D	E	F	G
1974														
September	1.7	2.7	0.6	1.5	4.5	9.5	-	-	-	-	-	74.3	5.2	-
October	-	3.1	-	3.2	2.1	3.3	-	-	-	-	-	85.1	3.1	-
November	-	0.3	-	0.2	-	-	-	-	-	-	-	8.1	0.3	91.0
December	-	0.1	-	0.4	-	-	0.4	-	0.1	0.03	-	12.1	0.6	86.2
1975														
January	-	0.06	-	0.05	0.02	-	0.4	-	0.2	0.04	1.7	30.5	0.6	65.6
February	-	0.2	0.02	0.6	0.3	-	2.1	-	0.2	0.02	2.1	27.0	0.6	66.8
March	-	0.22	0.08	1.6	1.0	-	8.0	-	0.1	0.02	2.6	22.9	1.6	61.7
April	-	0.09	0.3	4.0	2.8	-	18.3	-	0.1	0.03	2.2	67.2	4.0	-
May	1.9	1.7	1.2	5.2	5.2	-	21.6	12.5	-	0.02	-	42.1	8.6	-
June	1.5	1.4	1.8	4.4	5.5	16.5	3.1	11.4	-	-	-	45.2	9.2	-
July	4.3	4.8	3.9	4.3	12.4	23.2	-	10.3	-	-	-	22.6	11.1	-
August	5.7	3.9	1.8	2.5	12.5	26.4	-	-	-	-	-	40.1	7.1	-

Appendix XIII. Net energy production of major algal producers. Pro-rated values represent percent distribution over the growth period. (Calculations based on data from Table 11.)

	<i>Cladophora</i> sp.	<i>Enteromorpha</i> <i>minima</i>	<i>Enteromorpha</i> <i>prolifera</i>	<i>Monostroma</i> <i>oxyspermum</i>	<i>Rhizoclonium</i> <i>implexum</i>	<i>Spirogyra</i> sp.	<i>Pyraliella</i> <i>littoralis</i>
1974							
September	8.0	10.6	4.5	2.9	7.2	10.3	-
October	-	9.9	-	5.1	2.7	2.9	-
November	-	5.2	-	2.0	-	-	-
December	-	1.4	-	2.4	-	-	0.8
1975							
January	-	0.9	-	3.5	1.1	-	1.1
February	-	3.3	1.0	6.3	2.1	-	8.5
March	-	5.1	3.2	16.8	8.2	-	31.9
April	-	7.2	5.2	15.8	8.9	-	28.1
May	14.1	10.3	13.4	15.8	12.7	-	25.7
June	11.7	8.9	21.7	14.4	14.4	29.5	3.8
July	40.9	22.7	36.2	10.3	23.8	30.4	-
August	25.3	14.4	14.4	4.7	18.7	26.9	-

....Continued

Appendix XIII. Continued.

	Association						
1974	A	B	C	D	E	F	G
September	-	-	-	-	8.0	6.3	-
October	-	-	-	-	7.5	3.1	-
November	-	-	-	-	4.0	1.9	26.9
December	-	11.2	15.5	-	3.8	2.1	15.7
1975							
January	-	29.4	28.3	117.33	11.7	2.7	14.8
February	-	31.8	17.6	31.5	15.3	4.4	22.2
March	-	19.4	20.7	38.7	12.9	10.2	20.4
April	-	8.1	10.9	12.4	14.6	9.9	-
May	38.4	-	7.2	-	7.1	16.3	-
June	36.9	-	-	-	8.1	18.5	-
July	24.7	-	-	-	3.0	16.5	-
August	-	-	-	-	4.1	8.1	-

Appendix XIV. Primary production and photosynthetic efficiency data for constructing seasonal energy flow pathways.

Fall (September)

	Gross Production	Respiration	Net Production		P/S ^c
			Dis. ^a	Part. ^b	
<i>Cladophora</i> sp.	103.78	22.83	5.26	75.69	0.17
<i>Enteromorpha</i> <i>minima</i>	55.84	13.74	2.53	39.57	0.09
<i>Enteromorpha</i> <i>prolifera</i>	148.80	38.98	7.14	102.68	0.24
<i>Monostroma</i> <i>oxyspermum</i>	72.85	10.13	5.02	57.70	0.13
<i>Rhizoclonium</i> <i>implexum</i>	80.98	17.64	5.07	58.26	0.13
<i>Spirogyra</i> sp.	151.94	53.63	13.76	84.55	0.21
<i>Pylaiella</i> <i>littoralis</i>	-	-	-	-	-
Association A	-	-	-	-	-
Association B	-	-	-	-	-
Association C	-	-	-	-	-
Association D	-	-	-	-	-
Association E	143.64	38.78	13.63	91.23	0.22
Association F	70.50	21.15	5.42	43.93	0.10
Association G	-	-	-	-	-

^a Dis. = dissolved organic exudation

^b Part. = particulate organic

^c P/S = photosynthetic efficiency

....Continued

Appendix XIV. Continued.

