The Dynamics of Phytoplankton Blooms in Puget Sound, a Fjord in the Northwestern United States*

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Abstract

This paper describes a quantitative investigation of relationships between the growth of phytoplankton, and climatic and hydrodynamic conditions in temperate fjords with marked tides, as exemplified by Puget Sound, Washington (USA). Algal growth in the open waters of the central basin of the Sound is dominated by a number of intense blooms beginning in late April or May and recurring throughout the summer. Rarely, and only briefly, does nitrate become exhausted. The phytoplankton production rate in the central basin of Puget Sound is about 465 g C m^{-2} year^{-1}. During the springs of 1966 and 1967, oceanographic measurements were carried out at a mid-channel station with sufficient frequency to allow investigation of physical and biological processes with time scales of the order of a day. The principal investigative tool is a numerical model in which the hydrodynamical conditions are represented by an approximate analysis of the gravitational convection mode of circulation. Algal concentration is represented as a continuous function of space and time in the model which ascribes changes in phytoplankton density to variations in photosynthetic and respiratory activity, algal sinking, grazing by herbivores, and to mixing and advection. Computations adequately reproduce the principal features of phytoplankton concentrations observed during 75 days and 35 days in the springs of 1966 and 1967, respectively. Numerical experiments assess the relative importance of various processes which govern the level of primary production in Puget Sound. It is concluded that phytoplankton growth is limited by a combination of factors, including vertical advection and turbulence, modulation of underwater light intensity by self-shading and inorganic particulates, sinking of algal cells, and occasional rapid horizontal advection of the population from the area by sustained winds. The high primary productivity of the Sound is due to intensive upward transport of nitrate by the estuarine mechanism. These results should be generally applicable to other temperate fjords because of the largely conventional choice of the biological functions.

Introduction

Density-driven circulation in a fjord is characterized by a near-surface brackish-water zone of several meters thickness flowing seaward over a deeper, landward-moving zone of salt water from the sea. Observations of primary production in fjords suggest that phytoplankton growth is closely coupled to circulation as well as to the physical and chemical properties of the water. Under conditions of moderate stability, when insolation is adequate and the brackish zone of the fjord is not excessively turbid, algae may grow with sufficient vigor to exhaust the surface zone temporarily of plant nutrients. However, turbulent entrainment of nutrient-rich oceanic water from depth will tend to replenish the supply of these ions. On the other hand, cells growing near the surface are only temporary residents of the brackish zone inasmuch as they are advected persistently seaward, on the average. At the same time, the estuarine mechanism will resupply the near-surface zone with viable cells from depth. Some fraction of this "seed stock" may originate external to the inlet, entering the fjord with the intrusion of oceanic water at the mouth; the remaining fraction may consist of cells formerly growing in the surface zone, which have sunk or were mixed to depth in the vicinity of a sill and were subsequently carried landward with intruding saline water.

The principal objective of this paper is to examine quantitatively the relationship between the circulation and other environmental factors and primary production in fjords which characterize coastlines of the formerly glaciated regions in temperate and subpolar zones of both hemispheres. We use the central basin of Puget Sound in the state of Washington as an example. Puget Sound is a complex system of interconnected fjords and channels which constitutes the southern terminus of a more extensive inlet system along the northeastern Pacific coastline from Washington northward to Alaska. The Sound as a whole com-
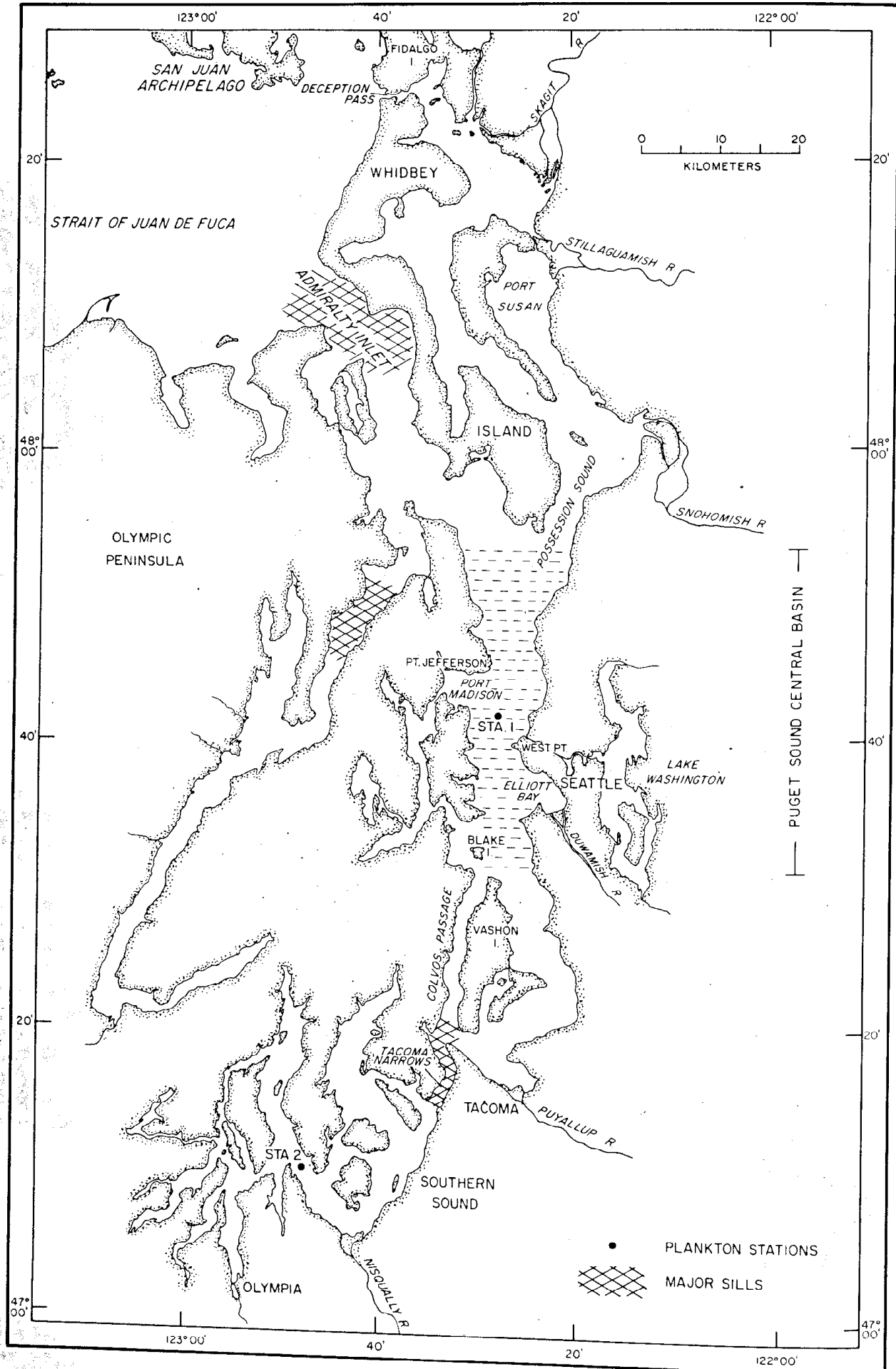

Fig. 1. Map of Puget Sound

municates with the Pacific Ocean by way of the Strait of Juan de Fuca to the north (Fig. 1). The principal entrance to the Sound is through Admiralty Inlet. The intensity of the incursion of oceanic water through the channel at Admiralty Inlet is determined partly by tidal characteristics and partly by the rate of fresh-water runoff from drainage areas contiguous to the Sound.

Throughout all seasons of the year, the principal basins of Puget Sound exhibit some degree of stratification. The density structure is primarily associated with salinity differences between near-surface zones of brackish water and deeper zones of more saline oceanic water.

The tides in Puget Sound are of the mixed type, with a progressive increase in range from Admiralty Inlet to the inner regions. In the vicinity of Seattle, the mean and diurnal tidal ranges are 2.5 and 3.5 m, respectively. In the neighborhood of the sills at Admiralty Inlet, the Tacoma Narrows, and at Deception Pass, strong turbulence and high tidal currents (up to 5 knots) are the rule. Elsewhere, throughout the open water of the Sound, tidal current speeds are usually less than 1 knot.

Nontidal currents in Puget Sound are induced by wind stress, river discharge, and gravitational convection. The circulation pattern induced by runoff usually results in a net seaward outflow of brackish surface water and a net inflow of denser, more saline water at depth. The greatest amounts of freshwater are supplied to the Sound by rivers along the northeastern shore. During the spring and early summer, runoff into the central basin is derived largely from melting snow in the surrounding mountains rather than local rainfall.

