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Call #: GC1 .P7
Location: 5th floor BASE
Journal Title: Progress in oceanography.
Volume: 25 Issue: 1-4
Month/Year: 1990
Pages: 175-210
Article Author:
Article Title: SMALL,; PRIMARY PRODUCTION, PLANT AND DETRITAL BIOMASS, AND PARTICLE-TRANSPORT IN THE COLUMBIA RIVER ESTUARY

Imprint: Oxford, New York, Pergamon Press, [1963]

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Prog. Oceanog. Vol. 25, pp. 175-210, 1990.
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0079 - 6611/90 $0.00 + .50

Primary production, plant and detrital biomass, and particle transport in the Columbia River Estuary

LAWRENCE F. SMALL[1], C. DAVID MCINTIRE[2], KEITH B. MACDONALD[3], J. RUBEN LARA-LARA[1,4], BRUCE E. FREY[1,5], MICHAEL C. AMSPOKER[2,6] and TED WINFIELD[7]

[1]*College of Oceanography, Oregon State University, Corvallis, OR 97331, USA*

[2]*Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, USA*

[3]*PO Box 60310, San Diego, CA 92106, USA*

[4]*Current address: Centro de Investigacion Cientifica y Educacion Superior de Ensenada, Ensenada, Baja California, Mexico 22830*

[5]*Current address: Oregon Health Sciences University, Portland, OR 97201, USA*

[6]*Current address: Biology Department, Westminster College, Fulton, MO 65251, USA*

[7]*Woodward-Clyde Consultants, 500 12th Street, Oakland, CA 94607, USA*

Abstract – The dynamics of primary production and particulate detritus cycling in the Columbia River Estuary are described, with particular reference to mechanisms that account for patterns within the water column, on the tidal flats, and in the adjacent wetlands. Analysis of patterns in phytoplankton flora and biomass and in distribution of detrital particulate organic matter (DPOC) in the water column indicated that salinities of 1-5 delineated an essentially freshwater flora from a marine or euryhaline flora, and that living phytoplankton was converted to DPOC at the freshwater-brackishwater interface. Similarly, the benthic diatom assemblages on tidal flats reflected either the fresh or the brackish nature of the water inundating the flats. Emergent vascular plants were grouped into six associations by cluster analysis, the associations being separated mainly on the bases of different relative abundances of freshwater, euryhaline or brackishwater species, and on whether samples occurred in high or low marsh areas.

Annual rates of net areal 24-hr production averaged 55, 16, and 403gC $m^{-2}y^{-1}$ for phytoplankton, benthic algae, and emergent vascular vegetation, respectively. Total production over the whole estuary was 17,667 metric tons C y^{-1} for phytoplankton, 1,545mt C y^{-1} for benthic algae, and 11,325mt C y^{-1} for emergent vascular plants, for a grand total of 30,537mt C y^{-1}. Phytoplankton biomass turned over approximately 39 times per year on average, while benthic algae turned over about twice and emergent plants once per year.

Budgets for phytoplankton carbon (PPOC) and DPOC were developed based on PPOC and DPOC import and export, grazing loss, and *in situ* production and conversion of PPOC to DPOC. It

is suggested that 36,205mt y^{-1} of PPOC is converted to DPOC in the estuary, principally at the freshwater-brackishwater interface. About 40,560mt y^{-1} of PPOC is exported to the ocean, and 159,185mt y^{-1} of DPOC is transported into the marine zone of the estuary (no data are available on DPOC export to the ocean). Thus, the estuary acts principally as a conduit for the transport of particles to the sea, and only secondarily as a converter of viable phytoplankton cells to detrital carbon and as a trap for DPOC.

CONTENTS

1. INTRODUCTION

This paper describes the primary production and particulate detrital dynamics of the Columbia River Estuary over an annual cycle, and discusses mechanisms that account for patterns within the water column, on the tidal flats, and in the adjacent wetlands. Comparisons among the rates and biomasses associated with phytoplankton, benthic algae, vascular plants and detritus were possible because these rates and biomasses (measured by different methods for the three plant groupings and for detritus) could all be resolved ultimately in carbon units. Expressions of all plant productivities as mgC $m^{-2}y^{-1}$, for example, allowed areal comparisons among the phytoplankton, benthic algae and vascular plants within any selected region of the estuary or over the whole estuary. Total annual estuarine primary production, or annual production within a given estuarine region, was then easily computed from areal rates and a knowledge of the areal extent

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2. SAM

2.1 *Phytoplankton*

Nine cruises were conducte
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stations defined as either those
where depths were <4m.

Water samples were collec
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total suspended particle mass a
analysis before and after hot per
and SMALL, 1980); and 6) parti
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shore-mounted recording pyran
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measured with a submersible s

Direct measurement of phy
selected stations (Fig.1) by 4-
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50, 30, 15, 6 and 1% of inciden
$m^{-3}h^{-1}$ and then was integrated ov

of production by the three plant groupings. Production and transport of detrital carbon could be assessed in similar fashion. Such system-wide analysis is rare for estuarine systems, and is the first such attempt for the Columbia River Estuary.

Basic physical and sedimentological features of the study area, as well as the few older studies on primary biomass and production, are reviewed in SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD (1990). Based on the physical and sedimentological features, eight different regions in the main body of the estuary and three separate zones (including the eight regions) have been delineated, and we use these to help quantify and understand the patterns of primary production and detrital distribution. The Estuarine Channels Region and Mid-Estuary Shoals Region described in SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD (1990) were indistinguishable in terms of chlorophyll concentration and areal primary productivity, so these two regions (Regions 3 and 5) were combined into a composite Mid-Estuary Region (3+5) in this paper. The Mid-Estuary Region comprised the mixing zone in the main body of the estuary.

Analyses of species assemblages of benthic, planktonic and emergent vascular plants in selected parts of our study area also have aided us in delineating marine, brackishwater and freshwater zones, and interpreting productivity and biomass data. Finally, annual budgets of phytoplanktonic and suspended particulate detrital carbon are attempted, based on our regional and estuary-wide estimates of phytoplanktonic and detrital production, transport, and losses.

2. SAMPLING AND ANALYTICAL METHODOLOGY

2.1 *Phytoplankton*

Nine cruises were conducted approximately every other month from April 1980 through July 1981. Stations were occupied throughout the study area (Fig.1), although there were no stations in the Baker Bay/Trestle Bay Region (SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD, 1990) because water depths were too shallow for the boat. The number of stations sampled per cruise varied from 25 to 47. Stations were located in both shallow and deep water, with deep-water stations defined as either those with water depths >4m or as those along the main estuarine axis where depths were <4m.

Water samples were collected by submersible pump. Properties measured for spatial and temporal variability included the following: 1) temperature; 2) salinity by refractometer; 3) dissolved nutrients [NO_3^- +NO_2^-, $PO_4^{3-}$and $Si(OH)_4$] analyzed from filtered water by automated colorimetric analysis (ATLAS, HAGER, GORDON and PARK, 1971); 4) chlorophyll *a* and phaeophytin *a* by fluorometry on extracted and non-extracted samples (STRICKLAND and PARSONS, 1972); 5) total suspended particle mass and organic and inorganic fractionation of the total, by gravimetric analysis before and after hot peroxide digestion (PETERSON, 1977; LARA-LARA, ALVAREZ-BORREGO and SMALL, 1980); and 6) particulate organic carbon and nitrogen analysis by pyrolysis and gas chromatography (CHN analyzer). In addition, incoming solar radiation was measured with a shore-mounted recording pyranometer, and the output was corrected to give available photosynthetically active radiation (300-700nm) at the water surface. Light attenuation at each station was measured with a submersible spherical quantum meter.

Direct measurement of phytoplankton productivity was conducted around midday at six selected stations (Fig.1) by 4-hr ^{14}C uptake experiments. Water samples were taken from different depths and placed in on-deck incubation tanks screened in such a way as to admit 100, 50, 30, 15, 6 and 1% of incident light. Phytoplankton net productivity was computed as mg C $m^{-3}h^{-1}$ and then was integrated over depth and the daylight portion of each day (LARA-LARA, 1982)

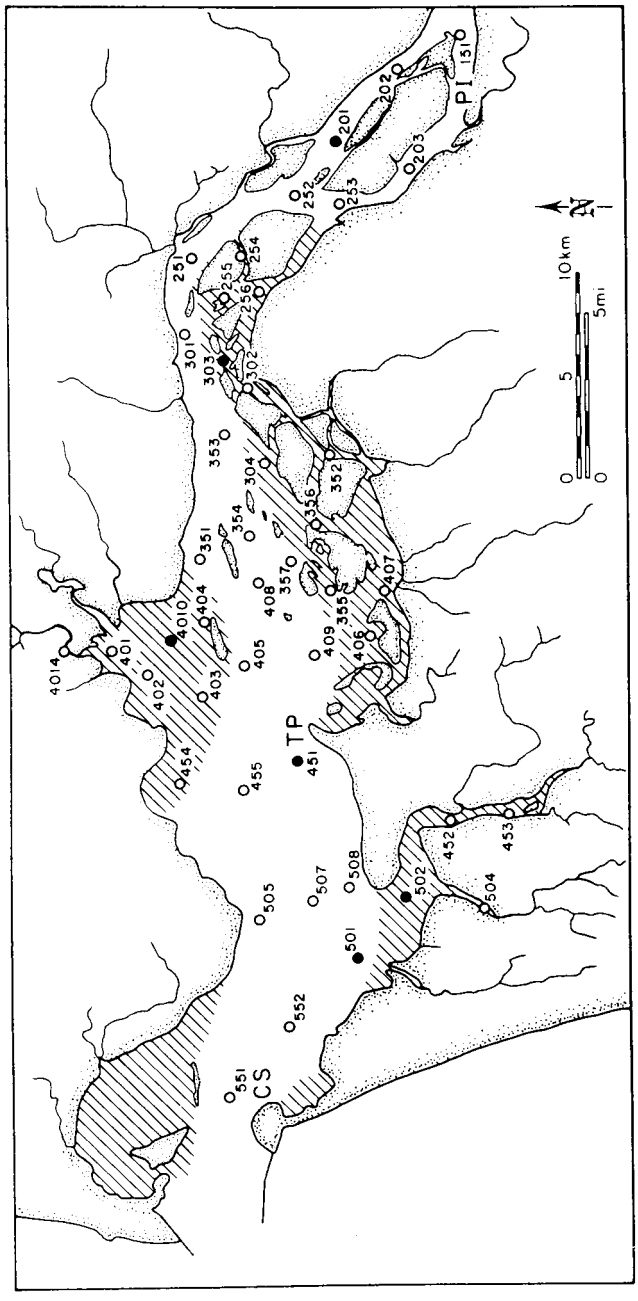

FIG. 1. Sampling stations for phytoplankton studies: ○ = biomass measurements only; ● = primary production and biomass measurements; CS (Clatsop Spit), TP (Tongue Point) and PI (Puget Island) are the three locations from which phytoplankton species were determined. The cross-hatched areas are those containing the shallow-water stations (<4m). Placenames are left off this figure for clarity.

to yield productivity in units
Multiple regression analysis
BRENNE, 1981) in order to id
accounted for most of the va
empirical models for predicti
annual net phytoplankton pr
estimated by integrating dail
annual cycle. These annual
respiration proceeded for 24
1983), and that gross daylight
each sampling month at the l

Samples for identification
species associations (see later
of Tongue Point (mid-estuary
Island (at the riverine end of
solution and major species w

Transport of phytoplankto
through the Fluvial, Cathlame
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the river-estuary continuum.
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which assumed vertical hetero
Mid-Estuary Regions (OFFICE
transports of chlorophyll *a*.

Transports were computed
Estuary Region (3+5) into the

$$T_{(3+5)1} = Q_0 C_{(3+5)} + E$$

where Q_0 is river flow ($m^3 s$
chlorophyll *a* (mg m^{-3}) in Reg
Regions (3+5) and 1. The e
between regions, assuming tha
salt. Thus,

$$E_{(3+5)1} = Q_0 S_{(3+5)}/[S$$

where S_1 and $S_{(3+5)}$ are respecti

Mean chlorophyll transpor
converted to carbon-based rate
work on phytoplankton from th
to metric tons d^{-1}. Chlorophyll *a*
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were used (ANDERSON, 1964, 1
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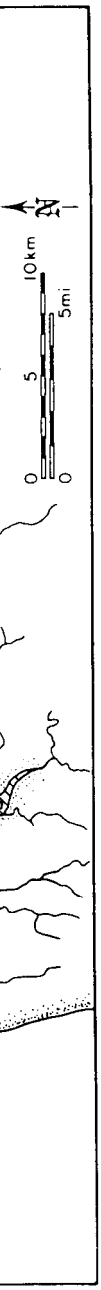

FIG. 1. Sampling stations for phytoplankton studies: ○ = biomass measurements only; ● = primary production and biomass measurements; CS (Clatsop Spit), TP (Tongue Point) and PI (Puget Island) are the three locations from which phytoplankton species were determined. The cross-hatched areas are those containing the shallow-water stations (<4m). Placenames are left off this figure for clarity.

to yield productivity in units of mg C $m^{-2}d^{-1}$, at both deep (>4m) and shallow (<4m) stations. Multiple regression analysis was then done by a "forward stepwise" procedure (ROWE and BRENNE, 1981) in order to identify those environmental variables (from a group of ten) which accounted for most of the variability in daily primary productivity. This led to development of empirical models for predicting daily primary productivity in both deep and shallow areas. Mean annual net phytoplankton production during daylight hours in each region of the estuary was estimated by integrating daily areal productivities (both measured and predicted) through the annual cycle. These annual daylight values were converted to 24-hr rates by assuming that respiration proceeded for 24 hours at 29% of gross daylight production (DAVIS and MCINTIRE, 1983), and that gross daylight production proceeded for the average number of daylight hours in each sampling month at the latitude of the Columbia River Estuary (46°15'N).

Samples for identification of the major diatom species (>10μm) and for determination of species associations (see later) were collected in 1-liter bottles at several locations in the vicinity of Tongue Point (mid-estuary), and at locations near Clatsop Spit (the estuary mouth) and Puget Island (at the riverine end of our study area) (Fig.1). Water samples were fixed in Lugol's solution and major species were later identified and counted under 1250X magnification.

Transport of phytoplankton was estimated from calculated sequential fluxes of chlorophyll *a* through the Fluvial, Cathlamet Bay, Mid-Estuary and Entrance Regions [Regions 8, 7, (3+5) and 1, respectively; see SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD, 1990] in the main body of the river-estuary continuum. A two-parameter model based on salt transport, which assumed complete vertical mixing along the length of the river-estuary continuum (OFFICER, 1980) was used to evaluate horizontal exchange between each adjacent region. Other more complex models which assumed vertical heterogeneity in the Entrance Region only, and again in the Entrance and Mid-Estuary Regions (OFFICER, 1980), were explored, but they yielded only marginally different transports of chlorophyll *a*.