Winter (December)

	Gross Production	Respiration	Net Production		P/S ^c
			Dis. ^a	Part. ^b	
<i>Cladophora</i> sp.	-	-	-	-	-
<i>Enteromorpha</i> <i>minima</i>	26.63	6.55	1.20	18.88	0.22
<i>Enteromorpha</i> <i>prolifera</i>	-	-	-	-	-
<i>Monostroma</i> <i>oxyspermum</i>	92.74	12.89	5.98	73.87	0.89
<i>Rhizoclonium</i> <i>implexum</i>	-	-	-	-	-
<i>Spirogyra</i> sp.	-	-	-	-	-
<i>Pylaiella</i> <i>littoralis</i>	45.45	14.14	4.51	26.62	0.35
Association A	-	-	-	-	-
Association B	13.14	3.40	1.75	7.99	0.11
Association C	6.47	1.85	0.49	4.13	0.05
Association D	-	-	-	-	-
Association E	37.21	7.05	3.53	26.63	0.34
Association F	24.01	7.20	1.85	14.95	0.19
Association G	23.58	4.20	1.55	17.83	0.22

^a Dis. = dissolved organic exudation

^b Part. = particulate organic

^c P/S = photosynthetic efficiency

....Continued

Appendix XIV. Continued.

Spring (March)

	Gross Production	Respiration	Net Production		P/S ^c
			Dis. ^a	Part. ^b	
<i>Cladophora</i> sp.	-	-	-	-	-
<i>Enteromorpha</i> <i>minima</i>	125.11	30.78	5.66	88.67	1.16
<i>Enteromorpha</i> <i>prolifera</i>	94.78	24.83	4.58	65.37	0.86
<i>Monostroma</i> <i>oxyspermum</i>	428.56	59.57	27.68	341.31	4.56
<i>Rhizoclonium</i> <i>implexum</i>	140.11	30.54	8.76	108.81	1.35
<i>Spirogyra</i> sp.	-	-	-	-	-
<i>Pylaiella</i> <i>littoralis</i>	489.42	172.17	48.61	286.64	3.92
Association A	-	-	-	-	-
Association B	33.18	8.59	4.42	20.17	0.30
Association C	9.93	22.84	0.74	6.35	0.09
Association D	116.50	25.00	8.81	82.69	1.13
Association E	131.47	35.50	12.47	83.50	1.18
Association F	114.99	34.50	8.85	71.64	0.99
Association G	30.61	5.45	2.01	23.15	0.31

^a Dis. = dissolved organic exudation^b Part. = particulate organic^c P/S = photosynthetic efficiency

....Continued

Appendix XIV. Continued.

Summer (June)

	Gross Production	Respiration	Net Production		P/S ^c
			Dis. ^a	Part. ^b	
<i>Cladophora</i>	166.15	36.55	8.42	121.18	0.16
sp.					
<i>Enteromorpha</i>	159.67	39.28	7.23	113.16	0.15
<i>minima</i>					
<i>Enteromorpha</i>	183.13	48.46	8.80	126.35	0.17
<i>prolifera</i>					
<i>Monostroma</i>	263.61	36.64	17.02	209.95	0.29
<i>oxyspermum</i>					
<i>Rhizoclonium</i>	150.86	32.89	9.44	108.53	0.15
<i>implexum</i>					
<i>Spirogyra</i>	505.69	178.51	45.81	281.37	0.41
sp.					
<i>Pylaiella</i>	138.73	43.70	13.77	81.26	0.01
<i>littoralis</i>					
Association	439.84	117.62	43.22	289.30	0.42
A					
Association	-	-	-	-	-
B					
Association	-	-	-	-	-
C					
Association	-	-	-	-	-
D					
Association	230.09	62.12	21.84	146.13	0.21
E					
Association	208.13	62.44	16.02	129.67	0.18
G					

^a Dis. = dissolved organic exudation

^b Part. = particulate organic

^c P/S = photosynthetic efficiency