Phytoplankton is found in appreciable concentrations (usually > 0.2 mg chlorophyll a/m^3, even at depth) in nearly all parts of Puget Sound throughout the year, but the algae proliferate during the spring and summer months. Field studies of phytoplankton production have been performed in a few locations in Puget Sound and the San Juan Archipelago (Phifer, 1933; Barlow, 1958; Larrance, 1964) and in British Columbia waters to the north (LeBrasseur, 1954; McAllister, 1956; Gilmartin, 1964; Parsons *et al.*, 1969b; Takahashi *et al.*, 1973). However, the present investigation is based largely upon hydrographic and biological data acquired during a Puget Sound field study initiated in 1963 by G.C. Anderson and K. Banse (unpublished). The field work was motivated partly by the fact that, in the early 1960's, the municipality of metropolitan Seattle (METRO) began the construction of a central sewage treatment plant with a large outfall at West Point on the eastern shore of the central basin (Fig. 1). The observational program was undertaken to establish baseline conditions of environmental and biological variables, as well as to investigate processes of primary production in Puget Sound.

Measurements were taken at two stations, one near midchannel in the central basin off Seattle,

the other located in the southern part of the Sound (Fig. 1). From September, 1963 through December, 1965, the stations were visited approximately biweekly to observe insolation, standard physical and chemical water properties, and concentrations of chlorophyll a and zooplankton. Half-day measurements (local apparent noon to sunset) were also made of the rate of carbon uptake by phytoplankton in water samples drawn from several depths. The carbon uptake rates above the 1% light depth at the northern station, in the central basin, were 460 and 470 g C m^{-2} year^{-1} in 1964 and 1965, respectively, which is extraordinarily high for an unpolluted temperate site. For the same years, the uptake rates in the southern Sound, at Station 2, were 270 and 280 g C m^{-2} year^{-1}, respectively.

The data indicate that primary production at the southern station was fairly uniform from March through September. In contrast, the observations at the northern station showed that the annual cycle of phytoplankton growth was dominated by a number of intense blooms between early May and September. The onset of the blooms was exceptionally late for the latitude of 48° N. Moreover, the algal concentrations were changing drastically within time periods shorter than the sampling interval. Therefore, during some of the spring months of 1966 and 1967, the same parameters were studied on an almost daily basis at the northern station.

The collections were supplemented with experiments designed to elucidate specific details of the primary production process in Puget Sound: Hirota (1967) measured algal production and generation times of individual phytoplankton species in floating plastic columns of 1.1 m diameter and 17 m length, which were deployed at the northern station. The development of phytoplankton was thus studied without the complications which are introduced by advection. During the cruise sequence in May, 1967, Booth (1969) recorded changes in the species distribution of phytoplankton at the northern station. Finally, during a three-vessel survey in May, 1969, the horizontal distribution of surface chlorophyll was mapped throughout the central basin during blooms for a period of 13 days (Munson, 1970).

Those observations acquired during the springtime cruises in 1966 and 1967 which are relevant to our inquiry are described in the next section. The third section elaborates on the hydrography of the central basin segment and summarizes an analysis of gravitational convection circulation in the main channel during the periods of observation. The fourth section presents a numerical model of phytoplankton production which utilizes the circulation analysis and quantitative descriptions of other environmental variables. Results of simulations with the numerical model are given in the fifth section. The paper closes with conclusions regarding the relationship between environmental conditions, including circulation, and primary production in Puget Sound. Recommendations are also made of the critical
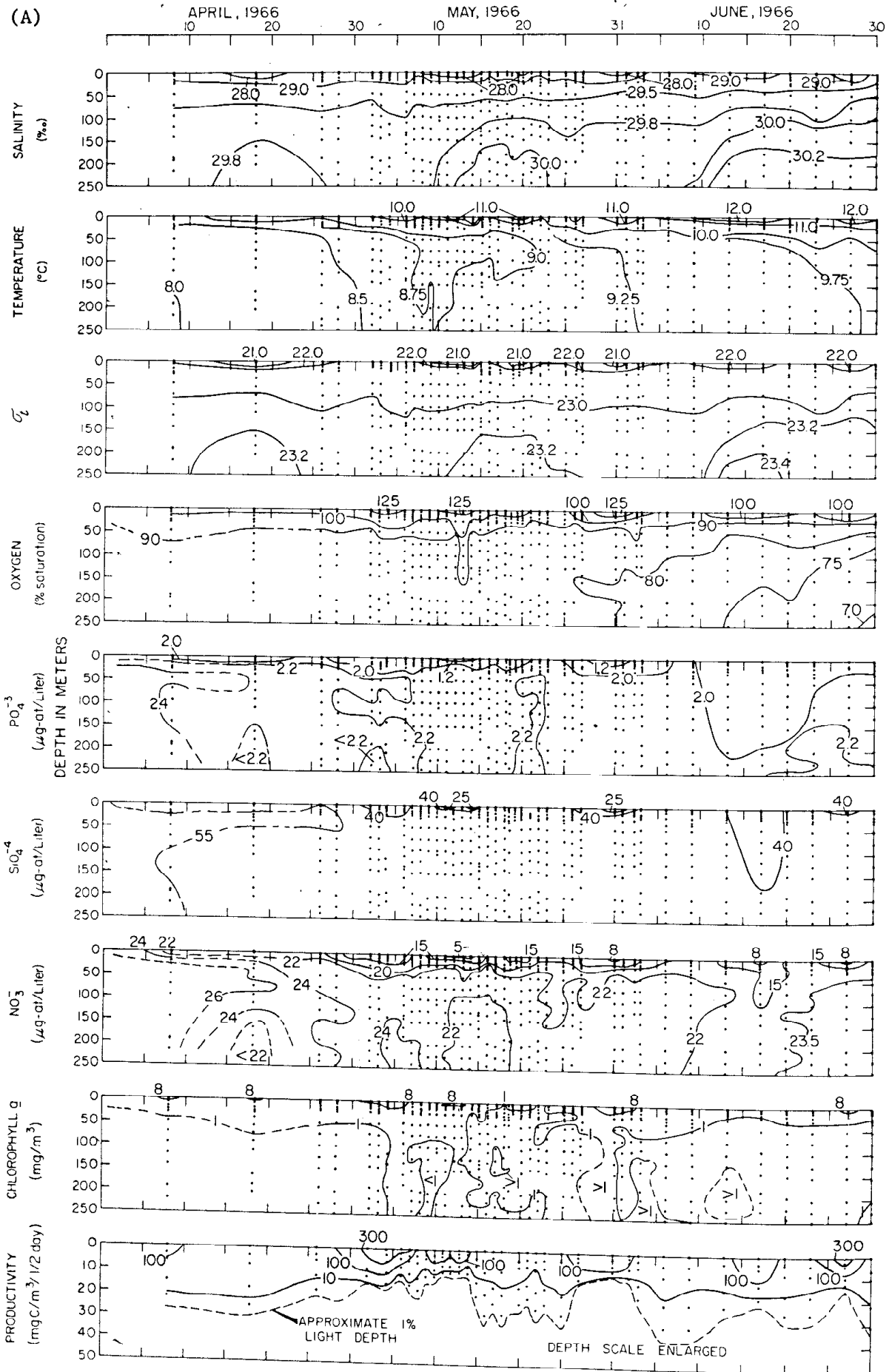
Fig. 2. Variations of salinity, temperature, density, oxygen saturation, phosphate, silicate, nitrate, chlorophyll *a*, and carbon uptake rate at Station 1. Dots indicate sampling depths. (A) April to June, 1966
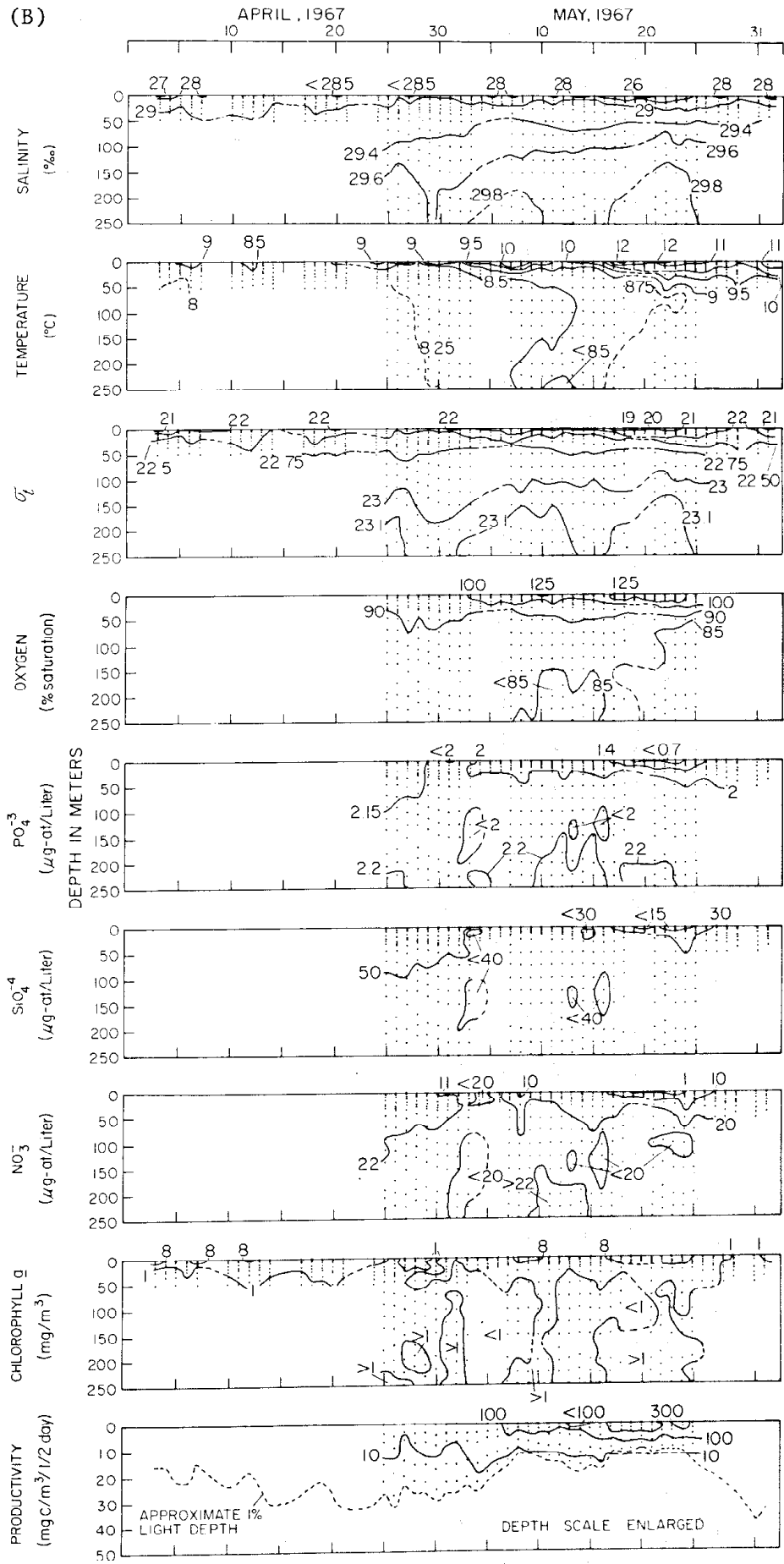
Fig. 2. (B) April and May, 1967