Transports were computed as follows, using the transport of chlorophyll *a* from the Mid-Estuary Region (3+5) into the Entrance Region 1 [i.e. $T_{(3+5)1}$] as an example:

$$T_{(3+5)1} = Q_0 C_{(3+5)} + E_{(3+5)1}[C_{(3+5)} - C_1],$$

where Q_0 is river flow (m^3s^{-1}), $C_{(3+5)}$ and C_1 are respectively the mean concentrations of chlorophyll *a* (mg m^{-3}) in Regions (3+5) and 1, and $E_{(3+5)1}$ is the exchange rate (m^3s^{-1}) between Regions (3+5) and 1. The exchange rate was calculated from the mean salinity difference between regions, assuming that exchange of chlorophyllous particles would mimic exchange of salt. Thus,

$$E_{(3+5)1} = Q_0 S_{(3+5)}/[S_1 - S_{(3+5)}],$$

where S_1 and $S_{(3+5)}$ are respectively the mean salinities (ppt) in Regions 1 and (3+5).

Mean chlorophyll transports for each region and each sampling month were computed, converted to carbon-based rates through use of a carbon:chlorophyll ratio of 40 based on earlier work on phytoplankton from the Columbia River Estuary (LARA-LARA, 1982), and extrapolated to metric tons d^{-1}. Chlorophyll *a* concentrations in the adjacent ocean, for calculation of transport from the Entrance Region into the ocean, were not measured in this study, so historical values were used (ANDERSON, 1964, 1972; SMALL and CURL, 1972; HOLTON, CUTSHALL, GORDON and SMALL, 1978; SMALL, unpublished data). Historical values were inappropriate for use in the near-ocean region after the volcanic eruption of Mt. St. Helens, so no transport rates for May 1980 were calculated through the Entrance Region.

Loss of phytoplankton carbon resulting from grazing is addressed in SIMENSTAD, SMALL and MCINTIRE (1990).

2.2 *Benthic Algae*

Seaweeds and other macroalgae are rare in the Columbia River Estuary, and therefore have not been considered in this study. However, benthic microalgal assemblages, which consist almost entirely of diatoms, are prominent on the tidal flats of the intertidal regions. Data related to these assemblages were generated for a 13-month period from monthly replicated sampling at five intensive study sites and during a 3 month period at 31 survey sites (Fig.2).

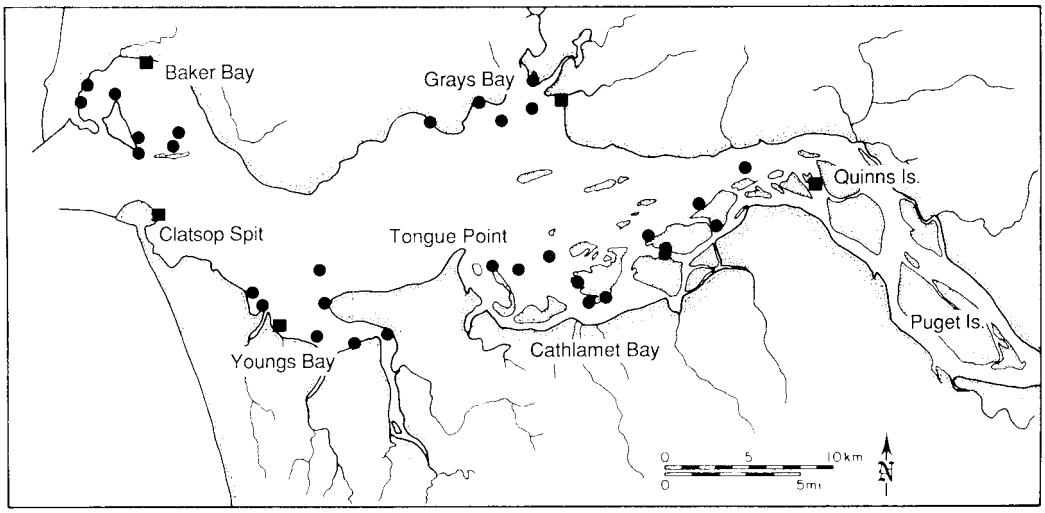

FIG.2. Sampling sites for benthic algal studies: ■ = intensive study sites; ● = survey sites.

The sampling strategy at each intensive study site involved the collection of sediment cores both for the analysis of chlorophyll *a* and phaeopigment concentrations (STRICKLAND and PARSONS, 1972), and for measurements of primary productivity. MCINTIRE and AMSPOKER (1986) give the detailed methodology and assumptions implicit in the methods used for measuring benthic algal productivity. Basically, mean hourly rates of oxygen production and consumption were measured in flow-through respirometer chambers that were either darkened or exposed to full sunlight. Oxygen values were converted to hourly carbon-based rates using a photosynthetic quotient of 1.2. Net rates for the daylight period were derived by multiplying mean net hourly rates by the number of hours per day that production took place (MCINTIRE and AMSPOKER, 1986). Hourly rates of night-time respiration were multiplied by the number of night-time hours to yield total respiration during the night-time period, after which total night-time respiration was subtracted from net daylight production to yield net production for the 24 hour period. The annual rate of net benthic algal production was calculated by integrating the 24 hour rates over the annual cycle.

At the survey sites, chlo
measured along transects at
Regression equations derive
predict rates of benthic alga
survey sites. As at the intens
24 hour carbon-based rates a
tions at all sites were conve
carbon:chlorophyll ratio of 8
84 in benthic algae was more
cells in their generally high li
(chlorophyll) to maintain the

In addition to the sample
taken at different locations i
determine species association
each in Baker Bay (Region 2
(Region 7) and the fluvial sec
8) (Fig.2). A statistical analys
Spit, Tongue Point and Puge

where SIMI is an index of si
sample, and p_{ik} is the propor
MOORE, 1977). SIMI can var
the samples have identical sp

Other variables monitored
water and the concentration
sediment samples were obtai
transects on the tidal flats at
above MLLW.

2.3 *Vascular Plants*

Species composition data
of two successive growing s
convenient to partition the
sediments of the intertidal a
marshlands and swamplands
were relatively rare on the ti
of approximately 58.7km^2, of
freshwater regions. THOMAS
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and subtidal regions.

Estuary, and therefore have
assemblages, which consist
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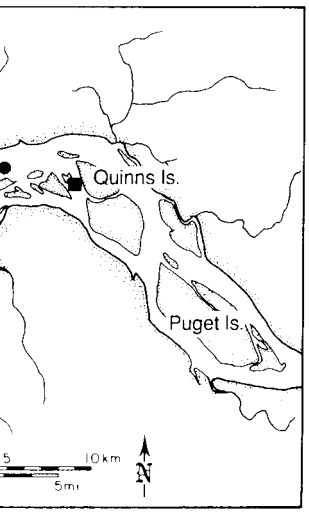
nthly replicated sampling at
sites (Fig.2).



es; ● = survey sites.

collection of sediment cores
ntrations (STRICKLAND and
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ultiplying mean net hourly
NTIRE and AMSPOKER, 1986).
of night-time hours to yield
night-time respiration was
24 hour period. The annual
24 hour rates over the annual

At the survey sites, chlorophyll *a* and phaeopigment concentrations in the sediment were measured along transects at 0.3m, 0.5m and 0.7m above mean lower low water (MLLW). Regression equations derived from data collected from the intensive study sites were used to predict rates of benthic algal productivity from measurements of sediment chlorophyll at the survey sites. As at the intensive study sites, predicted rates at the survey sites were converted to 24 hour carbon-based rates and ultimately to annual rates. In addition, chlorophyll *a* concentrations at all sites were converted to carbon-based biomass of benthic algae through use of a carbon:chlorophyll ratio of 84 (DAVIS and MCINTIRE, 1983). It should be noted that the ratio of 84 in benthic algae was more than double that in phytoplankton (40), indicating that benthic algal cells in their generally high light environment on tidal flats required less light-harvesting capacity (chlorophyll) to maintain their carbon biomass.

In addition to the samples for plant pigments and productivity, 49 sediment samples were taken at different locations in the estuary in order to identify the benthic diatom species and to determine species associations within five estuarine regions. The locations included several sites each in Baker Bay (Region 2), Youngs Bay (Region 4), Grays Bay (Region 6), Cathlamet Bay (Region 7) and the fluvial section of the estuary around Quinns Island and Puget Island (Region 8) (Fig.2). A statistical analysis of these 49 samples, plus those phytoplankton samples at Clatsop Spit, Tongue Point and Puget Island (Fig.1), involved calculation of the resemblance measure

$$SIMI = \frac{\sum_i p_{ij} p_{ik}}{\left[\sum_i p_{ij}^2 \cdot \sum_i p_{ik}^2\right]^{1/2}}$$

where SIMI is an index of similarity, P_{ij} is the proportional abundance of the i^{th} taxon in the j^{th} sample, and p_{ik} is the proportional abundance of the i^{th} taxon in the k^{th} sample (MCINTIRE and MOORE, 1977). SIMI can vary from zero, when the samples have no taxa in common, to 1 when the samples have identical species compositions and relative abundances.

Other variables monitored at the intensive study sites included salinity and temperature of the water and the concentration of organic matter in the top centimeter of sediment. In addition, sediment samples were obtained for an analysis of grain size. Samples were collected along 25m transects on the tidal flats at 0.3m, 0.5m and 0.7m above MLLW, and in the low marsh at 0.9m above MLLW.

2.3 Vascular Plants

Species composition data were collected from each of 22 study sites at the approximate peak of two successive growing seasons, in late July 1980 and early August 1981 (Fig.3). It was convenient to partition the vascular plants into the submergent species associated with the sediments of the intertidal and subtidal zones, and the emergent species that were part of the marshlands and swamplands. Submergent vascular plants exhibited a patchy distribution and were relatively rare on the tidal flats, while the emergent vegetation was abundant over an area of approximately 58.7km^2, of which 8.5km^2 were exposed to brackishwater and 50.2km^2 were in freshwater regions. THOMAS (1984) found 165 species in a region corresponding to the first 64 river kilometers. Of these species, only 11 were submergent forms associated with the tidal flats and subtidal regions.

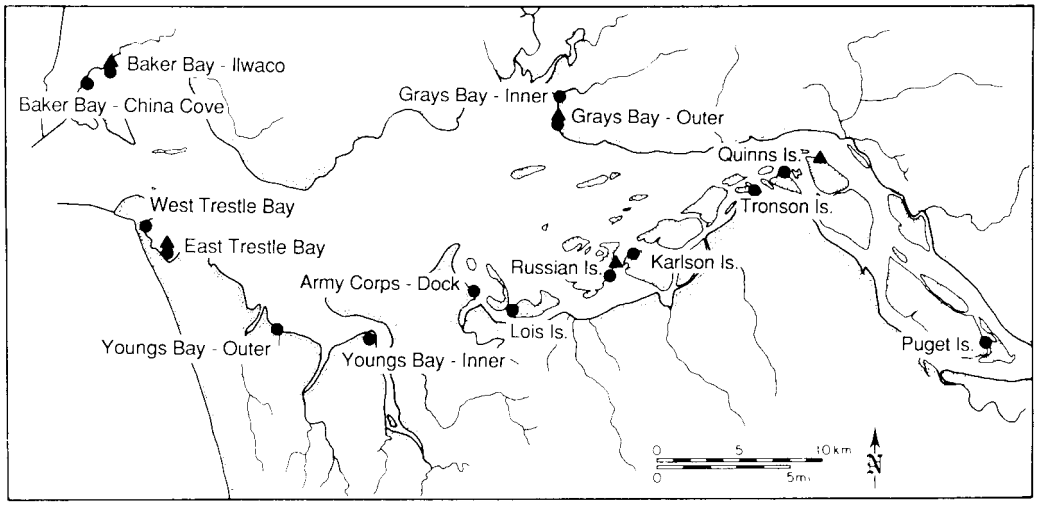


FIG.3. Sampling sites for emergent vascular plant studies (●): two different sites were sampled in Baker Bay-China Cove, West Trestle Bay, Grays Bay-Outer, and Grays Bay-Inner, while four different sites were sampled in East Trestle Bay. Also included are the sites for the litter bag experiments (▲).

Cluster analysis (MCINTIRE, 1973) was performed on 43 samples of the emergent vegetation (i.e. on mean percent species cover data collected from five replicate 0.5m^2 quadrats at each of 21 sites in 1980 plus 22 sites in 1981). This analysis was done in an attempt to identify species which tended to group together and to identify reasons for the groupings. Subsequently, a canonical analysis of discriminance (PIMENTEL, 1979) was performed to determine the affinities and lack of affinities among the groups delineated by cluster analysis.

Above-ground vegetation (both live and attached standing dead biomass from the same season's growth) was sampled by clipping all above-ground vegetation from nine 0.1m^2 quadrats at each sampling site during each of six sampling periods from spring through fall of 1980. The quadrats were randomly selected from visibly representative, ungrazed stands; high and low marsh areas were sampled separately. The biomasses of live and dead material were determined separately by weighing sorted clipped plant material dried to constant weight in an oven set at 93°C. Ash free dry weights (AFDW) were determined after ashing at 550°C, and carbon content was taken as 40% of dry weight (MACDONALD and WINFIELD, 1984). Below-ground biomass (roots and rhizomes) was estimated from two 8cm diameter sediment cores 20cm long collected from within two of the quadrats at each study site. Sampling variability associated with estimated mean biomass values was assessed using precision analysis (i.e. standard error/mean).

Annual net above-ground marsh plant production was estimated by the SMALLEY (1958) method, which takes into account incremental changes in both living and dead above-ground biomass over successive sampling periods throughout the growing season (TURNER, 1976; REIMOLD and LINTHURST, 1977). The SMALLEY method averages out different seasonal growth peaks among species, and thus tends to underestimate production slightly (MACDONALD and WINFIELD, 1984). Production in terms of carbon was estimated at 40% of production in terms of dry weight (MACDONALD and WINFIELD, 1984).

Import and export of live marsh plants was assumed to be zero. Grazing losses are given in SIMENSTAD, SMALL and MCINTIRE (1990).

2.4 *Detritus*

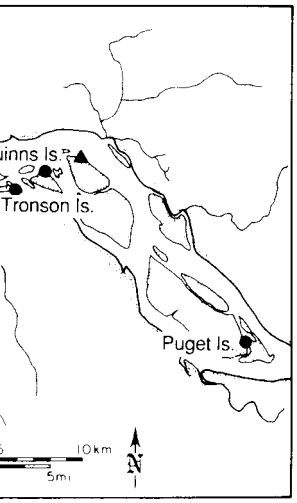
Estimates of detrital pa
estuarine regions were c
particulate organic carbo
computed through the rive
Loss of DPOC via grazing

Detrital carbon enters t
from the small tributary
experiments (DE LA CRUZ
TEAL, ALLEN, VAN ETTEN,
litter decomposition and tr
begun in May, July and Oc
litter bags were placed in b
of the estuary (Fig.3).

3.1 *Floristic Patterns*

3.1.1 Phytoplankton.
freshwater diatoms (AMSP
of the riverine flora. Of
October 1980 samples fr
marine planktonic diatom
Actinoptychus undulatus,
delicatulum, Biddulphia lo
Eucampia zoodiacus and *S*
Asterionella formosa, Fra
in low numbers (19.4%) in
flora had occurred. In A
dominated by freshwater
differences between the O
tions in freshwater dischar
the water column near To
Island (Fig.1) were similar
FREY and SMALL (1990) fo
decreased markedly on en
vicinity of Tongue Point).
than other species, which p
lower estuary, even thou
planktonic diatom species
MCINTIRE (1986).