variables to be examined in subsequent under-
takings in the Sound or in other deep, stratified
fjords.

Materials and Methods

Study Site

The central basin of Puget Sound is essentially
an elongated fjord whose bottom topography slopes
steeply to a depth of more than 200 m. Although
the width varies somewhat due to occasional
embayments, the basin is about 6 to 8 km wide,
on the average, and is characterized by a length-
to-width ratio of the order of 10 to 1. A 54 m
sill at the Tacoma Narrows at the southern end
separates the central basin from a system of
shallower basins and inlets. The northerly sill
at Admiralty Inlet is about 20 km long and 72 m
deep, and separates the central basin from the
Strait of Juan de Fuca which is connected with
both the Strait of Georgia and the northeast
Pacific Ocean. The central basin sampling station
(hereafter referred to as Station 1) is located
near mid-channel over a depression of 275 m depth,
near latitude 47°41.0'N; longitude 122°27.7'W
(Fig. 1). The distance from Station 1 to each
of the aforementioned sills is about 50 km. The
location of Station 1 was chosen as representative
of the main channel of the central basin on the
basis of experience with a hydraulic model of
Puget Sound in the Department of Oceanography at
the University of Washington (Rattray and Lincoln,
1955; Farmer and Rattray, 1963). Also, the loca-
tion was considered appropriate for biological
studies since relatively frequent measurements
of phosphate concentrations taken near or at the
station since the mid-1930's did not indicate any
long-term trend suggestive of pollution.

Methods and Data Summary

Prior to local apparent noon, samples were taken
just below the surface (100% light depth) and
from the 50, 25, 10 and 2% light depths with 6-1
non-toxic plastic bottles equipped with reversing
thermometers. Below the 2% light depth, collec-
tions were made at standard depths: 50, 75, 100,
125, 150, 200, 225 and 250 m. When the 2% light
depth was less than 20 m, samples were also
acquired at 25 m. The light depths were estimated
by assuming an exponential decrease in light
intensity with depth. The extinction coefficient
k_e was calculated from the standard expression
$k_e = 1.7/D$, where D is the maximum depth of visi-
bility of a 30-cm diameter Secchi disk.

The salinity of each water sample was deter-
mined from a conductivity measurement (Paquette,
1958). The temperature at each depth was calcu-
lated by averaging two protected thermometer
readings to which the standard expansion and in-
dex corrections had been applied. Dissolved oxy-
gen was measured by the modified Winkler method

(Thompson and Robinson, 1939); saturation values
were calculated from the tables of Truesdale and
Gameson (1957). Water samples for nutrient anal-
ysis were frozen. In the laboratory, phosphate
concentration was determined by the method of
Murphy and Riley (1962), and silicate was anal-
yzed by the method of Mullin and Riley (1955a),
with the modification that sodium silicofluoride
was used as a standard. Prior to 1967, nitrate
concentrations were found by the method of Mullin
and Riley (1955b); subsequently, the method of
Wood *et al.* (1967) was used. After addition of
powdered $MgCO_3$ on an HA Millipore filter (0.45-μm
pore size), the chlorophyll samples were filtered
on shipboard and were subsequently desiccated
and frozen. For the most part, the analysis fol-
lowed the procedure of Strickland and Parsons
(1965). The concentrations were computed from
the equations given by the SCOR-Unesco Working
Group 17 (1966). A correction for pigment degra-
dation products was not applied.

Photosynthetic carbon uptake rates were deter-
mined at each of the 5 depths above the 1% light
depth using subsamples of water enclosed in 1 dark
and 2 clear Pyrex reagent bottles of 125 ml volume
each. To each bottle was added approximately
1.5 μCi^{14}C in a 0.5 ml solution of Na_2CO_3. The
ampoules containing the tracer were prepared from
$Ba^{14}CO_3$ (Steemann Nielsen, 1952), and absolute
activity determined by gas phase techniques (Gold-
man, 1963). The samples were incubated from local
apparent noon to sunset in a shallow water-filled
tray covered with 0.5-cm thick plate glass and
located on the roof of the deck house. The prin-
cipal method for maintaining the water bath at
ambient surface sea-water temperature was re-
circulation through a cooling apparatus. Wire
screens (McAllister and Strickland, 1961) were
used to simulate the light intensities at the
depths from which the water samples had been taken.
At the end of the incubation period (sunset), the
content of each bottle was filtered over an HA
Millipore filter (0.45-μm pore size); the filters
were stored in plastic trays over silica gel. The
radioactivity of the filters was measured with a
gas-flow counter with micromil window, after
exposing them to fuming HCl and an additional
period of desiccation. The results were corrected
for background activity, variations in inorganic
carbon content of seawater (from salinity), coin-
cidence loss, isotope effect (5%), and dark uptake.

The measurements made with these methods during
the springs of 1966 and 1967 are summarized in
Fig. 2. The choice of contour intervals is based
on confidence limits for single observations.
These are derived from numerous pairs of samples
taken during 1964 at 4 depths at Station 1 and an
auxiliary station 1 mile to the south which was
occupied a few hours later. The confidence inter-
vals for carbon uptake, however, are derived from
the duplicate light bottles on Station 1.

Incident radiation was measured from noon to
sunset with a portable Belfort Solarimeter mounted
beside the incubator. The measured values were
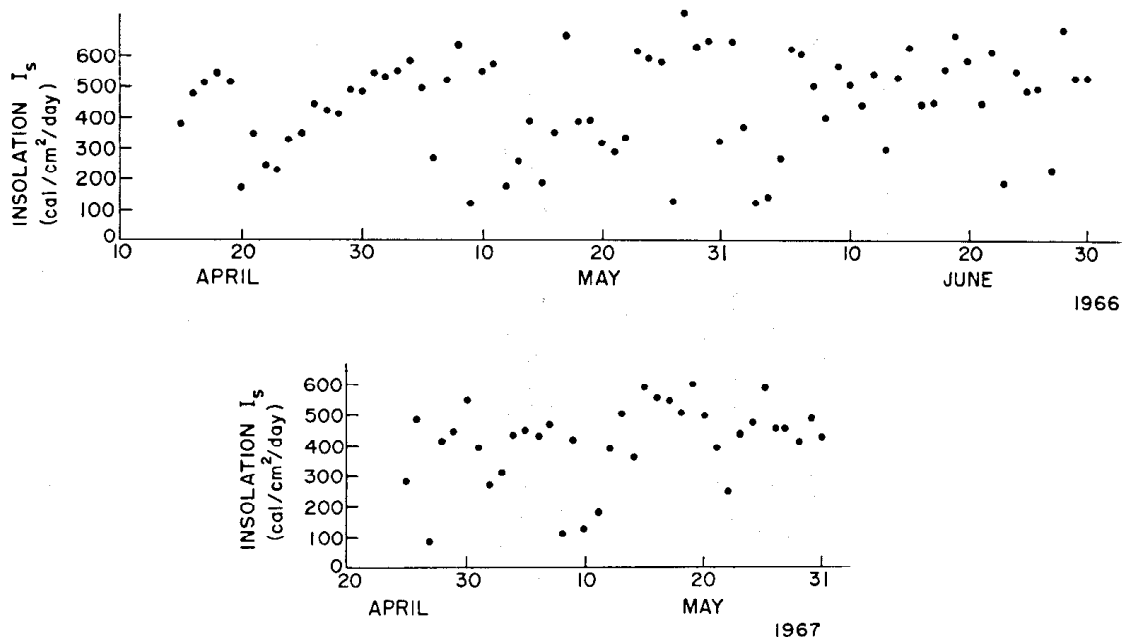doubled to obtain approximate whole-day values

Fig. 3. Daily values of insolation at Station 1, April to June, 1966, and April and May, 1967

of I_s, the above-surface radiative flux. For those days when no cruises were conducted, values of I_s are available from daily insolation measurements at Seattle-Tacoma airport (47°27'N; 122°18'W). During the springtime of 1966, the shipboard measurements were consistently lower than the airport readings by factors of 0.84 and 0.97 on days of good and inclement weather, respectively. Therefore, the integrated radiation intensities used for each day during the 1966 study period were the daily airport values, corrected by the appropriate "weather factors" above. No correction factor was found to be necessary for 1967. Fig. 3 shows inferred daily values of I_s for the study periods of both years.

Finally, zooplankton was collected in the late morning hours or the early afternoon by vertical tows with a 215-μm mesh closing-net of 0.75 m diameter. Hauls were made from near the bottom (from 200 to 250 m) to the 1% light depth, and from there to the surface. Also, during 1966, 4 collections were made above the 1% light depth after sunset. A filtration efficiency of the net of 90% was assumed. The dry weights determined on formalin-preserved subsamples were corrected for the ever-present contamination from phytoplankton by subtracting twice the ash content found upon ignition of the samples. This procedure assumes that all phytoplankton collected were diatoms with an ash content of 50%. The ash content of zooplankton was neglected because sorted material acquired locally, preserved in the same manner as our samples, contained only about 2% ash (M. Jawed, personal communication), which is a small fraction of the total. The calculated dry weight of zooplankton was considered to be close to the ash-free dry weight. The carbon content of the zooplankton was taken to be one-half of the ash-free dry weight.

Aliquots of the 1966 samples from the surface layer were also microscopically counted. Dry weights of the animals were calculated from length measurements and various formulae (largely based on the data of Conover, 1959, and Robertson, 1968). The concentration of herbivores was then estimated on the basis of species identification. Because Robertson's raw data for copepods were obtained from freshly dried material, the herbivore concentrations used herein are largely unaffected by the loss of organic matter after preservation (e.g. Lasker, 1966), in contrast to the ash-free dry weights found chemically. A regression of concentration of herbivores from daytime samples on chemically-determined zooplankton for 1966 was applied to the chemical data for 1967; the regression did not include samples where brachyuran larvae contributed more than 25% of the microscopically estimated mass. The results are shown in Fig. 4. The calculated concentration may be too high an estimate of herbivores on those dates for which total zooplankton is low, and too low an estimate for dates with high zooplankton concentration. Finally, concentrations of copepod nauplii and ciliates were determined from a few water samples collected for phytoplankton enumeration, and were converted into mass to estimate the total zooplankton present.

Results

To emphasize certain features of the field data exhibited in Fig. 2, the amounts of chlorophyll a and primary production above the 1% light depth have been plotted together with the daily variation in tidal amplitude and the degree of stratification in the upper layer as measured by the density difference $\Delta\sigma_t$ between the surface and
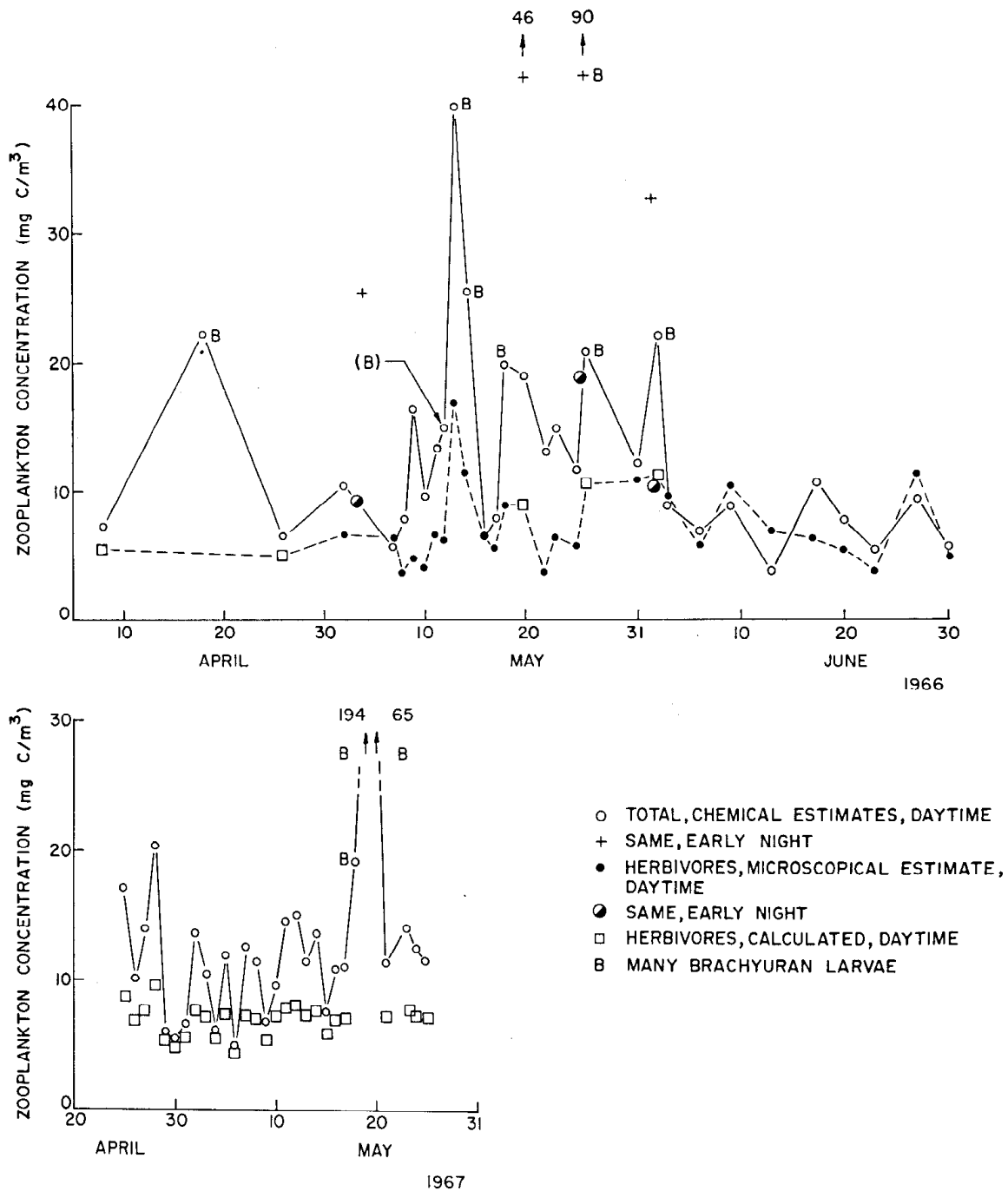
Fig. 4. Average concentration of total and herbivorous zooplankton above 1% light depth in 1966 and 1967. Numbers associated with arrows indicate data off scale

25 m (Fig. 5). Also, graphs of salinity, tempera-
ture, oxygen and nitrate just below the surface
and at the 10% light depth are shown in Fig. 6
as functions of time. The 10% light depth was
chosen because the rate of photosynthesis is
especially sensitive to the physical and chemical
parameters above this depth.

Salinity, Temperature, and Density

It can be seen from Figs. 5 and 6 that the salin-
ity of the near-surface zone at Station 1 under-
goes rather large excursions in time. These

variations are largely associated with changes
in the hydrographs of rivers to the south (up-
stream) of the station, although some are pro-
duced by wind effects. During high runoff, it is
not uncommon for shallow lenses of relatively
freshwater to appear locally off the major river
mouths. Under the right circumstances, these
lenses can retain a degree of identity for some
days while moving seaward in the surface layer,
until they are finally eroded by increasing tur-
bulence in the vicinity of the northern sill at
Admiralty Inlet. However, it is more usual for
freshwater from the rivers and land runoff to be
mixed by tidal effects and wind with saline water

from depth to form a brackish surface zone over the main channel. Within this zone, the isohaline surfaces have fairly gentle slopes in the along-inlet direction.