3.1.2. Benthic Algae. I
of the Columbia River Estu
in sediment samples from
(*Navicula diserta* and *N. s*



ent sites were sampled in
ys Bay-Inner, while four
e sites for the litter bag

of the emergent vegetation
e 0.5m^2 quadrats at each of
attempt to identify species
roupings. Subsequently, a
d to determine the affinities
is.
ad biomass from the same
on from nine 0.1m^2 quadrats
g through fall of 1980. The
azed stands; high and low
d material were determined
nt weight in an oven set at
550°C, and carbon content
elow-ground biomass (roots
s 20cm long collected from
ciated with estimated mean
error/mean).
ed by the SMALLEY (1958)
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Grazing losses are given in

2.4 *Detritus*

Estimates of detrital particulate organic carbon (DPOC) in the water column in the different estuarine regions were obtained by subtracting phytoplankton carbon (PPOC) from total particulate organic carbon (TPOC) done by CHN analyzer. Transports of DPOC were then computed through the river-estuary continuum in the same manner as the phytoplankton carbon. Loss of DPOC via grazing is treated in SIMENSTAD, SMALL and MCINTIRE (1990).

Detrital carbon enters the estuary directly from the marshes bordering the estuary as well as from the small tributary rivers and from the main stem of the Columbia River. Litter bag experiments (DE LA CRUZ, 1973; RICE and TENORE, 1981; RUBLEE and ROMAN, 1982; VALIELLA, TEAL, ALLEN, VAN ETTEN, GOEHRINGER and VOLKMANN, 1985) were performed to estimate rates of litter decomposition and transfer of material to the detrital pool. Different experimental sets were begun in May, July and October, 1980, and continued for 33, 28 and 38 weeks, respectively. The litter bags were placed in both low and high marsh areas, and in brackish and freshwater regions of the estuary (Fig.3).

3. RESULTS AND DISCUSSION

3.1 *Floristic Patterns*

3.1.1 Phytoplankton. Phytoplankton greater than 10μm was composed primarily of freshwater diatoms (AMSPOKER and MCINTIRE, 1986) which represented a downstream extension of the riverine flora. Of seven plankton samples that were analyzed quantitatively, only the October 1980 samples from open water near Clatsop Spit (Fig.1) contained an abundance of marine planktonic diatoms (75.1% of the total number of cells). The marine forms included *Actinoptychus undulatus, Actinocyclus ehrenbergi, Asteromphalus heptactis, Bacteriastrum delicatulum, Biddulphia longicruris, Chaetoceros decipiens, C. curvatulus, Ditylumbrightwellii, Eucampia zoodiacus* and *Skeletonema costatum.* The few freshwater planktonic species, namely *Asterionella formosa, Fragilaria crotensis, Melosira granulata* and *M. italica*, that were present in low numbers (19.4%) in the Clatsop Spit collection indicated that some mixing with the upriver flora had occurred. In April 1981 a collection of phytoplankton from the same location was dominated by freshwater taxa (e.g. *A. formosa, Stephanodiscus* sp., and *M. italica*). The differences between the October and April samples apparently were related to seasonal fluctuations in freshwater discharge. Plankton samples obtained in October 1980 and April 1981 from the water column near Tongue Point and in October 1980 from the upper estuary near Puget Island (Fig.1) were similar and contained mostly freshwater taxa. In a related study, LARA-LARA, FREY and SMALL (1990) found that cell densities of nine selected species of freshwater diatoms decreased markedly on encountering salinities of 1 to 5 (commonly found at the surface in the vicinity of Tongue Point). *Melosira granulata* and *A. formosa* apparently were more salt-tolerant than other species, which probably explains why these two species were consistently found in the lower estuary, even though in low numbers during low riverflow in summer. A listing of planktonic diatom species found in the Columbia River Estuary can be found in AMSPOKER and MCINTIRE (1986).

3.1.2. Benthic Algae. Distributional patterns and species listings for the benthic diatom flora of the Columbia River Estuary were given by AMSPOKER and MCINTIRE (1986). The dominant taxa in sediment samples from Baker Bay (Fig.2) included both typical brackishwater diatom species (*Navicula diserta* and *N. salinicola*) and species tolerant of a wide range of salinity (*Achnanthes*

hauckiana and *A. lemmermanni*). This flora exhibited very little seasonal change. The occurrence of both brackishwater and freshwater benthic diatoms in sediment samples from Youngs Bay indicated that this region was exposed to intermittent periods of fresh and brackish water input. Seasonal changes in the species composition in Youngs Bay also were relatively small. Dominant benthic diatoms in Grays Bay included two freshwater species (*Achnanthes lanceolata* and *Navicula submuralis*), and two salinity-tolerant species (*Achnanthes hauckiana* and *Navicula gregaria*). The abundance of *A. lanceolata* and *N. submuralis* and the occurrence of many other typical freshwater species in the samples (e.g. *Achnanthes minutissima, Cymbella minuta,* and *Gomphonema parvulum*) was evidence for the lack of a saltwater influence in the bay. The dominant benthic diatoms in Cathlamet Bay were *N. submuralis, N. gregaria, Fragiliaria pinnata, A. lanceolata* and *Amphora ovalis* var. pediculus. Of these taxa, *N. gregaria* is euryhaline and the rest are typical freshwater species. Variations among the samples from Cathlamet Bay were primarily related to temporal changes in the deposition of planktonic diatoms from the water column. Diatom samples obtained upriver from Cathlamet Bay at sites on Quinns Island and several other small islands in the Fluvial Region indicated that this region was exposed to freshwater conditions throughout the period of study. Dominant taxa included typical freshwater species (e.g. *A. lanceolata, A. ovalis* and *Navicula capitata*) and two euryhaline species (*A. hauckiana* and *N. gregaria*).

Of the five regions compared for benthic diatom similarity (Table 1), the brackishwater flora from Baker Bay (Region 2) exhibited the lowest similarity to the floras from the other regions (SIMI<0.3). Baker Bay is shallow and essentially cut off from freshwater flow by the north channel of the estuary, through which most of the tidal exchange occurs (JAY and SMITH, 1990). Most of the river flow passes through the estuary in the south channel; thus, Youngs Bay flora was more similar to the floras from the freshwater regions (i.e. Grays Bay, Cathlamet Bay, and the Fluvial Region) than to the flora from Baker Bay. There is also freshwater input into Youngs Bay from the Lewis and Clark River and Youngs River, whereas Baker Bay has only two tiny freshwater tributaries. The benthic diatom assemblages from the Cathlamet Bay, Grays Bay, and Fluvial Regions were all quite similar (SIMI>0.7).

TABLE 1. Matrix of similarity values (SIMI; see text) of benthic samples pooled by region, and between pooled samples from each region and the plankton samples from three locations. The regions are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB), and the Fluvial Region (F). Plankton samples are from the water column near Puget Island (PI), Tongue Point (TP), and Clatsop Spit (CS). The matrix is partitioned into comparisons within benthic samples (upper left triangle), between benthic and plankton samples (upper right rectangle), and within-plankton samples (lower right triangle)

SITE	YB	CB	GB	F	PI	TP	CS
BB	0.367	0.201	0.083	0.230	0.006	0.005	0.008
YB		0.472	0.472	0.677	0.523	0.577	0.157
CB			0.854	0.845	0.145	0.136	0.049
GB				0.790	0.114	0.101	0.034
F					0.255	0.235	0.079
PI						0.903	0.263
TP							0.264

Comparisons between the benthic and planktonic floras (Table 1) indicated that, with the exception of two values related to Youngs Bay, similarities were low. The abundance of a freshwater plankter (*Melosira italica*) in some of the benthic samples from Youngs Bay accounted for the relatively high similarities to planktonic samples from Tongue Point and Puget Island. There was a high similarity (SIMI=0.9) between the two plankton sample sets from Tongue Point and Puget Island, but low similarity between these samples and the plankton samples from Clatsop Spit (Table 1). These data indicate that the radical change in the planktonic flora occurs in the mixing zone seaward of Tongue Point. LARA-LARA, FREY and SMALL (1990) showed that the most dramatic decrease in cell abundance occurs in summer through the 1-5 salinity gradient, which is located in the vicinity of Tongue Point. The similarity between the benthic floras in the Cathlamet Bay and Fluvial Regions, and their dissimilarity with the benthic floras down the estuary in Baker Bay, for example, further supports the idea that species composition is controlled by downstream salinity. WILDERMAN (1987) observed that salinity was a primary determinant of benthic algal distributions in the Severn River Estuary of Chesapeake Bay, and this study, coupled with the present study and others along the Oregon coast (MCINTIRE, 1973, 1978), further supports the hypothesis of WHITING and MCINTIRE (1985) that similar distributional patterns can be expected to occur throughout comparable estuaries in the temperate region of the Northern Hemisphere.

3.1.3 Vascular Plants. Cluster analysis of emergent vascular plant data from 1980 and 1981 indicated that a six-cluster structure was the most interpretable pattern in the data matrix. Cluster 1 consisted primarily of low marsh sites in brackish water (i.e. sites in Baker Bay, Trestle Bay, and outer Youngs Bay; see Fig.3). However, the dominance of *Carex lyngbyei*, a euryhaline species, at four sites in the middle estuary (Army Corps Dock, Grays Bay, Karlson Island, and Quinns Island; see Fig.3) also grouped these samples with the brackishwater sites. According to analyses of benthic diatom communities these areas were basically freshwater areas. Other abundant taxa in the samples of cluster 1 included *Triglochin maritimum, Scirpus americanus*, and *Eleocharis palustris*. Cluster 2 included seven samples from high marsh sites in the middle of the study area (Grays Bay, Russian Island, and Tronson Island). Some of the dominant species in these samples were *Oenanthe sarmentosa, Lotus corniculatus, Mimulus guttatus, Carex lyngbyei*, and *Deschampsia caespitosa*. Samples from low marsh sites in the middle of the study area (Lois Island, Grays Bay, and Karlson Island) composed cluster 3. *Carex lyngbyei* was abundant in all of these samples, while the other dominant taxa included *Alisma plantago-aquatica, Sagittaria latifolia, Eleocharis palustris*, and *Juncus oxymeris*. Clusters 4 and 5 were one-sample groups which were separated from the other clusters on the basis of dominant species. Cluster 4 represented a marsh on Puget Island dominated by *Typha latifolia*, whereas cluster 5 was a sample from a low marsh near the Army Corps Dock site where *Myosotis laxa* and *Equisetum* sp. were abundant. Cluster 6 was composed of eight samples from Trestle Bay, six of which were from the high marsh. The abundant species in these samples were *Lathyrus palustris, Potentilla pacifica, Carex lyngbyei, Juncus balticus* and *Agrostis alba*. Complete species listings for the Columbia River Estuary were given by THOMAS (1984).

Canonical analysis of discriminance displayed the six-cluster structure of the emergent plant data in two dimensions (Fig.4). This analysis illustrates the affinity between the brackishwater groups (clusters 1 and 6), and indicates the discrete and unique nature of the high marsh samples from the middle of the study area (cluster 2). The low marsh samples from the mid-estuary (cluster 3) and the sample from the *Typha* marsh on Puget Island (cluster 4) were closer to the brackishwater and freshwater locations. The abundance of *Myosotis laxa* and *Equisetum* sp. in a sample from the low marsh near the Army Corps Dock was primarily responsible for the separation of cluster 5 from all other clusters.

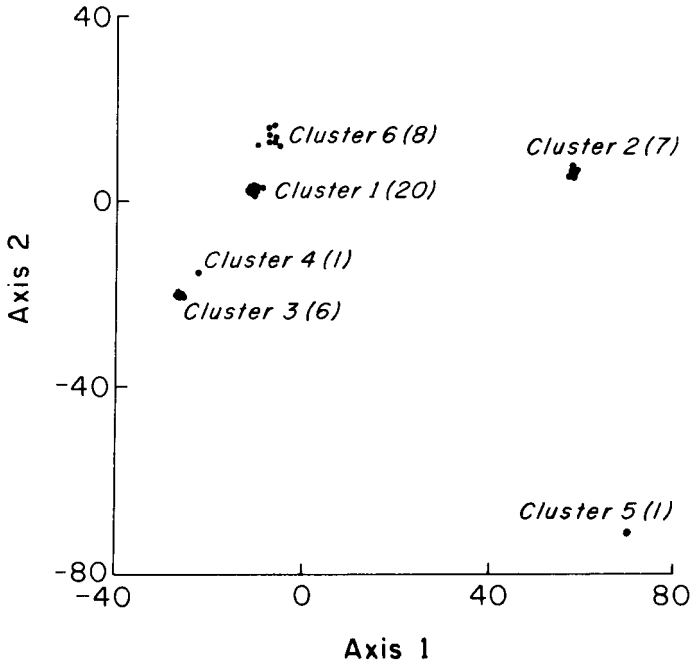

FIG.4. Two-dimensional ordination of the six-cluster structure of emergent plant distribution, produced by canonical discriminant analysis (see text); numbers in parentheses indicate the number of sample sets in each cluster (combined July 1980 and August 1981 data sets).

3.2 *Plant Biomass*

3.2.1 Phytoplankton. The distribution of chlorophyll *a* in the different regions along the main body of the estuary (Fig.5) showed prominent seasonal changes similar to those shown earlier by HAERTEL, OSTERBERG, CURL and PARK (1969), as well as significant decreases from the Fluvial to the Entrance Region. The sharp decline from the Cathlamet Bay Region to the Mid-Estuary Region in May and July 1980 reflected the effect of the salinity barrier on freshwater phytoplankton. The relatively high concentrations in May were the result of normal springtime increase plus an unknown quantity of chlorophyll *a* from the enormous pulse of water and sediment that entered the Columbia River shortly after the eruption of Mt. Saint Helens on May 18, 1980.

The bays and tributary rivers also showed a seasonal pattern in chlorophyll *a* concentration (Fig.6). In most cases during the period from spring through fall, the bays had lower chlorophyll *a* concentrations than the small rivers that flowed into them, suggesting that conditions for growth of freshwater phytoplankton in the rivers did not carry over into the more brackish water of the bays. This pattern was not observed during the winter months.