At depth, the salinity of the water which flows into Puget Sound from the Strait of Juan de Fuca is controlled by tidal mixing over the northern sill at Admiralty Inlet. During neap tides, the tidal velocity is the factor most closely related to mixing which, in turn, determines the density of intruding water at depth. However, tidal amplitude is the more relevant parameter at the time of spring tides, when the tidal excursion is of the same order as the length of the sill (about 20 km). These phenomena are reflected in the time history of salinity changes at depth near Station 1, with the lowest values appearing fortnightly about 2 days after the highest tidal amplitudes. The pattern is most apparent in the 1967 data in Fig. 2, but it is evident also in the data of 1966, particularly in the density observations. Apparently, greater quantities of fresher surface water are vertically mixed and refluxed into Puget Sound around the time of spring tides than around the neap tides, when the density-driven circulation is less drastically affected by turbulence.

The overall average salinity at depth shows a gradual increase with time in the springs of both 1966 and 1967. This trend reflects a seasonal increase associated with the usual rise in salinity at depth in the Strait of Juan de Fuca (see Herlinveaux and Tully, 1961). The salinity at intermediate depths also undergoes a gradual increase during the spring periods; the net increase is somewhat less than 0.5‰ at 50 m during both periods. However, a study of salinity changes at intermediate depth at Station 1 indicates that the salinity at 25 m very seldom decreases in phase with the large variations near the surface. Similarly, the salinity at 100 m only rarely decreases during the spring tides, thereby demonstrating a rather loose coupling of the intermediate layer with the deeper water and the mixing processes at the sill in Admiralty Inlet. Also, the temperature minima (Fig. 2) and the occasional higher concentrations of phosphate and nitrate in the intermediate layer suggest that the water at intermediate depth is not formed simply by mixing between the deep and the surface waters within the main channel.

The temperature of the surface layer fluctuates so markedly as nearly to obscure the overall seasonal increase. The highest temperatures are observed in water of low salinity, when highly stratified conditions are obtained and there is sufficient solar radiation for heating of the surface layer. During the springtime periods investigated here, temperatures above the 10% light depth varied over a range of 4.5C°, with the exception of one very short interval in each year.

The density distribution in space and time is determined primarily by the distribution of salt; the role of temperature is mainly to enhance the stability of the surface layer during warm weather. However, water at all depths throughout the central basin exhibits at least some degree of stratification. Changes in the degree of stratification as measured by the density differences over the upper 25 m are only partially correlated with variations in tidal amplitude (Fig. 5).

Dissolved Oxygen and Nutrient Salts

Concentrations of dissolved oxygen have been expressed in the figures as percentages of saturation at sea-level pressure. As a general rule, the water in the central basin of Puget Sound is undersaturated because of low oxygen concentrations in the source waters in the Strait of Juan de Fuca. As a result of offshore upwelling during late spring and early summer, declining concentrations of oxygen (well below 50%) and increasing concentrations of nutrient salts appear at depth in the Strait from about April onward (Herlinveaux and Tully, 1961). Mixing intensity at the Admiralty Inlet sill is sufficient to raise the oxygen concentration of intruding source water to levels exceeding 80% during most of the periods treated here (Fig. 2). Later in the summer, the saturation values in the water at depth in Puget Sound fall to about 60%. On occasions of intense algal blooms in stratified, relatively warm water (Fig. 5), the oxygen saturation level at the surface can exceed 150%, a value which is unusually high for a marine environment.
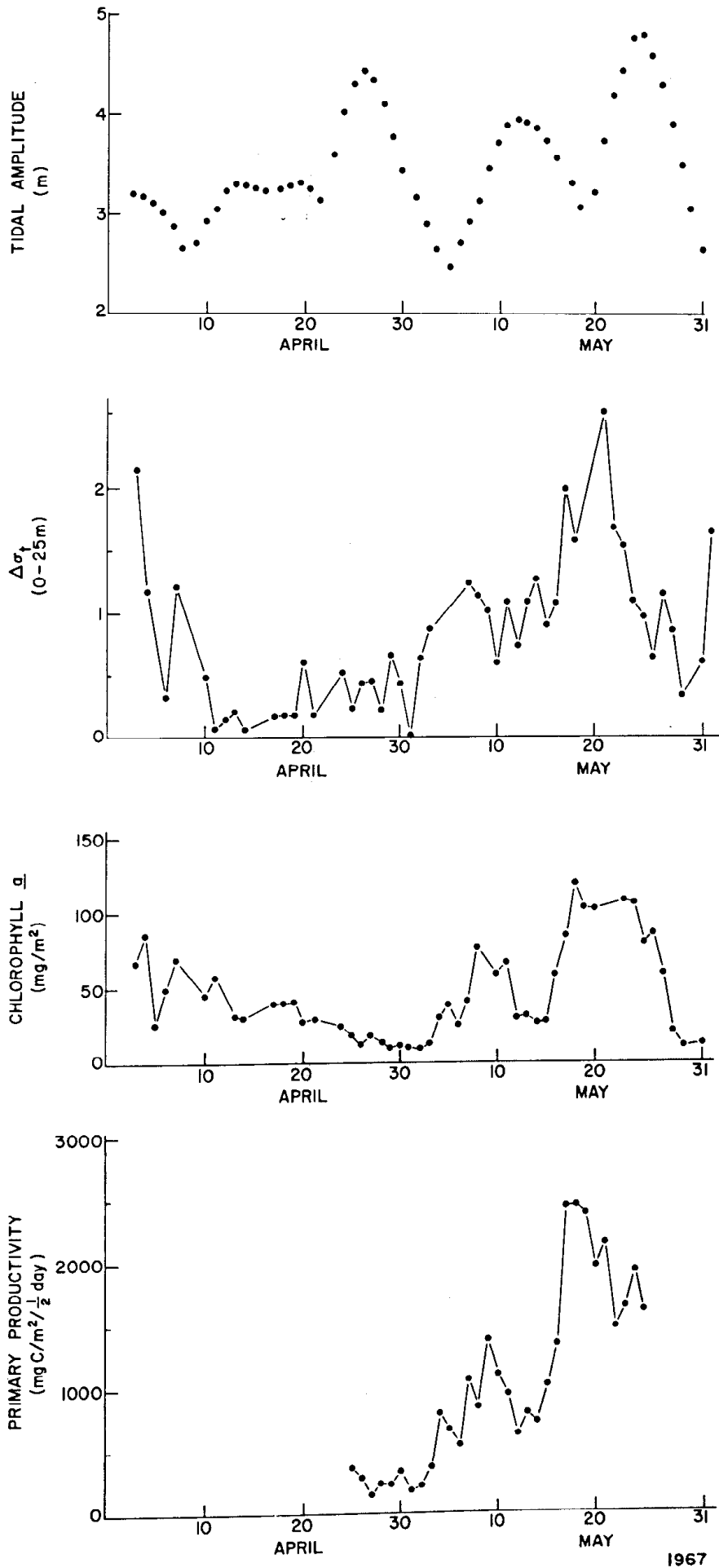
Of the nutrient salts which were measured, nitrate is likely to be most important in limiting phytoplankton growth. When algal blooms are not extant, the springtime surface concentration of nitrate may be as high as 15 to 20 µg-at/l. The somewhat higher concentrations near the beginning of the observation periods in 1966 and 1967 (Fig. 6) reflect the fact that, in the late wintertime, nitrate levels in excess of 25 µg-at/l prevail throughout the central basin. On the occasions of intense algal blooms, nitrate concentrations sometimes fall to nearly undetectable levels. At the same time, phosphate and silicate may decrease markedly, but the concentrations remain above levels known to be limiting to phytoplankton growth. Exhaustion of nitrate was not observed to persist for more than about 36 h in 1966 or 48 h in 1967. Munson (1970), however, recorded nitrate depletion at the 100 and 50% light depths at Station 1 for periods up to approximately 72 h during an algal bloom in May, 1969. After that interval of time, a drastic decline in the specific rate of photosynthesis was observed.