3.2.2 Benthic Algae. In benthic communities that consist of complex mixtures of microalgae, detritus, and associated animals and heterotrophic microorganisms, the concentration of chlorophyll *a* in the sediment provides a good index to the biomass of the autotrophic organisms (DAVIS and MCINTIRE, 1983). The mean concentrations of chlorophyll *a* in the top centimeter of sediment at the five intensive study sites (Fig.2) are shown in Table 2. When data from all sites and tidal levels

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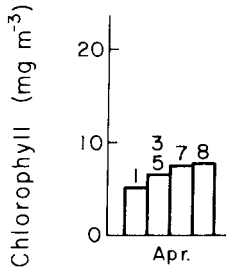

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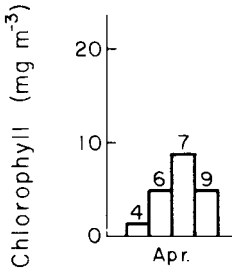

FIG.6. Mean wat
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were pooled by sampling month, chlorophyll *a* concentration exhibited very little seasonal change. The mean concentration over all sampling months was 15.4 6 2.7μg cm^{-3}. Mean values for observations pooled by site over all months and tidal levels, however, ranged from 1.4μg cm^{-3} at Clatsop Spit to 26.4μg cm^{-3} in Youngs Bay (Table 2). If it is assumed that the chlorophyll concentration in the top centimeter of sediment is a reliable index to the capacity for benthic autotrophy, these data indicated that the most productive sites were Youngs Bay and Baker Bay.

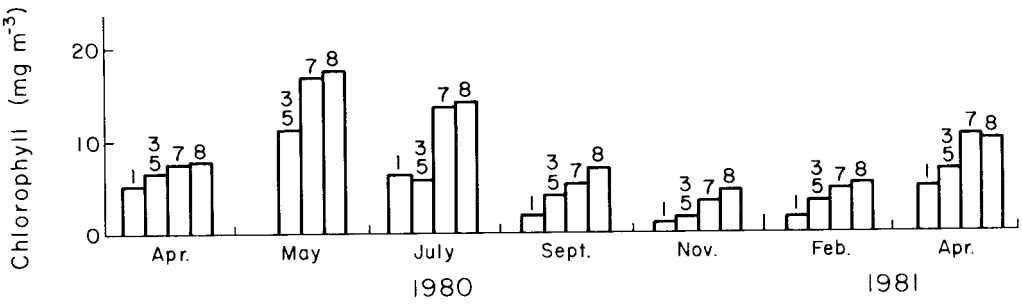

FIG.5. Mean water column chlorophyll *a* concentrations (mg m^{-3}) by sampling months and by regions along the main estuarine axis. May 1980 concentrations reflected the eruption of Mt. Saint Helens to some unknown extent. Regions are: Entrance (1), Mid-Estuary (3+5), Cathlamet Bay (7), and Fluvial (8). Regions 3 and 5 were combined because they were not differentiated during sampling for chlorophyll.

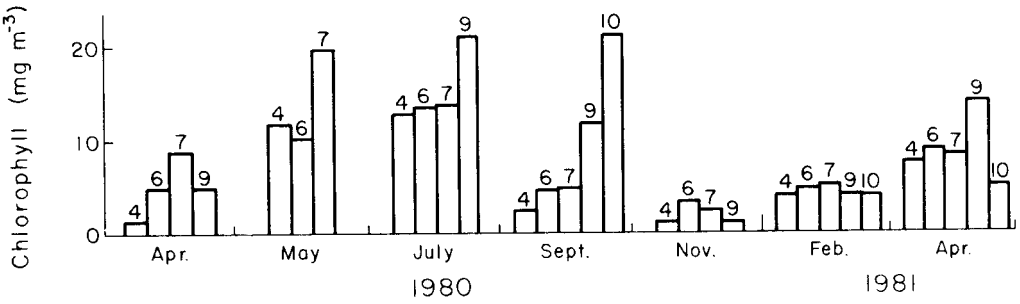

FIG.6. Mean water column chlorophyll *a* concentrations (mg m^{-3}) by sampling months and by regions in the shallows (cross-hatched areas in Fig.1) and tributary rivers. Regions are: Youngs Bay (4), Grays Bay (6), Cathlamet Bay shallows (7), Youngs plus Lewis and Clark Rivers (9), and Deep River (10). Water-column chlorophyll was not sampled in Baker Bay/Trestle Bay (2).

TABLE 2. Mean concentrations of chlorophyll *a* (mg cm^{-3}), number of samples, and standard error of the means for the five intensive benthic algal study sites (Fig.2). Data pooled by sampling time (month), site, and tidal level (transect) represent means of measurements in the top cm of sediment. Data pooled by sediment depth represent means of all observations for the top cm of sediment and at depth horizons of 4.5-5.5cm and 9-10cm below the surface

Variable	Number of Samples	Mean	Standard Error
Time			
April	90	17.6	1.5
May	114	17.8	1.1
June	114	19.0	1.4
July	114	13.7	0.9
August	114	14.3	1.0
September	114	17.5	1.7
October	114	15.2	1.2
November	48	19.2	1.9
January	96	13.1	1.3
February	114	13.8	1.3
March	114	11.8	1.0
April	114	12.2	1.0
Site			
Clatsop Spit	204	1.4	0.1
Youngs Bay	270	26.4	0.8
Baker Bay	270	25.1	0.7
Grays Bay	252	10.3	0.4
Quinns Island	264	9.0	0.5
Tide Level Transect			
Marsh (0.9m above MLLW)	258	21.0	0.7
Upper (0.7m above MLLW)	354	16.0	0.8
Mid (0.5m above MLLW)	336	14.0	0.7
Lower (0.3m above MLLW)	312	10.7	0.5
Sediment Depth Horizon			
0-1cm	1260	15.2	0.4
4.5-5.5cm	798	8.1	0.2
9-10cm	798	5.2	0.2

The extremely low biomass and productive capacities at the Clatsop Spit site (Table 2) were related to the sediment composition and other sediment properties in that exposed area. Sediment composition was over 99% sand along all transects, the grain size averaged larger than at any other site, the sediment was very well sorted, and there was no stabilizing marsh area (Table 3). All these factors pointed to a very physically energetic and hence biologically unproductive sedimentary environment. The patterns that emerged from analysis of data from the 31 survey sites (Fig.2) were consistent with the data obtained at the intensive study sites (MCINTIRE and AMSPOKER, 1986).

Although the top centimeter of sediment contained most of the chlorophyll *a* at all sites, on average, there was pigment at least to the 10cm depth (Table 2). One-centimeter sections of sediment cores at the 9-10cm depth horizon averaged about one third the chlorophyll *a* concentration of the top centimeter. MCINTIRE and AMSPOKER (1986) demonstrated that the ratios

TABLE 3. Summary of
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all seasons (except for

Site	n
Clatsop Spit	
Upper	8
Mid	1
Lower	8
Youngs Bay	
Marsh	7
Upper	8
Mid	1
Lower	8
Baker Bay	
Marsh	8
Upper	8
Mid	1
Lower	8
Grays Bay	
Marsh	8
Upper	8
Mid	1
Lower	8
Quinns Island	
Marsh	8
Upper	8
Mid	1
Lower	8

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showed great differences b
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3.2.3 Vascular Plants.
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n	Standard Error
6	1.5
8	1.1
0	1.4
7	0.9
3	1.0
5	1.7
2	1.2
2	1.9
1	1.3
8	1.3
8	1.0
2	1.0
4	0.1
4	0.8
1	0.7
3	0.4
0	0.5
0	0.7
0	0.8
0	0.7
7	0.5
2	0.4
1	0.2
2	0.2

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TABLE 3. Summary of sediment grain size analysis for the five intensive benthic algal study sites. Transects and sites are the same as those indicated in Table 2. Mean grain size (phi), sorting, and skewness are all defined by INMAN (1952). The values are the means of n observations taken over all seasons (except for the one sample taken only in May 1980 for the middle transect at each site)

Site	n	Mean % Composition			Grain size (phi)	Sort	Skew
		Sand	Silt	Clay			
Clatsop Spit							
Upper	8	99.7	0.3	0.1	2.47	0.25	0.04
Mid	1	99.4	0.6	0.0	2.37	0.32	0.23
Lower	8	99.6	0.4	0.1	2.36	0.30	0.07
Youngs Bay							
Marsh	7	11.3	75.0	13.7	6.03	1.79	0.22
Upper	8	9.2	78.3	12.5	5.84	1.65	0.35
Mid	1	27.1	63.1	9.8	4.70	1.76	0.19
Lower	8	56.2	36.4	7.3	4.34	2.08	0.51
Baker Bay							
Marsh	8	35.9	42.8	21.3	6.02	2.59	0.36
Upper	8	57.5	31.9	10.7	4.61	1.89	0.46
Mid	1	72.3	21.2	6.4	3.73	0.62	0.30
Lower	8	30.5	55.0	14.6	5.69	2.10	0.38
Grays Bay							
Marsh	8	55.9	35.1	9.0	4.72	1.55	0.10
Upper	8	69.4	26.8	4.9	4.29	1.31	0.60
Mid	1	86.4	10.6	3.0	3.26	0.74	0.04
Lower	8	43.0	51.7	5.4	4.69	1.25	0.37
Quinns Island							
Marsh	8	28.5	63.1	8.4	4.94	1.60	0.26
Upper	8	92.5	6.4	1.2	2.21	1.11	0.33
Mid	1	97.2	2.8	0.0	1.63	-	-
Lower	8	81.2	15.6	3.2	2.78	1.02	0.81

of chlorophyll *a* between the top centimeter and the two lower depth horizons often varied by season, height above MLLW, and particularly sampling site. Youngs Bay and Baker Bay both showed great differences between the top centimeter and the lower sediment depths, while Grays Bay and Quinns Island showed little difference among the depths (well-mixed sediment profiles through much of the year). Clatsop Spit showed a well-mixed sediment profile with only very small concentrations of chlorophyll *a* in the top centimeter. Even though the chlorophyll *a* at subsurface sediment depths was probably viable pigment capable of mediating photosynthesis, light penetration into sediment was limited to no more than one centimeter (McINTIRE and AMSPOKER, 1986); hence, primary productivity on the tidal flats likely was limited to the top centimeter at any given time.

3.2.3 Vascular Plants. Maximum above-ground biomasses occurred in either June or July at all sampling sites (Table 4). These values were similar to a maximum biomass of 687g dry weight m^{-2} recorded in a *Carex*-dominated tidal marsh in the Fraser River Estuary, B.C. (KISTRITZ, HALL and YESAKI, 1983). Except for the Trestle Bay site, the high marsh contained a greater biomass than the adjacent low marsh during the maximum biomass period, in regions where both marsh areas were represented. Substantial biomass was still present at most sites in October, although a great fraction of this material was dead by that time of year. By winter most of the above-ground vegetation was gone except for short overwintering shoots of *Carex*. Above-ground vegetation began to reappear in March or April.

TABLE 4. Mean (6 standard error) live and attached dead vascular plant above-ground biomass (g dry wt m2) in 1980. L=Low marsh, H=High marsh, M=Middle marsh. Standard errors are not shown when they are less than 0.5

Site	April		May		June		July		October	
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Baker Bay										
China Cove *Carex* (L)	68±06	5±01	575±102	26±07	82±801	52±08	523±060	108±25	226±33	382±045
China Cove *Scirpus* (L)	29±02	4	340±023	2±01	386±046	36±05	356±074	117±24	39±22	228±046
Ilwaco (L)	32±04	9±01	622±073	8±03	597±125	29±07	717±061	128±33	237±45	429±056
Trestle Bay										
West (L)	191±14	18±01	645±076	0	794±141	49±07	545±078	55±12	196±30	224±039
West (H)	250±09	40±03	509±061	12±02	782±109	43±08	730±060	87±07	485±762	227±042
West *Carex* (L)	140±06	12±01	479±042	19±04	1,089±137	48±05	1,417±160	313±58	10±03	148±018
East (L)	101±06	9±03	320±064	0	706±029	28±03	679±090	102±21	460±84	179±050
East (M)	429±04	41±03	540±038	6±03	279±094	26±08	816±101	84±16	487±59	190±034
East (H)	125±11	32±04	445±043	0	551±058	24±07	639±070	132±23	176±14	229±032
Youngs Bay										
Outer (L)	136±21	14±02	924±100	100±11	2,358±145	170±28	1,646±302	323±45	479±134	631±108
Inner (L)	136±14	10±01	433±094	23±08	718±149	113±19	772±135	209±46	156±32	221±061
Grays Bay										
Outer (L)	-	-	317±051	4±01	416±101	28±06	555±106	86±25	186±31	48±012
Outer (H)	126±11	8±01	470±043	0	971±120	26±05	700±106	120±44	402±89	184±074
Inner (L)	90±09	13±02	476±047	3±02	319±051	16±03	316±058	75±19	290±82	95±031
Inner (H)	171±10	5±01	573±089	9±07	1,021±082	83±012	839±105	54±13	479±87	265±022
Cathlamet Bay										
Army Corps Dock (L)	48±03	10±02	536±076	0	595±060	32±06	822±172	80±20	192±39	97±023
Lois Island (L)	7±01	1	204±021	0	33±037	33±06	274±067	36±17	28±13	16±006
Russian Island (H)	26±03	1	419±028	0	819±060	53±04	959±086	134±20	232±61	312±059
Karlson Island (L)	28±03	3	114±028	2±02	547±088	20±06	527±082	49±10	268±40	85±017
Tronson Island (H)	77±16	12±04	295±049	13±08	712±096	56±05	539±091	53±11	223±24	66±015
Fluvial Region										
Quinns Island (L)	30±02	2	342±041	20±05	624±054	49±06	701±161	77±10	153±24	46±010
Puget Island (H)	-	-	-	-	-	-	1,383±278	119±34	-	-

Below-ground biomas
ground biomass. Even tho
small sample size, in some
than in summer, associate
suggested downward trans
rhizomes and roots in autu
KIBBY, 1981). This patter
areas, where presumed tr
(MACDONALD and WINFIEL
peak standing stock was tr
River Estuary.

A summary of the seas
in Fig.7. On-ground litter

TABLE 5. Mean dry weig
soil core data. There w

Baker Bay
China Cove *Carex* (L)
China Cove *Scirpus* (L)
Ilwaco (L)

Trestle Bay
West (L)
West (H)
East *Carex* (L)
East (L)
East (M)
East (H)

Youngs Bay
Outer (L)
Inner (H)

Grays Bay
Outer (L)
Outer (H)
Inner (L)
Inner (H)

Cathlamet Bay
Army Corps Dock (L)
Lois Island (L)
Russian Island (H)
Karlson Island (L)
Tronson Island (H)

Fluvial Region
Quinns Island (L)
Puget Island (H)

Below-ground biomass (Table 5) did not show seasonal changes as clearly as the above-ground biomass. Even though sampling variability could not be assessed adequately because of small sample size, in some areas there appeared to be greater below-ground biomass in October than in summer, associated with decreasing above-ground biomass from summer to fall. This suggested downward translocation of organic compounds from above-ground vegetation to the rhizomes and roots in autumn, as reported for other *Carex* marshes in Oregon (GALLAGHER and KIBBY, 1981). This pattern seemed particularly pronounced in *Carex*- and *Scirpus*-dominated areas, where presumed translocation represented 38.5% of annual above-ground production (MACDONALD and WINFIELD, 1984). KISTRITZ, HALL and YESAKI (1983) also found that 38% of the peak standing stock was translocated into roots in the *Carex*-domianted tidal marsh in the Fraser River Estuary.

A summary of the seasonal biomass patterns, averaged over all study sites in 1980, is shown in Fig.7. On-ground litter concentrations are also shown.