We have no information on the concentrations of ammonium ion. It is unlikely, however, that the levels would have been high enough to support vigorous photosynthesis during episodes of nitrate depletion, since ammonium is taken up preferentially over nitrate (e.g. MacIsaac and Dugdale, 1969) and should have been exhausted first. Also, our data on net-collected zooplankton can be used,
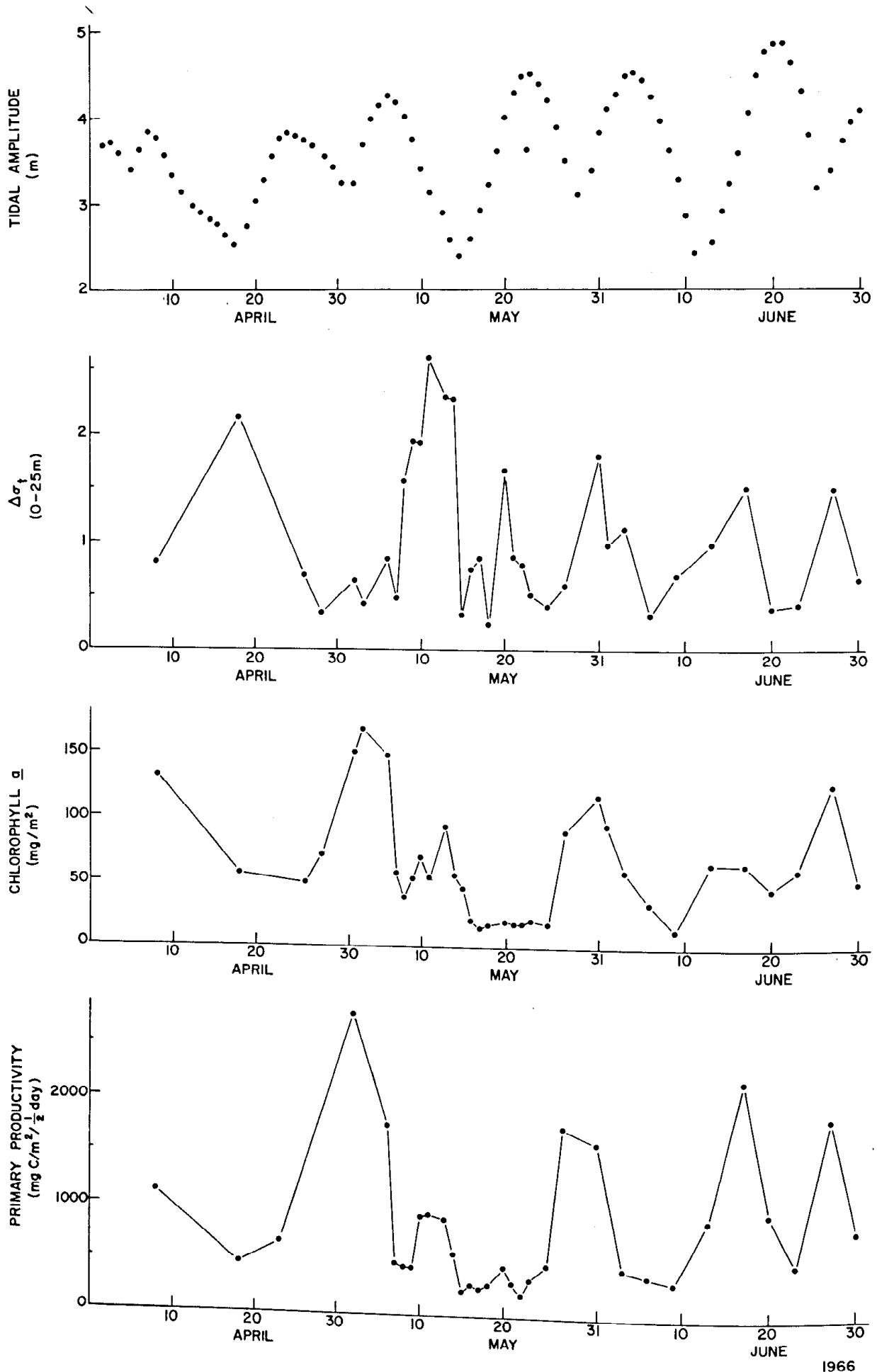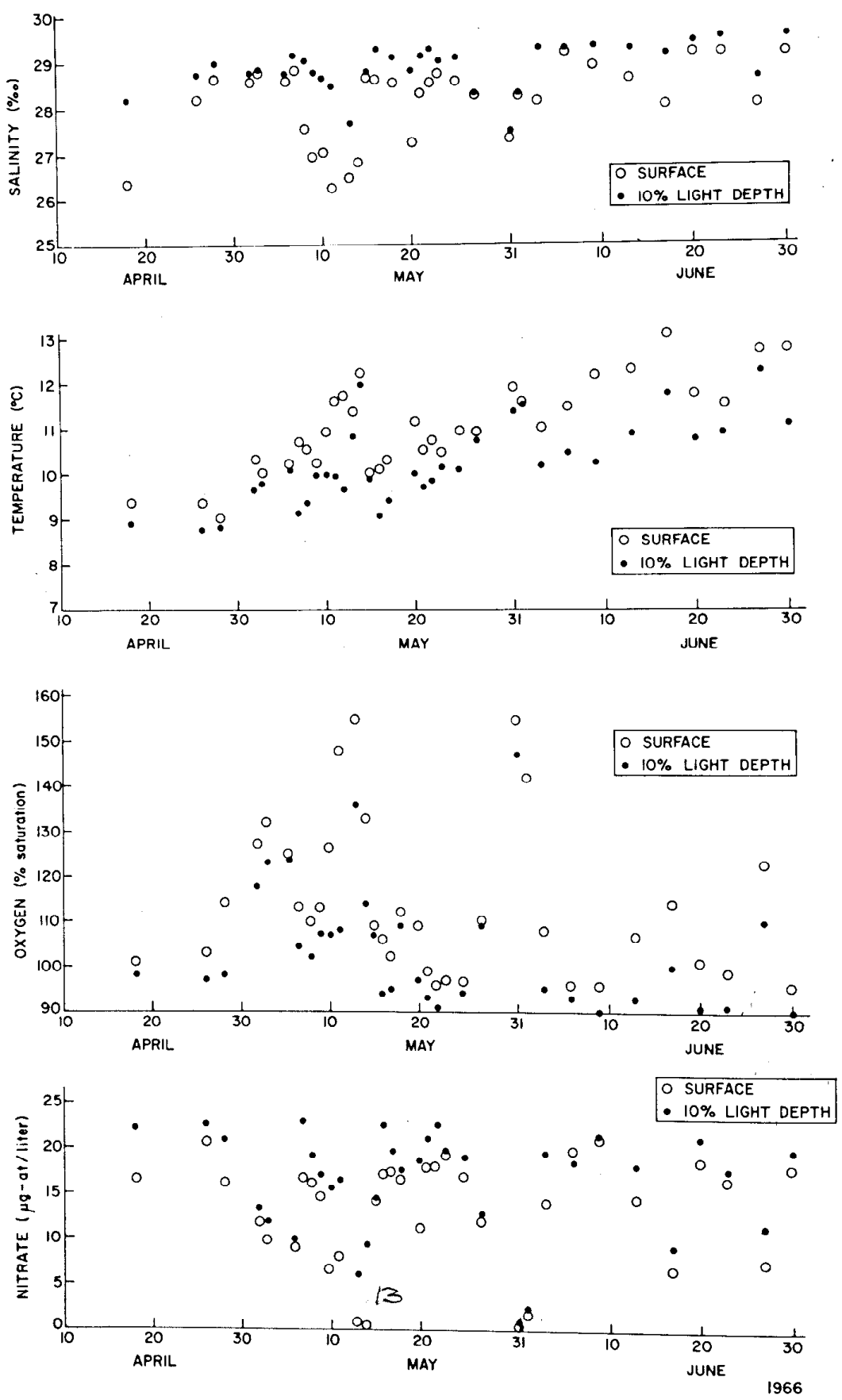
Fig. 5. Tidal amplitude range, density difference (surface and 25 m), chlorophyll *a*, and carbon-uptake rate integrated from surface to 1% light depth in 1966 and 1967

Fig. 5. (1967 data)

Fig. 6. Salinity, temperature, oxygen and nitrate at surface and 10% light depth in 1966 and 1967
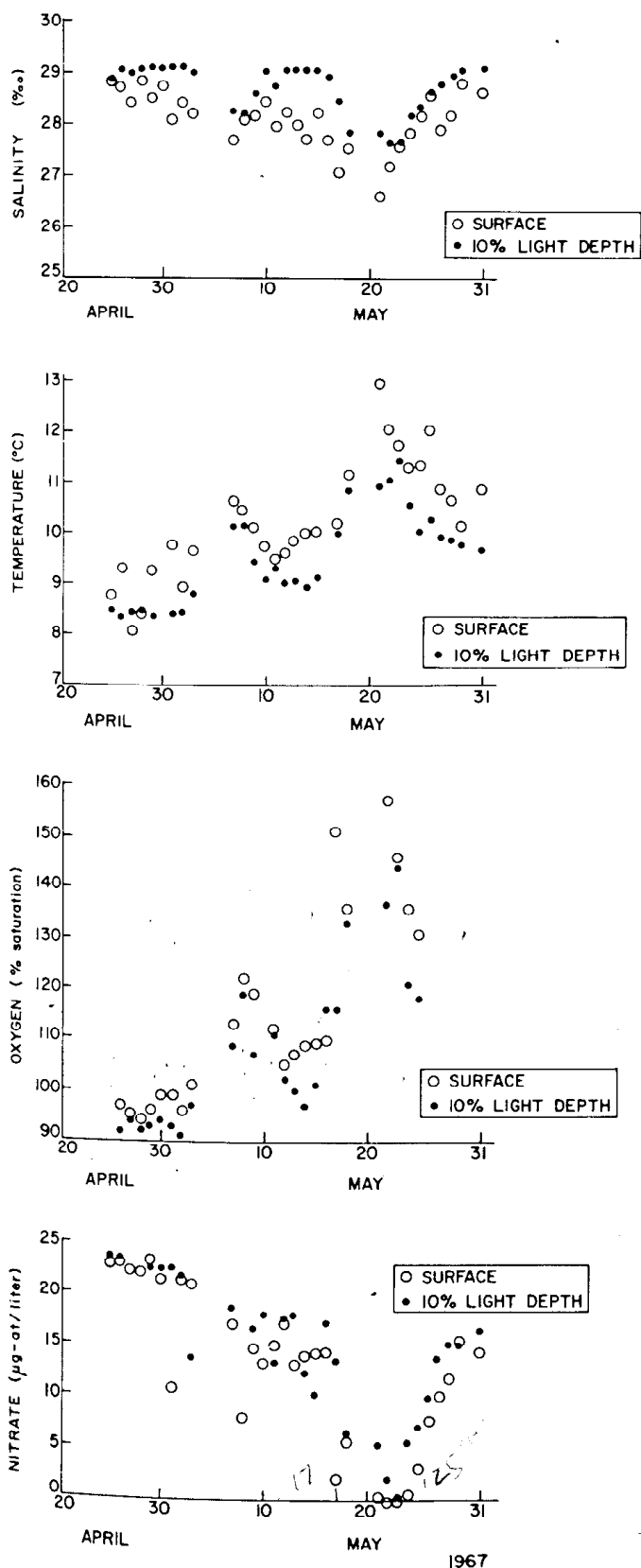
Fig. 6. (1967 data)

together with reasonable grazing coefficients and data on chemical composition of algae, to show that, on the occasions when nitrate was undetectable, regeneration of nitrogen as ammonium could only support photosynthesis at a rate lower than observed by an order of magnitude.

Chlorophyll

The chlorophyll concentrations in the surface zone varied considerably on a time scale of the order of a few days. Fig. 7 shows changes of pigment concentration integrated from the surface to the depth of disappearance of the Secchi disk and the corresponding Secchi disk depths. As will be shown later, the marked variations in Secchi disk depth are a function not only of the nature and amount of dissolved and suspended substances but also of the density of algal cells (chlorophyll). The vertical profiles of chlorophyll a indicate that the highest concentrations almost always occur at or near the surface, but very rarely exceed 15 mg chlorophyll a/m^3 despite high nutrient concentrations and high photosynthetic rates.

A phenomenon of particular interest in Puget Sound is the large amount of chlorophyll at depth (Fig. 2). For the greater part of the year, the concentration below 50 m is between 0.5 and 1.5 mg chlorophyll a/m^3. As a consequence, there is nearly always more pigment in the water column below the euphotic zone than within it. The chlorophyll distribution below the euphotic zone is generally more irregular than the distributions of nutrient salts, possibly because of the additional complication of sinking of the particulate matter. Although some of the relatively high pigment values near the bottom (approximately 2 mg chlorophyll a/m^3) occur in the slightly freshened water appearing shortly after the spring tides, an unambiguous correlation does not exist. In the same periods, concentrations of the nutrient salts in the bottom water tend to be lowered, again suggesting large admixtures of surface water and rapid advection at depth to the site of Station 1.

We suggest that a significant fraction of the chlorophyll at depth consists of viable cells, since exposure of deep water to light results in vigorous phytoplankton growth within a few days' time. Appreciable algal cell concentrations have also been observed at depth in similar hydrographic situations outside the sill in Admiralty Inlet and in the San Juan Archipelago by Gran and Thompson (1930). The rapidity of the southward transport of dense water from the northern sill to the central basin, as indicated by the relation between chlorophyll and salinity in the bottom water, is probably important to the viability of this deep population. The cells at depth may have grown originally in the surface zones of Puget Sound or in the Strait of Juan de Fuca and were mixed downward by turbulence over the Admiralty Inlet sill. Sinking could also
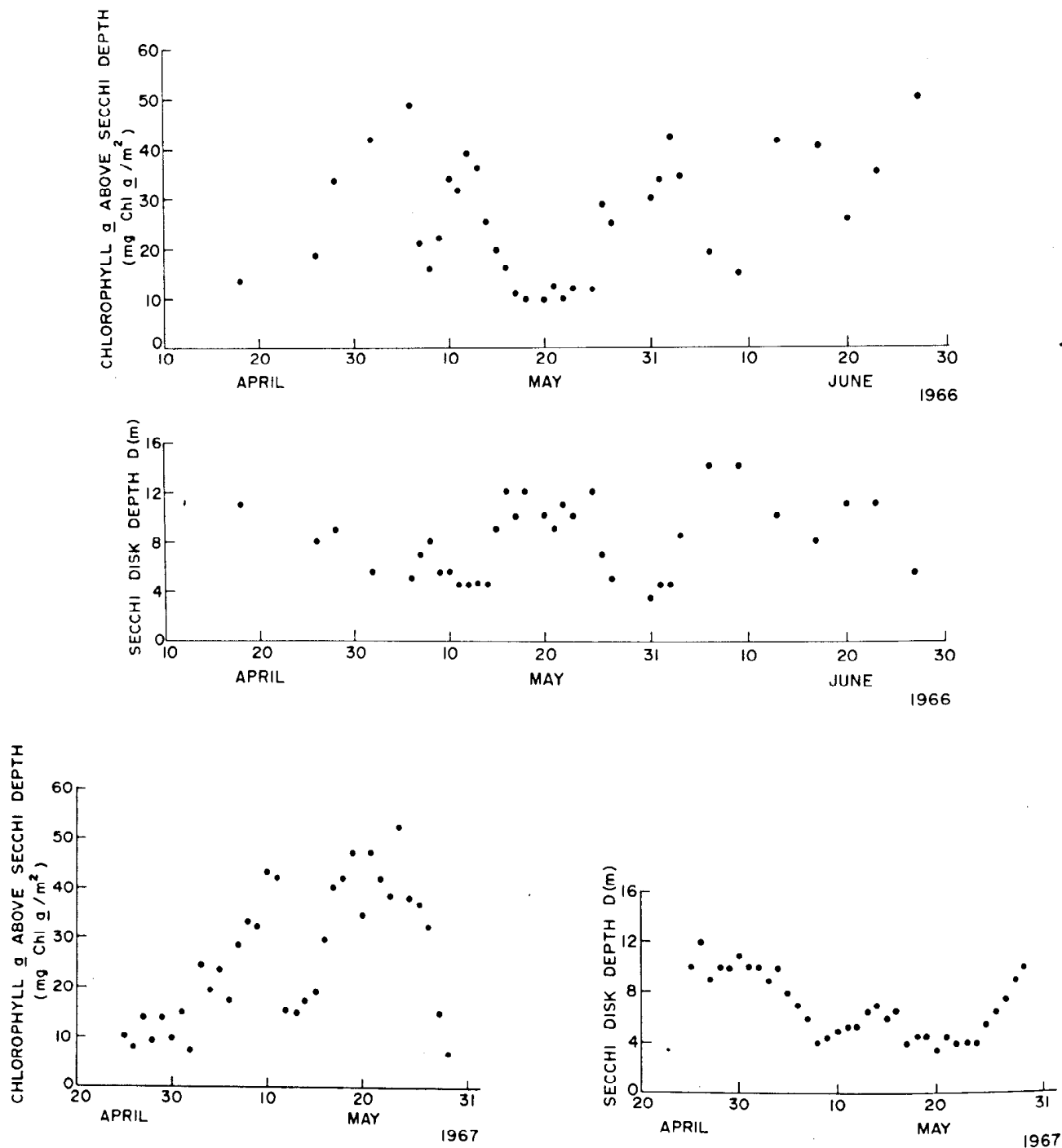
Fig. 7. Integrated chlorophyll *a* from surface to observed Secchi disk depth and measured Secchi disk depth at Station 1, April to June, 1966, and April and May, 1967

conceivably be a source of cells at depth, but it will later be shown to be much less important than advection effects.

All chlorophyll concentrations reported herein probably include breakdown products of chlorophyll *a*. A few deep-water samples, acquired at Station 1 during the winter of 1970-1971 and spring 1973, were analyzed for chlorophyll breakdown products by the methods of Yentsch and Menzel (1963) and Lorenzen (1967); subsamples were exposed to light as mentioned above. The results showed that a fairly large fraction (1/2 to 2/3) of the "chloro-phyll *a*" concentration below the euphotic zone consisted of phaeopigments.