TABLE 5. Mean dry weight (g dry wt m^{-2}) of live vascular plant root material in 1980, computed from soil core data. There were too few replicate samples for meaningful calculations of standard errors

	April	June	July	October
Baker Bay				
China Cove *Carex* (L)	2632	2910	2863	3754
China Cove *Scirpus* (L)	2362	1058	-	2815
Ilwaco (L)	3077	2348	2916	2445
Trestle Bay				
West (L)	3296	2614	2910	3062
West (H)	-	863	1372	1495
East *Carex* (L)	-	2012	1817	3006
East (L)	-	213	1439	867
East (M)	-	1738	326	757
East (H)	755	1529	934	1503
Youngs Bay				
Outer (L)	3272	1346	1533	2940
Inner (H)	1537	970	1781	2181
Grays Bay				
Outer (L)	-	678	414	1296
Outer (H)	2374	1101	2797	1869
Inner (L)	1070	700	897	366
Inner (H)	1821	1439	1734	2135
Cathlamet Bay				
Army Corps Dock (L)	2565	1340	813	1153
Lois Island (L)	1364	183	930	594
Russian Island (H)	3205	2614	2881	938
Karlson Island (L)	1757	1388	1413	264
Tronson Island (H)	3507	-	1654	942
Fluvial Region				
Quinns Island (L)	1324	914	1606	1074
Puget Island (H)	-	-	1686	-

Army Corps Dock (L)	48±03	10±02	536±076	0	595±060	32±06	822±172	80±20	192±39	97±023														
Lois Island (L)	7±01	1	204±021	0	33±037	33±06	274±067	36±17	28±13	16±006														
Russian Island (H)	26±03	1	419±028	0	819±060	53±04	959±086	134±20	232±61	312±059														
Karlson Island (L)	28±03	3	114±028	2±02	547±088	20±06	527±082	49±10	268±40	85±017														
Tronson Island (H)	77±16	12±04	295±049	13±08	712±096	56±05	539±091	53±11	223±24	66±015														
Fluvial Region																								
Quinns Island (L)	30±02	2	342±041	20±05	624±054	49±06	701±161	77±10	153±24	46±010														
Puget Island (H)	-	-	-	-	-	-	1,383±278	119±34	-	-														

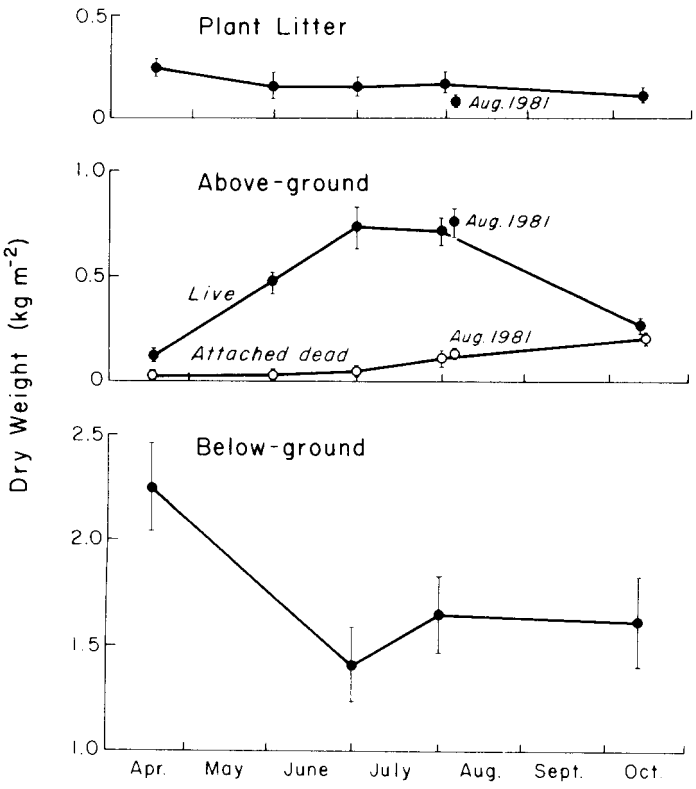

FIG. 7. Abundance of live and dead emergent plant material averaged over all study sites (except Puget Island) by 1980 collection dates; Puget Island was represented by one species and was very different from other sites (Cluster 5 and Fig.4). August 1981 data are shown for comparison. Vertical bars represent standard errors of the means.

3.3 Primary Production

3.3.1 Phytoplankton. The best empirical models of phytoplankton productivity obtained from multiple regression analyses were, for deep-water (>4m) stations:

$$\text{LogP} = 1.548 + 0.001\text{R} - 0.103\text{k} + 0.056\text{C} + 0.028\text{T} - 0.001\text{S}$$

and for shallow-water (<4m) stations:

$$\text{LogP} = 1.605 + 0.003\text{R} - 0.127\text{k} + 0.033\text{C}$$

where P = day-time produc
extinction coefficient of lig
temperature (°C), and S = t
the variability of daily pro
variability. It was evident t
ton productivity, because R
stations, and 80% at the sha
that light was the major va

The productivity model
and times in which we hac
measurements of producti
productivity at the deep-v
regional differences in Ma
(Fig.8). The eruption of Mt
1980 by dramatically decre
SMALL, 1983). However,
volcano effect by substitu
obtained at comparable tim
and incident light values m
was a progressive decline i
late spring and summer. Th
Region that was observed i
but not in the July data (Fig
within any given month w

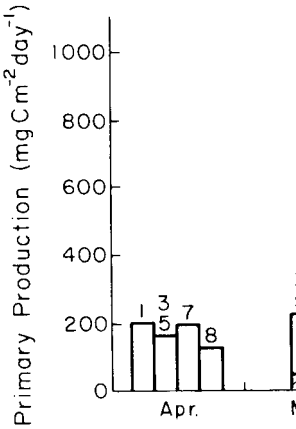

FIG. 8. Mean phytoplankt
for regions) along the m
because of the Mt. Saint

where P = day-time productivity (mgC $m^{-2}d^{-1}$), R = daily solar radiation input (gcal $cm^{-2}d^{-1}$), k = extinction coefficient of light (m^{-1}), C = chlorophyll *a* concentration (mg m^{-3}), T = surface water temperature (°C), and S = total seston load (g m^{-3}). The deep-water model accounted for 90% of the variability of daily productivity, while the shallow-water model accounted for 85% of the variability. It was evident that light availability exerted the primary control on daily phytoplankton productivity, because R and k together accounted for 75% of the variability at the deep-water stations, and 80% at the shallow-water stations. FREY, LARA-LARA and SMALL (1983) also noted that light was the major variable affecting phytoplankton productivity.

The productivity models were used to extend our number of productivity estimates into areas and times in which we had estimates of the appropriate environmental variables but no direct measurements of productivity. Both measured and model-predicted values for phytoplankton productivity at the deep-water stations, when grouped by estuarine regions, showed strong regional differences in May and July 1980, in addition to the expected seasonal differences (Fig.8). The eruption of Mt. Saint Helens markedly reduced the daily photosynthetic rates in May 1980 by dramatically decreasing the light penetration in the water column (FREY, LARA-LARA and SMALL, 1983). However, we calculated potential production rates for May 1980 without the volcano effect by substituting into the productivity model the values for k and total seston obtained at comparable times from other years, and by using the actual chlorophyll *a*, temperature and incident light values measured in May 1980. These adjusted rates are shown in Fig.8. There was a progressive decline in production from the Fluvial Region toward the estuary mouth during late spring and summer. The sharp break between the Cathlamet Bay Region and the Mid-Estuary Region that was observed in the chlorophyll data (Fig.5) was apparent in the corrected May data but not in the July data (Fig.8). Throughout the rest of the year, primary production for all regions within any given month was remarkably similar.

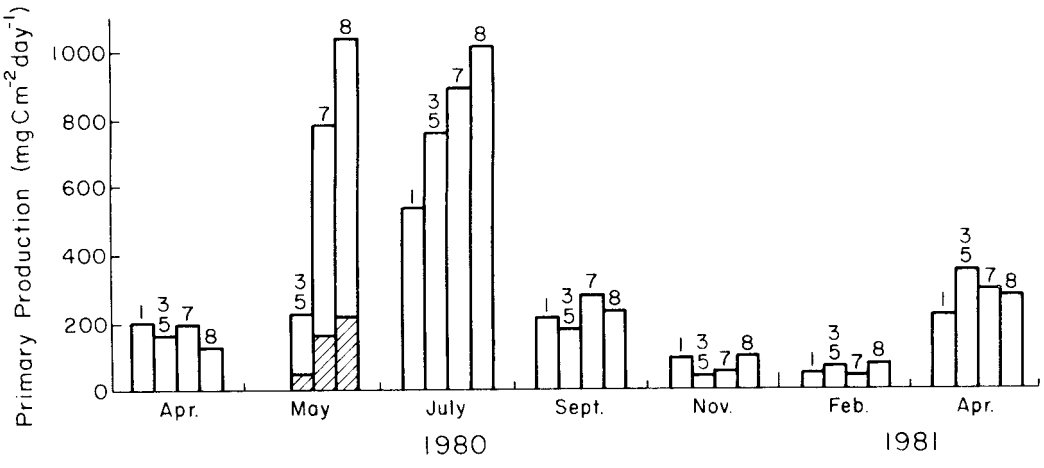

FIG.8. Mean phytoplankton production (mg C $m^{-2}d^{-1}$) by sampling months and by regions (see Fig.5 for regions) along the main estuarine axis. Actual rates in May 1980 (cross-hatching) are reduced because of the Mt. Saint Helens eruption; rates without the volcano effect have been computed and are also shown for May 1980.

On a per unit area basis from May through September 1980, both measured and model-predicted productivity values showed that the small rivers were the most productive shallow-water regions (Fig.9). However, because they are so small, these rivers did not significantly affect productivity estimates for the main body of the estuary. For example, in summer, Youngs River and Lewis and Clark River both discharge into Youngs Bay, and Deep River discharges into Grays Bay, without apparently changing the lower areal productivity of either bay. In winter, the areal productivities of the bays and rivers were uniformly low.

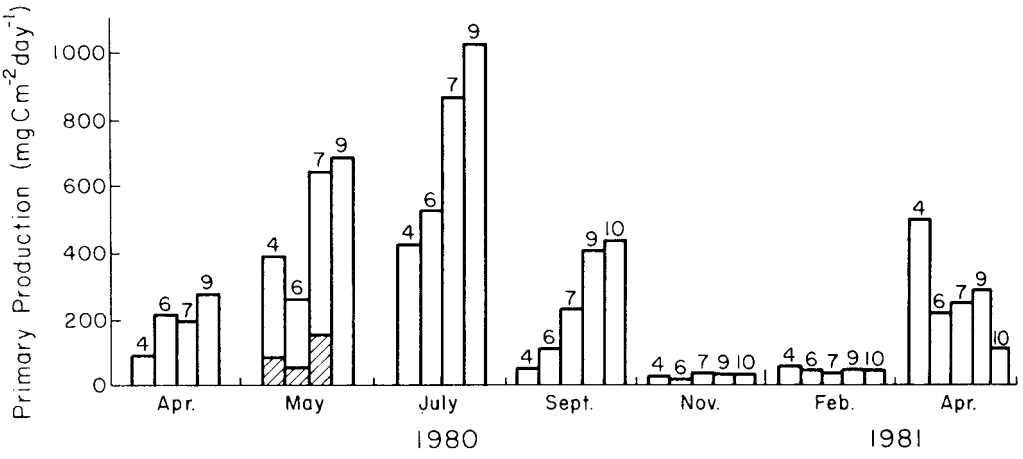

FIG.9. Mean phytoplankton production (mg C $m^{-2}d^{-1}$) by sampling months and by regions (see Fig.6 for regions) in the shallows (cross-hatched areas in Fig.1) and tributary rivers. Actual rates in May 1980 (cross-hatching) are reduced because of the Mt. Saint Helens eruption, but the tributary rivers were not affected; rates in the shallows without the volcano effect have been computed and are also shown for May 1980.

At our time of sampling in May 1980, the effect of the volcanic eruption had not reached into either the Youngs River or the Lewis and Clark River, and their productivity was very high relative to the productivity in the adjoining Youngs Bay, which was affected by the volcanic load (Fig.9). Grays Bay was also affected by the volcano, but presumably Deep River was not (although no measurements were made in Deep River in May 1980).

3.3.2 Benthic Algae. Gross benthic algal productivity averaged 41 mg C $m^{-2}h^{-1}$ over all months, intensive sampling sites and tidal level transects, while net productivity averaged 20 mg C $m^{-2}h^{-1}$ (Table 6). Net productivity throughout the daylight period averaged 130 mg C $m^{-2}d^{-1}$. The winter months (November and February) yielded the lowest production rates, as expected. Tidal flats in Youngs Bay had the highest mean daily productivity, while those in Clatsop Spit had by far the lowest. Mean production rates in the marsh transects tended to be higher than those in the upper intertidal transects, which in turn tended to be higher than those in the lower intertidal.

Correlation coefficients relating hourly gross primary productivity (GP) to both total oxygen uptake and chlorophyll *a* content (C) in 1cm cores in all intertidal areas (not including the marsh) were both 0.81, and significant at $p<0.05$. This led MCINTIRE and AMSPOKER (1986) to develop the following regression equation with chlorophyll *a* as the independent variable:

$$GP = 0.63 + 0.28\ C$$

TABLE 6. Mean rates
productivity (mg C m
by sampling time (mo
variability in rates at e
pooled monthly rates, s

Variable
Time
May
June
July
August
September
October
November
February
March
April
Site
Clatsop Spit
Youngs Bay
Baker Bay
Grays Bay
Quinns Island
Tidal Level Transect
Marsh (0.9m above MI
Upper (0.7m above MI
Lower (0.3m above M

The mean GP:C ratio of 0.
by an order of magnitude
mean GP:C ratios for four
and Quinns Island) only v
The ratio in Baker Bay w
from the remainder of the
ratios were subsequently
where only chlorophyll *a*

Benthic algal producti
the concentration of organ
as mean grain size and sor
to chlorophyll *a* in the 4.5
however, the correlation

The correlations betwe
as high as in the intertidal
productivity and, respecti
centimeter of marsh sedir

TABLE 6. Mean rates of hourly gross and net primary productivity (mg C $m^{-2}h^{-1}$) and daily net productivity (mg C $m^{-2}d^{-1}$) for the five intensive benthic algal study sites (Fig.2). Data are pooled by sampling time (month), site, and tidal level transect. Because of the large natural temporal variability in rates at each site and tidal level transect, and the large spatial variability within the pooled monthly rates, standard errors are large (not reported herein) and the mean values can be used only for gross comparisons

Variable	Sample Size	Hourly Gross	Hourly Net	Daily Net
Time				
May	14	75.7	53.7	280.9
June	14	39.1	27.8	157.1
July	12	51.6	36.6	206.8
August	14	37.5	26.6	130.3
September	14	48.1	34.2	156.0
October	14	53.4	37.9	147.1
November	7	28.4	20.2	68.3
February	14	11.1	7.9	29.3
March	14	38.9	27.6	116.5
April	14	31.5	22.4	102.1
Site				
Clatsop Spit	17	5.2	3.7	15.9
Youngs Bay	29	84.2	59.8	257.7
Baker Bay	29	42.5	30.2	130.0
Grays Bay	29	33.0	23.4	101.0
Quinns Island	29	29.6	21.0	90.6
Tidal Level Transect				
Marsh (0.9m above MLLW)	39	55.0	39.1	168.3
Upper (0.7m above MLLW)	48	43.2	30.7	132.3
Lower (0.3m above MLLW)	44	29.4	20.9	90.1

The mean GP:C ratio of 0.28 was fairly typical for sediment-associated microalgae (though lower by an order of magnitude than ratios typical for phytoplankton at light saturation). However, the mean GP:C ratios for four of the five intensive study sites (Clatsop Spit, Youngs Bay, Grays Bay and Quinns Island) only varied between 0.32 and 0.37, all higher than the 0.28 overall mean ratio. The ratio in Baker Bay was just 0.17, indicating once again that this bay was relatively isolated from the remainder of the estuary in both biological and physical attributes. Appropriate GP:C ratios were subsequently used to estimate benthic algal productivity at the survey sites (Fig.2), where only chlorophyll *a* was measured directly.

Benthic algal productivity in the intertidal regions was also related significantly ($p<0.05$) to the concentration of organic matter in the top centimeter of sediment, to sediment properties such as mean grain size and sorting coefficient, and to the ratios of chlorophyll *a* in the top centimeter to chlorophyll *a* in the 4.55-5.55 and 9-10cm depth horizons (McINTIRE and AMSPOKER, 1986); however, the correlation coefficients were all relatively low, from 0.42 to 0.68.

The correlations between benthic algal productivity and other variables in the marsh were not as high as in the intertidal areas. For example, the correlation coefficients between hourly gross productivity and, respectively, total oxygen uptake and chlorophyll *a* concentration in the top centimeter of marsh sediments were 0.57 and 0.27. Such poor correlations likely were due to

variable detrital inputs and differential shading from stands of vascular marsh plants through the seasons. Neither surface light intensities on the tidal flats or marshes nor salinity of the water periodically inundating the flats were significantly correlated with benthic algal productivity. Measured light intensities (mean of 1428μE $m^{-2}s^{-1}$) were almost always above the intensity required to saturate photosynthesis (300μE $m^{-2}s^{-1}$), so no productivity:light relationship was expected. In addition, the benthic algal flora in estuaries characteristically is tolerant of a wide salinity range.

3.3.3 Vascular Plants. Except for the short overwintering shoots of *Carex* and dead material from the previous season, the marshes are bare in winter. Above-ground vegetation grows rapidly in the spring of each year, reaches maximum biomass in the summer, then dies back in the late fall (Table 4). The grand mean of the annual above-ground production in the estuary, taken as the mean of the average production at each site (Table 7), was 1038g dry wt $m^{-2}y^{-1}$, or 415.3 g C $m^{-2}y^{-1}$. Mean areal production without the data from an isolated stand of *Typha latifolia* in the Fluvial Region was 402.7gC $m^{-2}y^{-1}$ (Table 8), which is probably a more representative value. Production at each site was by no means uniform (Table 7). The high marsh exhibited higher production than the low marsh in Grays Bay, for example, whereas stands of highly productive *Carex* dominated the annual production in the low marshes of Baker and Trestle Bays. The low marsh of outer Youngs Bay was the most productive site of all, while the low marsh of inner Youngs Bay exhibited relatively modest annual production. The tidal flat bordering the low marsh of outer Youngs Bay was also the most productive of the benthic microalgal sites (Table 6).

3.3.4 Annual Primary Production Dynamics in the Estuary. Total annual net primary production for the Columbia River estuary was estimated as 30,537 metric tons C y^{-1}, with approximately 17,667mt C y^{-1} being produced by phytoplankton, 1,545 mt C y^{-1} by benthic algae, and 11,325 mt C y^{-1} by emergent vascular plants (Table 8). On an areal basis, phytoplankton averaged about 55g C $m^{-2}y^{-1}$ (using 24-hour productivities), or about 100g C $m^{-2}y^{-1}$ (using daylight productivity values only). This latter value was two to nine times lower than comparable production in estuaries of eastern USA and Canada (LARA-LARA, 1982; NIXON, 1988). The only similar rate in the literature is 120g C $m^{-2}y^{-1}$ for the Fraser River Estuary, British Columbia (PARSONS, LEBRASSEUR and BARRACLOUGH, 1970). Benthic algal production in the Columbia Estuary averaged approximately 16 g C $m^{-2}y^{-1}$, and emergent vascular plants averaged 403 g C $m^{-2}y^{-1}$ (Table 8). Even though the vascular plants had by far the highest production per unit area, the total annual estuarine production by vascular plants was less than that for phytoplankton because of the relatively small total marsh area in the estuary. Total annual estuarine production by benthic algae was lowest of all by virtue of its low areal production rate and the small area occupied by tidal flats in the estuary.

The areal phytoplankton production in the Cathlamet Bay and Fluvial Regions was substantially higher than in the other regions (Table 8). However, the Mid-Estuary Region contributed most (about 6,291mt C y^{-1}) to the total annual production for the whole system, because of the large mid-estuarine area. Because there was no phytoplankton sampling in the very shallow water of the Baker Bay/Trestle Bay Region, production rates were estimated as simple averages of values from the adjoining Entrance and Youngs Bay Regions. If these values are excluded from the estuary-wide production means, the areal means increase slightly but the means for total annual production are reduced from about 17,667 to 16,690mt C y^{-1}. LARA-LARA, FREY and SMALL (1990) estimated net phytoplankton production at 29,876mt C y^{-1} for the daylight period only, suggesting that, on an annual average basis over the complete estuary, nighttime respiration was 29,876-17,667 = 12,209mt C y^{-1}, or 41% of the annual net daylight production.

TABLE 7. Net annual pri
excluding grazi

Site
Baker Bay
China Cove *Carex* (L)
China Cove *Scirpus* (L)
Ilwaco (L)
Trestle Bay
West (L)
West (H)
East *Carex* (L)
East (L)
East (M)
East (H)
Youngs Bay
Outer (L)
Inner (L)
Grays Bay
Outer (L)
Outer (H)
Inner (L)
Inner (H)
Cathlamet Bay
Army Corps Dock (L)
Lois Island (L)
Russian Island (H)
Karlson Island (L)
Tronson Island (H)
Fluvial Region
Quinns Island (L)
Puget Island (H)

*End of season total standi

Estimates of areal benth
ton production in the Your
less than the areal phytopl
benthic algae was very lov
Estuary Regions. Benthic
Bay/Trestle Bay, Youngs
benthic algal production i

Areal production by er
areal production rates in t
annual production in the lo
isolated stand of *Typha la*

TABLE 7. Net annual primary production (in terms of dry wt and carbon) of emergent vascular plants, excluding grazing losses. L = Low marsh; H = High marsh;, M = Middle marsh

Site	g dry wt $m^{-2}y^{-1}$	g C $m^{-2}y^{-1}$
Baker Bay		
China Cove *Carex* (L)	873	349.2
China Cove *Scirpus* (L)	475	190.0
Ilwaco (L)	850	340.0
Trestle Bay		
West (L)	861	344.4
West (H)	853	341.2
East *Carex* (L)	1730	692.0
East (L)	790	316.0
East (M)	1176	470.4
East (H)	803	321.2
Youngs Bay		
Outer (L)	2528	1011.2
Inner (L)	981	392.4
Grays Bay		
Outer (L)	641	256.4
Outer (H)	1005	402.0
Inner (L)	545	218.0
Inner (H)	1104	441.6
Cathlamet Bay		
Army Corps Dock (L)	912	364.8
Lois Island (L)	364	145.6
Russian Island (H)	1094	437.6
Karlson Island (L)	577	230.8
Tronson Island (H)	768	307.2
Fluvial Region		
Quinns Island (L)	778	311.2
Puget Island (H)	1502*	600.8*

*End of season total standing crop of isolated stand of *Typha latifolia*.

Estimates of areal benthic algal production were similar to those for 24 hour areal phytoplankton production in the Youngs Bay and Baker Bay/Trestle Bay Regions (Table 8), but were much less than the areal phytoplankton production estimates in the other regions. Areal production by benthic algae was very low across the predominantly sandy substrates of the Entrance and Mid-Estuary Regions. Benthic algal production in the relatively extensive tidal flat areas of Baker Bay/Trestle Bay, Youngs Bay and Cathlamet Bay represented approximately 82% of total benthic algal production in the estuary.

Areal production by emergent vascular plants in Youngs Bay marshes was about twice the areal production rates in the other regions (Table 8). This was primarily the result of very high annual production in the low marsh of outer Youngs Bay (Table 7). High areal production in an isolated stand of *Typha latifolia* was not included in the mean areal production for the Fluvial

TABLE 8. Annual rates of net areal production (mg C $m^{-2}y^{-1}$) and total production (mt C y^{-1}) by region for phytoplankton, benthic algae and emergent vascular plants. See text for estimation protocols

Region		Phytoplankton			Benthic Algae		Emergent Vascular Plants	
		g C $m^{-2}y^{-1}$ (daylight)	g C $m^{-2}y^{-1}$ (24 hour)	mt C y^{-1} (24 hour)	g C $m^{-2}y^{-1}$ (24 hour)	mt C y^{-1} (24 hour)	g C $m^{-2}y^{-1}$ (24 hour)	mt C y^{-1} (24 hour)
(1)	Entrance	80.3	47.5	1,474.9	1.6	3.4	-	-
(2)	Baker Bay/ Trestle Bay	(72.1)	(42.7)	(706.3)	40.8	536.9	373.8	1,322.5
(3+5)	Mid-Estuary	84.9	50.2	6,290.5	1.4	70.8	-	-
(4)	Youngs Bay	63.9	37.8	482.8	29.9	359.5	701.8	2,444.6
(6)	Grays Bay	66.3	39.2	1,376.8	10.9	148.2	329.5	781.0
(7)	Cathlamet Bay	124.5	73.6	4,442.5	9.5	366.8	297.2	5,539.7
(8)	Fluvial	152.7	90.3	2,8982.7	16.1	59.2	311.2*	1,236.7
Mean		96.2	54.5		15.7		402.7*	
Mean (excluding Region 2)		99.6	56.4					
Total				17,666.5		1,544.8		11,324.5
Total (excluding Region 2)				16,690.2				

*Not including data from an isolated stand of *Typha latifolia*.

Region as indicated earlier because the stand was atypical for the region (MACDONALD and WINFIELD, 1984). Approximately 71% of emergent plant production in the estuary took place in the Youngs Bay and Cathlamet Bay Regions. If annual production in the Baker Bay/Trestle Bay and Fluvial Regions were included, the percentage of the total production increased to about 93%.

The annual turnover of the phytoplankton and benthic algal biomasses for each region and for the whole estuary can roughly be computed as the ratio of mean annual areal carbon production to mean areal carbon biomass (P/B). The annual turnover of emergent marsh vegetation is, of course, unity because our method of calculating annual production involves appearance and disappearance of above-ground biomass over the annual growing period. With the exception of Youngs Bay, P/B ratios for phytoplankton were similar (Table 9), and indicated that phytoplankton carbon-based biomass turned over as a result of primary production about 30 times annually in the estuary. Benthic algae in the low marsh and tidal flats, on the other hand, turned over their biomasses in the upper centimeter of sediment approximately twice per year. The high P/B ratio in the Youngs Bay water column resulted from consistently high phytoplankton productivities and low biomasses. Youngs Bay was thus the most efficient region in producing phytoplankton, with the crop turning over its biomass on average 84 times per year. No concomitant high annual turnover was measured in the benthic algae of Youngs Bay. The generally enclosed morphometry of Youngs Bay, in contrast to the openness of Grays Bay, Cathlamet Bay and the rest of the estuary, is likely to increase the residence time of water in this bay and therefore give excellent conditions for the enhanced production of phytoplankton.

TABLE 9. Mean annual
benthic algae in the diff

Region	
(1)	Entrance
(2)	Baker Bay/Trest
(3+5)	Mid-Estuary
(4)	Youngs Bay
(6)	Grays Bay
(7)	Cathlamet Bay
(8)	Fluvial
Mean	
Mean without Youngs Bay	

3.4 *Import and Export o*

Transport of living pri
the phytoplankton. Mixi
study area, particularly o
phytoplankton. Similarly
continued to metabolize, a
assumed that bethic mic
estuary. Non-living cells
of the detrital pool.

Daily transport rates o
the Fluvial Region throug
exception was in July, whe
that through the Mid-Estu
(and phytoplankton carb
Region in July, and the
historical chlorophyll valu
for the higher transport
decreases in carbon transp
Estuary Region were the
two regions (Fig.5). The
chlorophyll *a* concentrati
eruption, though the relat

Annual transport of ca
integrating the daily trans
Mt. Saint Helens period
Entrance Region, and 40,

TABLE 9. Mean annual production/biomass (P/B) ratios (using carbon values) for phytoplankton and benthic algae in the different regions. The P/B ratios for emergent vascular plants were assumed to be 1.0. ND = no data

Region		Phytoplankton	Benthic algae
(1)	Entrance	31.07	2.63
(2)	Baker Bay/Trestle Bay	ND	1.74
(3+5)	Mid-Estuary	31.64	1.90
(4)	Youngs Bay	84.11	2.10
(6)	Grays Bay	30.08	2.31
(7)	Cathlamet Bay	34.35	2.10
(8)	Fluvial	24.76	2.32
Mean		39.34	2.16
Mean without Youngs Bay		30.38	

3.4 Import and Export of Living Plant Biomass

Transport of living primary producers through the Columbia River Estuary mainly involves the phytoplankton. Mixing of living benthic algal cells into the water column did occur in the study area, particularly over mudflats during tidal inundation, and these cells were evaluated as phytoplankton. Similarly, true phytoplanktonic cells undoubtedly settled onto substrates and continued to metabolize, and such cells were functionally considered benthic microalgae. It was assumed that bethic microalgae and living emergent vegetation were not transported in the estuary. Non-living cells, plants or plant fragments, regardless of origin, were considered part of the detrital pool.

Daily transport rates of phytoplanktonic particulate organic carbon (PPOC) decreased from the Fluvial Region through the Entrance Region in almost all sampling months (Table 10). The exception was in July, when the calculated transport through the Entrance Region was higher than that through the Mid-Estuary Region. This was brought about by a slightly lower chlorophyll (and phytoplankton carbon) concentration in the Mid-Estuary Region than in the Entrance Region in July, and the relatively high tidal exchange rate in the Entrance Region. Use of historical chlorophyll values for the adjacent ocean might have been responsible, at least in part, for the higher transport calculated through the Entrance Region in July. The rather sharp decreases in carbon transport in May and July between the Cathlamet Bay Region and the Mid-Estuary Region were the result of the sharp decreases in chlorophyll concentration between the two regions (Fig.5). The absolute transport rates for May were likely to have been inflated by chlorophyll *a* concentrations which were enhanced to some unknown degree by the volcanic eruption, though the relative transports between regions in May were probably unaffected.

Annual transport of carbon associated with living phytoplankton can be estimated roughly by integrating the daily transport rates for each sampling month over the full year. Excluding the Mt. Saint Helens period (May 1980), such transport was estimated as 41,430mt C y^{-1} into the Entrance Region, and 40,560mt C y^{-1} into the adjacent ocean (Table 10).

TABLE 10. Daily transport rates (mt C d^{-1}) of phytoplankton carbon through regions of the Columbia River Estuary for each sampling month. Estimates in parentheses are based on literature values for chlorophyll concentrations in the near ocean off the Columbia River, taken in different years. No export through the Entrance Region in May could be estimated because of the lack of data in adjacent ocean water after the volcanic explosion

Month	Transport Rates (mt C d^{-1})			
	Fluvial	Cathlamet Bay	Mid-Estuary	Entrance
April 1980	251.2	239.5	224.8	(214.5)
May	654.5	628.6	434.4	-
July	290.3	288.2	117.3	(179.1)
September	68.1	48.5	47.2	(43.3)
November	71.9	48.4	32.1	(15.3)
February 1981	133.0	125.3	106.8	(60.2)
Estimated annual export through the Mid-Estuary Region to the Entrance Region (without May)			41,430 mt C y^{-1}	
Estimated annual export through the Mid-Estuary Region to the Entrance Region (including May)			45,960 mt C y^{-1}	
Estimated annual export through the Entrance Region to the ocean (without May)			40,560 mt C y^{-1}	

3.5 *Detrital Biomass*

3.5.1 Water Column. Detrital particulate organic carbon (DPOC) represented 58 to 88% of total particulate organic carbon (TPOC) in the Fluvial Region; however, DPOC in the Entrance Region was 82 to 96% of TPOC (Table 11). Lysing phytoplankton was being added into the TPOC pool in the water column as the TPOC was being transported downstream. Allochthonous inputs of DPOC were derived from the fragmentation of emergent plant debris, resuspension of bottom sediments, fragmentation of excreta and carcasses of animals ranging in size from zooplankton to large vertebrates, and scouring of tidal flats and marshes. Although the concentrations of DPOC in May were very high, the DPOC:TPOC ratios were not unusual in comparison with other values throughout the year. The ratios in May in all four regions were higher than the ratios in April and July, however. In other estuarine systems, DPOC has also been reported to be the dominant suspended fraction (PARSONS and TAKAHASHI, 1973; POULET, 1976; VAN VALKENBURG, JONES and HENLE, 1978; CHERVIN, 1978; RAYMONT, 1980).

By elemental weight, the C:N ratio in living phytoplankton is approximately 5.7 (REDFIELD, KETCHUM and RICHARDS, 1963). There were no ratios observed as low as 5.7 in the top 10m of the water column in the Columbia River Estuary (not illustrated), but freshwater values at all times of year (except May 1980), and most other values in winter and early spring, were below 10. Ratios below 10 suggested significant contributions by live cells. The Mid-Estuary in summer, however, had particulate C:N ratios as high as 25, indicating that detrital carbon was being concentrated in this mixing zone, relative to phytoplanktonic carbon. Concentrations of detrital particles in this region, concomitant with a loss of chlorophyll *a* in the same region in summer, strongly suggested that 1) live freshwater phytoplankton was being converted to detrital carbon, and 2) non-living but carbon-rich detrital particles were being mixed into the water column from the sediments.

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Month	Fluvia
April 1980	632
May	4,781
July	674
September	1,098
November	1,327
February 1981	595

3.5.2 Tidal Flats. Th
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concentration of the five s
other four sites, the marsh
m^{-2} at Baker Bay. The upp
the lowest DPOC:TPOC ra
of living biomass. The You
(0.78), indicating that You
particulate organic carbon

The range of DPOC:TP
on location in the estuary,
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greater than those in the v
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3.5.3 Vascular Plants.
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There undoubtedly was s
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SIMENSTAD, SMALL and M
of 15% of annual emergent
tion to roots was estimated
the particulate detrital poo
vegetation in the marshes o

TABLE 11. Concentration (mg C m^{-3}) of detrital particulate organic carbon (DPOC) averaged over the water column, and DPOC as a fraction of total particulate organic carbon (TPOC), in four sequential, contiguous regions from the Fluvial to the Entrance

Month	DPOC (mg C m^{-3})				DPOC:TPOC			
	Fluvial	Cathlamet Bay	Mid-Estuary	Entrance	Fluvial	Cathlamet Bay	Mid-Estuary	Entrance
April 1980	632	655	686	748	0.69	0.72	0.77	0.82
May	4,781	4,948	5,060	5,214	0.88	0.89	0.92	0.94
July	674	684	957	968	0.58	0.60	0.82	0.82
September	1,098	1,125	1,260	1,309	0.77	0.82	0.90	0.96
November	1,327	1,342	1,405	1,425	0.86	0.89	0.93	0.95
February 1981	595	633	683	759	0.73	0.77	0.84	0.93

3.5.2 Tidal Flats. There were observable differences in DPOC in the top centimeter of sediment at the five intensive study sites (Table 12). Clatsop Spit had the lowest mean DPOC concentration of the five sites (29.8g C m^{-2}), but the highest DPOC:TPOC ratio (0.92). At the other four sites, the marsh transect registered the highest DPOC concentrations, up to 127.0g C m^{-2} at Baker Bay. The upper intertidal transect usually had the lowest DPOC concentrations and the lowest DPOC:TPOC ratios; thus, this transect usually had the highest relative concentrations of living biomass. The Youngs Bay site had the lowest mean DPOC:TPOC ratio over all transects (0.78), indicating that Youngs Bay had the highest living biomass concentration relative to total particulate organic carbon.

The range of DPOC:TPOC in the tidal flat sediments was 0.74 to 0.96 (Table 12), depending on location in the estuary, while the DPOC:TPOC range in the water column was 0.58 to 0.96, depending on both season and location in the study area (Table 11). This similarity occurred even though the absolute concentrations of DPOC and TPOC in the tidal flats were usually much greater than those in the water column. High concentrations of DPOC in the tidal flats and marshes suggested that scouring of these sediments into the water column would continue to increase the concentrations of water-column DPOC down the axis of the estuary, and at the same time increase the DPOC:TPOC ratio (Table 11).

3.5.3 Vascular Plants. The annual particulate detrital biomass generated from the emergent marsh vegetation can be estimated roughly as the difference between total annual above-ground carbon production and the sum of losses due to grazing and translocation of above-ground carbon compounds into rootstocks by fall. Attached standing dead plant material increased slightly along with the marked increase in live material during the April-July growing season (Fig.7), and this attached dead material was included as net production by the SMALLEY (1958) method. It became part of the detrital pool during fall die-back of the above-ground emergent plant biomass. There undoubtedly was some shedding during the growing season of dead above-ground material, but we had no direct measurements of this loss to the detrital pool. However, even if we assume that a quantity equal to the total standing dead biomass through the growing season was lost during the growing season, the loss amounts to only 0.84mt C, an insignificant fraction of the total annual emergent plant production of 11,324mt C y^{-2}.

SIMENSTAD, SMALL and MCINTIRE (1990) suggested that herbivore grazing removed an average of 15% of annual emergent plant carbon production in the Columbia River Estuary. Translocation to roots was estimated to remove 38%. The remaining 47% can be assumed to have entered the particulate detrital pool. Therefore, of the 11,324mt C y^{-1} produced as above-ground vegetation in the marshes of the Columbia River Estuary, about 5,322mt C y^{-1} becomes detritus.

TABLE 12. Concentrations (g C m^{-2}) of detrital particulate organic carbon (DPOC) in the top centimeter of sediment, and the ratio of DPOC to total particulate organic carbon (TPOC), for the five intensive benthic algal study sites, and for the transects within each intensive study site. Values are annual means

	DPOC (g C m^{-2})	DPOC:TPOC
Clatsop Spit	29.8	0.92
Upper (0.7m above MLLW)	27.4	0.87
Lower (0.3m above MLLW)	32.4	0.96
Youngs Bay	76.2	0.78
Marsh (0.9m above MLLW)	90.0	0.80
Upper (0.7m above MLLW)	70.7	0.74
Lower (0.3m above MLLW)	67.0	0.79
Baker Bay	104.9	0.85
Marsh (0.9m above MLLW)	127.0	0.86
Upper (0.7m above MLLW)	88.7	0.79
Lower (0.3m above MLLW)	98.3	0.89
Grays Bay	87.5	0.89
Marsh (0.9m above MLLW)	99.6	0.90
Upper (0.7m above MLLW)	75.8	0.89
Lower (0.3m above MLLW)	87.1	0.89
Quinns Island	66.8	0.89
Marsh (0.9m above MLLW)	109.7	0.89
Upper (0.7m above MLLW)	39.0	0.83
Lower (0.3m above MLLW)	50.0	0.93

Some of the vegetation washes off the marshes in large detrital pieces either to be redeposited on other marshes, to sink to the estuary bottom, or to be carried seaward. However, it would be expected that shredding, cutting, grinding and other means of mechanically reducing large fragments to small particles, in concert with microbial, metazoan and chemical decomposition, are the primary means of introducing marsh detritus into the estuarine water column. Decomposition rates as determined from the litter bag experiments were not significantly different in the low and high marshes but, as expected, less fibrous plants such as *Triglochin* decomposed most rapidly, fibrous genera such as *Festuca* and *Aster* decomposed the slowest, and the remaining important genera (*Carex, Potentilla, Agrostis, Juncus, Scirpus* and *Deschampia*) were intermediate. The major differences in decomposition rates were observed between plant litter in freshwater and brackishwater locations over a 38-week period. Loss of dry weight by *Carex lyngbyei* and *Scirpus* spp. litter in two freshwater locations (Quinns Island and Grays Bay), ranged from 92 to 96%, while loss in a brackishwater location (East Trestle Bay) was 66 to 68% (Fig.10). Mean rate of loss from all litterbag experiments was calculated as 0.33% d^{-1} in freshwater and 0.25% d^{-1} in brackishwater.

If we assume that carbon losses from the litter bags proceeded at the same rates as losses of dry weight over the year (RICE and TENORE, 1981; RUBLEE and ROMAN, 1982), and that a mean rate of 0.31% d^{-1} (weighted by the areal coverage of both brackishwater and freshwater marshes) can be applied throughout the estuary, the amount of annual emergent plant detrital accumulation

(5,322mt C y^{-1}) that was ul
roughly estimated as 3,60
estuary in large fragments
turnover time than measu

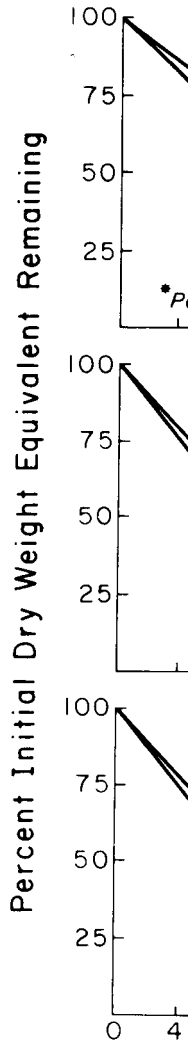

FIG.10. Dry-weight loss
represent

on (DPOC) in the top
carbon (TPOC), for the
nsive study site. Values

DPOC:TPOC
0.92
0.87
0.96
0.78
0.80
0.74
0.79
0.85
0.86
0.79
0.89
0.89
0.90
0.89
0.89
0.89
0.89
0.83
0.93

es either to be redeposited
rd. However, it would be
chanically reducing large
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d between plant litter in
s of dry weight by *Carex*
s Island and Grays Bay),
restle Bay) was 66 to 68%
lculated as 0.33% d^{-1} in

he same rates as losses of
1982), and that a mean rate
d freshwater marshes) can
ant detrital accumulation

(5,322mt C y^{-1}) that was ultimately turned into fine particles and dissolved organic carbon can be roughly estimated as 3,605mt C y^{-1}. The remaining 1,717mt C y^{-1} likely was washed into the estuary in large fragments or remained on the marsh floor as refractory material with a longer turnover time than measured in the litter bag experiments.

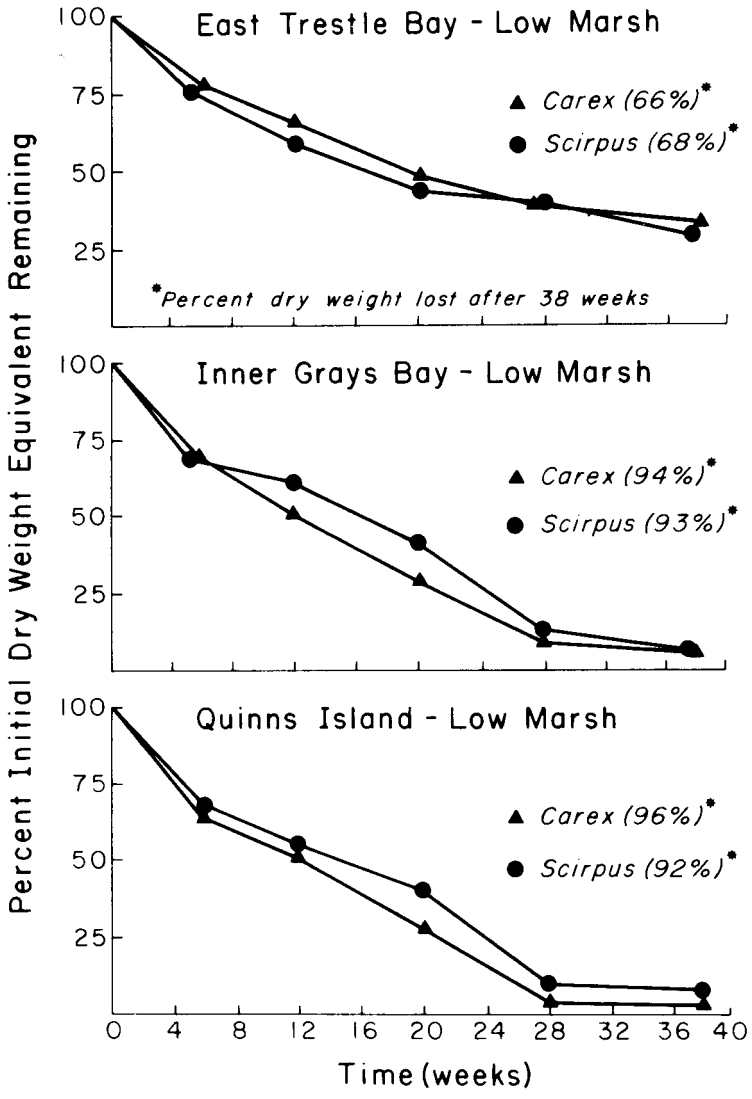

FIG.10. Dry-weight loss from *Carex* and *Scirpus* litter at three low-marsh sites; percentages represent losses of dry weight after 38 weeks in the litter bags.

3.6 Detrital Transport

In any given month except July 1980 and February 1981, DPOC transports through any given region were within 10% of the transports in an adjacent region (Table 13). Adjacent transports were often within 3% of one another, even in May 1980. Such conditions suggested near steady-state transport of DPOC down the axis of the estuary, although slight trends of increasing transport were observed in May, September and November. In July, there was a striking (39%) increase in detrital transport between the Mid-Estuary Region and the Cathlamet Bay Region which corresponded to a decrease in PPOC transport between these regions (Table 10). In February 1981, the detrital transport first increased slightly from the Fluvial Region to the Cathlamet Bay Region, then decreased over 15% in the Mid-Estuary Region. February is a month of generally high river flow (JAY, GIESE and SHERWOOD, 1990), and latter February 1981 was a time of particularly high discharge (up to 13,000m^3s^{-1}) (JAY and SMITH, 1990). High freshwater flow keeps the saltwater intrusion seaward, largely out of the Mid-Estuary Region (HAMILTON, 1990). This in turn likely retards vertical mixing to a large extent in mid-estuary, such that detrital particles (as well as phytoplankton cells) mostly settle out of the water column, and resuspension is minimal. An increase in resuspended detritus and a decrease in particle settling from surface waters, leading to increased detrital transport, might have occurred in the lower portion of the Mid-Estuary Region and in the Entrance Region in February 1981 because the mixing zone had been translocated to this area; however, we have no data in this area to verify this.

TABLE 13. Daily transport rates (mt C d^{-1}) of suspended detrital carbon (DPOC) through regions of the Columbia River Estuary for each sampling month

Month	Transport Rates (mt C d^{-1}) Fluvial	Cathlamet Bay	Mid-Estuary
April 1980	502.4	520.6	516.1
May	4,419.9	4,574.3	4,593.5
July	349.4	354.6	492.2
September	256.1	262.4	286.1
November	458.6	463.8	481.1
February 1981	440.3	468.4	405.1
Estimated annual export through the Mid-Estuary Region to the Entrance Region (without May)		159,185 mt C y^{-1}	
Estimated annual export through the Mid-Estuary Region to the Entrance Region (including May)		341,910 mt C y^{-1}	

3.7 Annual Dynamics of Particulate Carbon

The equation describing the annual phytoplanktonic carbon dynamics in the Columbia River Estuary is:

$$I_p + P_p - G_p - D_p - E_p = 0$$

where I_p = phytoplanktonic carbon imported to the study area, principally from upriver; P_p = phytoplanktonic net 24-hour carbon production in the study area; G_p = phytoplanktonic carbon removed by grazing in the study area; D_p = phytoplanktonic carbon converted to particulate and/or dissolved detrital carbon in the study area; and E_p = phytoplanktonic carbon exported from the study area. The dynamics can be depicted, and the terms evaluated, as in Fig.11a. The import term Ip (61,440mt C y^{-1}) excluded the May 1980 data. Phytoplanktonic production in the estuary (P_p) was 17,667mt C y^{-1} (Table 8), and export to the ocean (E_p) was 40,560mt C y^{-1} (Table 10). Grazing loss (G_p) was estimated at 2,342mt C y^{-1} (SIMENSTAD, SMALL and MCINTIRE, 1990). The unaccounted balance (D_p) of 36,205mt C y^{-1}, assumed to be planktonic carbon converted either to DPOC or to DOC in the study area, was almost as much as the annual amount exported to the ocean. It is instructive to note that, when recalculation was done to estimate export into the Entrance Region rather than into the adjacent ocean, D_p was 35,335mt C y^{-1}; thus, very little conversion of phytoplankton carbon to detrital carbon apparently took place in the Entrance Region on an annual basis. Most of the conversion presumably had already taken place upstream, a substantial part occurring directly at the freshwater-brackishwater interface, but some occurring via the production of fecal matter by zooplankton grazing on phytoplankton.

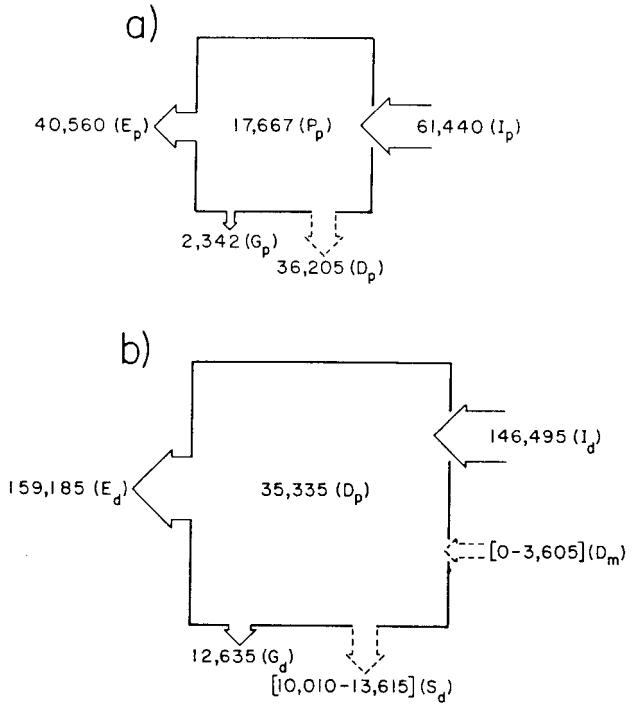

FIG.11. (a) Import of phytoplankton carbon to the estuary (I_p), phytoplankton carbon production in the estuary (P_p), export of phytoplankton carbon to the ocean (E_p), phytoplankton carbon lost to grazing in the estuary (G_p), and phytoplankton carbon converted to particulate detrital and/or dissolved organic carbon in the estuary (D_p), all as metric tons C y^{-1}. (b) Import of detrital particulate organic carbon (DPOC) to the estuary from the Columbia River (I_d), import of DPOC to the estuary from the adjacent marshes (D_m), conversion of phytoplankton carbon to DPOC and/or dissolved organic carbon in the estuary (D_p), export of DPOC to the Entrance Region (E_d), DPOC lost to grazing in the estuary (G_d), and DPOC sinking to the estuary bottom and/or converted to dissolved organic carbon (S_d), all as metric tons C y^{-1}. Note that export of DPOC is to the Entrance Region only, while export of phytoplankton carbon is to the ocean.

The equation describing the annual dynamics of detrital particulate organic carbon in the estuary is:

$$I_d + D_p + D_m - S_d - G_d - E_d = 0$$

where I_d = suspended detrital organic carbon imported from upriver; D_p = conversion to DPOC and/or DOC from phytoplankton carbon in the study area; D_m = conversion from marsh plant litter in the study area; S_d = net settling of detrital carbon onto the estuary bottom in the study area; G_d = suspended detrital carbon removed by grazing in the study area; and E_d = suspended detrital carbon exported from the study area.

The annual detrital particulate organic carbon dynamics in our study area is shown in Fig.11b. The annual transport of suspended detrital carbon into the Fluvial Region (I_d), was 146,495mg C y^{-1}, exclusive of the May 1980 data. D_p was 35,335mt C y^{-1} to the Entrance Region (as given earlier), but this was composed of both DPOC and DOC in unknown fractions. D_m was 3,605mt C y^{-1} if all marsh litter escaping the litter bags was particulate (D_m would be zero if organic carbon left the litter bags as DOC only). G_d was estimated at 12,635mt C y^{-1} (SIMENSTAD, SMALL and MCINTIRE, 1990), and detrital export into the Entrance Region (E_d) was 159,185mt C y^{-1} (Table 13).

DAHM, GREGORY and PARK (1981) estimated that the average annual contribution of total organic carbon (TOC) from the Columbia system to the northeastern Pacific Ocean was 4.9 x 10^{10}mol y^{-1}, with 89% of this export as DOC and 11% as POC (equivalent to our TPOC). The POC export converts to about 64.7 x 10^3mt y^{-1}, which was about a third of our TPOC estimate (DPOC + PPOC) of 199.7 x 10^3mt y^{-1} (Fig.11b). POC concentrations determined by DAHM, GREGORY and PARK (1981) averaged about 360mg m^{-3} throughout the estuary on 1 June 1974, about half the average concentrations we measured in April and July, 1980 (SIMENSTAD, JAY, MCINTIRE, NEHLSEN, SHERWOOD and SMALL, 1984). Furthermore, our fall and winter measurements in the estuary were higher than those recorded by DAHM, GREGORY and PARK (1981) at a station 128km upriver from the estuary mouth (they had no fall or winter estimates in the estuary proper). The different estimates of POC export to the ocean thus mainly reflected the different POC loads measured in different years. The volcanic eruption in May 1980 may have been the major cause of the difference. Even without considering the May 1980 concentrations, DPOC concentrations after the eruption were high, particularly in September and November 1980. Winter freshets could have resuspended abnormally large amounts of detrital carbon originally deposited as a result of the volcanic scouring in May. Flows in summer and fall are usually the lowest of the annual cycle (SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD, 1990), but July 1980 concentrations of DPOC were as high as those in April 1980 (before the eruption). April is in the high-flow season (SIMENSTAD, SMALL, MCINTIRE, JAY and SHERWOOD, 1990). Even the April 1980 concentrations, however (Table 11), were somewhat higher than the April 1974 POC concentrations at stations 128 and 230km upriver from the estuary mouth (DAHM, GREGORY and PARK, 1981); thus, real increase in the POC load between 1974 and 1980 cannot be discounted.

If we use 4.9 x 10^{10}mol y^{-1} as the best historical estimate of total organic carbon exiting the estuary (DAHM, GREGORY and PARK, 1981), this is equivalent to 588 x 10^3mt y^{-1}. Our estimate of TPOC export (199.7 x 10^3mt y^{-1}) was thus 34% of historical TOC export, in contrast to 11% of TOC export reported by DAHM, GREGORY and PARK (1981). By difference, DOC export in 1980 was 66% of historical TOC export, as opposed to 89% in 1974.

We had no direct measure of detrital settling (Sd) in our DPOC budget (Fig.11b), but if we solve for S_d in the detrital equation with the assumption that D_p was all in terms of DPOC, estimates of 10,010 to 13,615mt C y^{-1} are obtained, depending upon whether detrital input from

the marsh was considered to be in completely dissolved form or in particulate form. Either way, detrital carbon retained throughout the length of the study area was about 6 to 9% of the amount exported annually into the Entrance Region. However, some percentage of D_p might actually have been converted to dissolved organic carbon. If in fact about 35% of D_p was DOC, the net retention of detrital particulate carbon would be zero; thus, net retention of detrital carbon might range from zero to 9% of the amount transported annually into the Entrance Region. At present, we are unable to make a more precise estimate. The point remains, however, that import of DPOC into the study area, and transport of this allochthonous DPOC through the system, was far more significant than either production or settling of DPOC within the estuary itself. Thus, the physically dynamic Columbia River Estuary acts principally as a conduit for the transport of particles to the sea, and only secondarily as a converter of viable phytoplankton cells to detrital carbon and a trap for DPOC.

4. SUMMARY AND CONCLUSIONS

1. Floristic and biomass patterns of phytoplankton and distributions of detrital particulate organic carbon (DPOC) indicated that freshwater species decreased markedly on encountering salinities of 1 to 5 in the mixing zone of the Columbia River estuary. Phytoplankton carbon likely was converted to DPOC at the freshwater-brackishwater interface in the area of Tongue Point. Living phytoplankton seaward of Tongue Point were marine or brackishwater species.

2. An index of similarity showed that the benthic diatom assemblages from Cathlamet Bay, Grays Bay and the Fluvial Region of the estuary were similar freshwater assemblages. Diatoms in Youngs Bay were fairly similar to those from the freshwater regions because most of the river flow passes close to the mouth of Youngs Bay and because two tributary rivers empty into Youngs Bay. Benthic algae from Baker Bay, near the ocean and cut off from most freshwater outflow, were typical brackishwater species.

3. Cluster analysis of the emergent vascular vegetation showed that a six-cluster structure was the most interpretable pattern in the species data matrix. The clusters were separated generally by the different relative abundances of brackishwater, euryhaline, or freshwater species, and on whether samples were from high or low marsh areas.

4. Seasonal biomass and productivity patterns were evident for the phytoplankton and emergent vascular plants, with increases in spring and summer, decreases in fall and winter. Emergent plants showed the most dramatic seasonal change, with almost complete die-back of the summer's production in the fall/winter. Benthic algal biomass showed no measurable seasonal change, although benthic algal productivity was substantially greater in summer than in winter.

5. Annual rates of net areal 24 hour production averaged approximately 55, 16, and 403g C $m^{-2}y^{-1}$ for phytoplankton, benthic algae, and emergent vascular plants, respectively. Total production over the whole estuary, however, was approximately 17,667metric tons C y^{-1} for phytoplankton, 1,545mt C y^{-1} for benthic algae, and 11,325mt C y^{-1} for emergent vascular plants, for a total production estimate of 30,537mt C y^{-1}.

6. Phytoplankton biomass turned over approximately 30 times per year through all regions of the estuary except Youngs Bay, where turnover was 84 times per year. Benthic algal biomass turned over slightly more than twice per year on average, while the emergent vascular vegetation was assumed to turn over once per year.

7. Import of phytoplanktonic carbon (PPOC) to the estuary from upriver was 61,440mt C y^{-1}, which when added to the annual *in situ* production yielded 79,107mt C y^{-1} of PPOC accumulating in the estuary. Mean grazing loss was 2,342mt C y^{-1} and export to the ocean was

40,560mt C y^{-1}. Assuming steady state on an annual basis, 36,205mt C y^{-1} were unaccounted for. It was suggested that most of this was PPOC converted throughout the year to detrital particulate organic carbon (DPOC), principally at the freshwater-brackishwater interface in the estuary.

8. Analysis of DPOC dynamics in the estuary suggested that between 10,010 and 13,615mt DPOC y^{-1} were either retained within the estuary or were converted to dissolved organic carbon during transit from the Fluvial to the Entrance Region in the estuary. A maximum of 150,100mt C y^{-1} were estimated to enter the estuary as particles from upriver and off the marshes, 35,335mt y^{-1} were converted from PPOC to DPOC during transit to the Entrance Region, 12,635mt y^{-1} were consumed by zooplankton, and 159,185mt y^{-1} were transported into the Entrance Region from the upper reaches of the estuary. Combined DPOC and PPOC export from the estuary in 1980 was higher than that calculated in 1974 (DAHM, GREGORY and PARK, 1981), and this increase may have resulted from the Mt. Saint Helens volcanic eruption in May 1980.

9. The Columbia River estuary acts principally as a conduit for the transport of particles to the sea, and only secondarily as a converter of viable phytoplankton cells to detrital carbon and as a trap for DPOC.

5. ACKNOWLEDGEMENTS

These studies were supported by a grant from the Pacific Northwest River Basins Commission and U.S. Water Resources Council, administered through the Columbia River Estuary Data Development Program (CREDDP) and Columbia River Estuary Study Taskforce (CREST). Discussions with our colleagues in this program, particularly C. Simenstad, D. Jay, C. Sherwood, W. Nehlsen, J. Damron and D. Fox, were invaluable, and their help is gratefully acknowledged.

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Prog. Oceanog. Vol. 25, pp. 211-241
Printed in Great Britain.

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KIM K. JO

[1]*Oregon Department*

[2]*Fisheries Research*

[3]*College of Oceanogr*
Oregon Department

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