The comparison of the observations of 1966 and 1967 at Station 1 with the fortnightly data for 1964 and 1965 suggest that the two spring periods studied in detail in this paper did not deviate significantly from those of previous years with respect to hydrography, nutrient, or chlorophyll concentrations. This statement also holds for the zooplankton data reported below and for the general levels of observed carbon uptake.

Rate of Carbon Uptake

The primary production rates exhibited in Fig. 2 were converted to mass specific uptake rates, since these are a somewhat better indicator of the physiological condition of the algal population. The specific production rate was obtained by dividing the measured carbon uptake rate per unit volume of water by the product of the initial chlorophyll concentration and the incubation interval. This procedure may have led to over-estimates of specific production rates under circumstances favorable to production, when a significant synthesis of chlorophyll occurred throughout the incubation period. Bias may also be caused by fluctuation of light from saturation levels to very low intensities near the end of each measurement. The calculated specific rates near the surface exhibited a very large amount of scatter, with most of the values for 1966 and 1967 being in the range between 2 and 7 mg C/mg chlorophyll *a*/h.

Specific carbon uptake rates of natural phytoplankton populations are variable to some degree due to the dependence of production on temperature, light, nutrient levels, species distribution, and other environmental and physiological parameters (see e.g. Fogg, 1965). However, the rates implied by the Puget Sound measurements, on days with comparable light intensity, varied over a range greater than could be reasonably expected. In an effort to explain these anomalies, the ship's log for the 1966 cruises was examined for evidence of procedural difficulty during the simulated production measurements. According to the log, the cooling system of the incubator water-bath malfunctioned from time to time and, as a consequence, the water-bath temperature sometimes rose from the desired 10° – 12°C up to 16° – 18°C. This will produce serious overesti-mates of the production rate, particularly on days of high light intensity. When the photosynthetic mechanism is light-saturated, the overall reaction is controlled by enzymes rather than by photochemical processes and is, therefore, temperature-dependent (see e.g. Steemann Nielsen and Hansen, 1959a; Eppley, 1972). On those days when the inferred specific carbon uptake rate was exceptionally high, either the ship's log noted an overheating problem and sometimes described an attempt to correct it, or the log contained no statement to indicate that the temperature of the incubator was being monitored. Data from all such days were dropped from further consideration. Unfortunately, the data that survive this elimination process are too few in number to allow us to assign accurate values to maximum specific production rates throughout the cruise sequence. Inspection of the remaining data (Fig. 8) suggest that during April and the first part of May, 1966, the maximum specific production rate was about 4.0 mg C/mg chlorophyll *a*/h, and that it subsequently declined to about 3.0 during the early summer. This trend in specific production
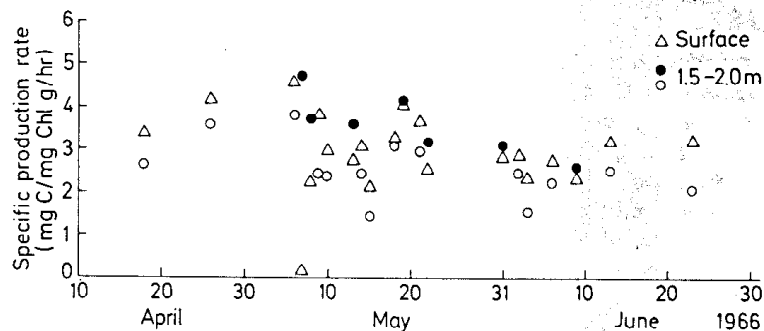

Fig. 8. Accepted measurements of specific rate of carbon uptake (noon to sunset) at 100 and 50% light depths, 1966. Filled circles: measurements suggesting photoinhibition at surface (greater production at 50% light depth)

rate is similar to that observed by Gilmartin (1964) for a British Columbia fjord.

The same sort of analysis could not be performed for 1967 since the ship's log for that cruise sequence could not be located. The measured specific production rates near the end of April and the beginning of May are not incompatible with p_{max} equal to about 4.0 mg C/mg chlorophyll *a*/h. However, large fluctuations and excessively high data values may again implicate the incubator temperature control.

No consistent relation between the specific rates at the 100, 50, and 10% light depths and the salinity, temperature and nitrate concentrations at these depths could be found for 1966 and 1967. Light adaptation in the lower part of the euphotic zone, if present, could not have been pronounced since water recently brought to the surface (as indicated by high salinity and nitrate and sometimes also low oxygen content) did not yield consistently low specific uptake rates. Moreover, a sequence of days with low insolation did not produce shade-adapted surface plankton (see Curl and Small, 1965, and Mandelli *et al.*, 1970, for similar results).

Zooplankton

During both the 1966 and 1967 observation periods, the average euphotic zone concentration of zooplankton was approximately 10 mg C/m³, as estimated by chemical analysis of samples from vertical hauls (Fig. 4). The average concentration of herbivorous zooplankton in the euphotic zone was about 7 mg C/m³ during the spring of 1966. Because the total zooplankton concentration determined for 1967 was similar to that of 1966, the calculated concentrations of herbivorous plankton are also similar.

Chemically estimated zooplankton concentrations below the 1% light depth for 1966 were approximately 1 to 2 mg C/m³ lower than those of the upper layer. On the basis of visual inspection of samples, it was assumed that half of the estimated zooplankton carbon represented herbivores.

Thus, the mean concentration of herbivores at depth during the spring of 1966 was estimated at about 4.0 mg C/m³. This value was also assumed to apply during the 1967 study period.

During the spring of 1966, 4 hauls were taken from the euphotic zone in the early evening and concentrations of chemically estimated zooplankton were found to be materially higher than the daytime values. However, on the three dates for which counts of herbivores are available, the data do not show uniformly a higher concentration at night (Fig. 4). Obviously, the few samples do not allow speculation about the importance of diel migration. Below the 1% light depth, the depth range of the hauls is so great as to preclude even a tentative statement concerning day-night concentration differences.

Supplementary Observations

A particularly useful index of phytoplankton concentration is the chlorophyll concentration integrated from the surface to the depth of the Secchi disk (Fig. 7). Although no direct analysis of the variability of this parameter was performed, a quantitative assessment was made from observations alongside a free-floating 17 m plastic cylinder, during the 1966 study period (Hirota, 1967). The cylinders were always deployed initially at Station 1, and the distance traveled during the experiment ranged from 9.5 to 17 km. The measurements, which were made during bloom episodes near Station 1, showed that a change of integrated chlorophyll concentrations by a factor of 2 over 24 h is not uncommon. Despite the diel fluctuations, however, days with and without algal blooms were easily distinguishable, inasmuch as their average integrated chlorophyll levels differed by factors of 4 to 6.

The data acquired by Hirota (1967) also indicated that the blooms observed near Station 1 are phenomena of considerable lateral extent. This is corroborated by the observation of chlorophyll distribution at 0.5 m depth by means of a multi-ship survey for 13 consecutive days in the spring of 1969 prior, during, and after a bloom (Munson, 1970). The survey covered much of the central basin of Puget Sound; the large horizontal extent of changes of pigment was substantiated by the visual appearance of the water as observed from an aircraft used in conjunction with the multi-ship survey.

The conclusion to be drawn from these observations is that near mid-channel in the central basin, at some distance from the sills, the growth and decline of large phytoplankton populations occur as general, widespread biological episodes, rather than as localized outbursts which may or may not propagate from their place of origin.

Hydrography and Circulation

An approximate mathematical analysis of gravitational convection in fjords has been published elsewhere (Winter, 1973), and only the final

results of the analysis, as applied to the central basin of Puget Sound, will be reviewed here. We begin with a presentation of certain additional hydrographic information relevant to the large-scale, nontidal circulation modes in the Sound.

We shall confine our considerations to a particular segment of the central basin which is 30 km in length, being bounded at its southern end near Blake Island and at its northern end near the southern tip of Whidbey Island (Fig. 1). This choice of segment boundaries reflects the fact that different sections of the Sound north of the Tacoma Narrows are characterized by different flow patterns. The central basin, as defined herein, constitutes an inlet segment which is characterized by the same general type of circulation pattern and hydrography. On the average, a significant fraction of the freshwater discharged from southern Puget Sound and the Puyallup River appears to enter the central basin near Blake Island, via Colvos Passage. The northern terminus of the segment marks the confluence with Possession Sound which carries freshwater from three of the largest rivers in the Puget Sound region.

Throughout the discussion in the sequel, we shall employ a coordinate system with the origin at the surface at the location of Station 1 near Seattle. The x-axis extends horizontally along the length of the Sound, the seaward direction being positive, and the z-axis is taken to be positive downward. With the objective of simplifying the circulation analysis, the main channel of the basin is idealized as a deep fjord segment which is sufficiently narrow and straight to preclude the occurrence of large cross-channel variations in the flow. Although the width of the segment is somewhat variable due to irregularities
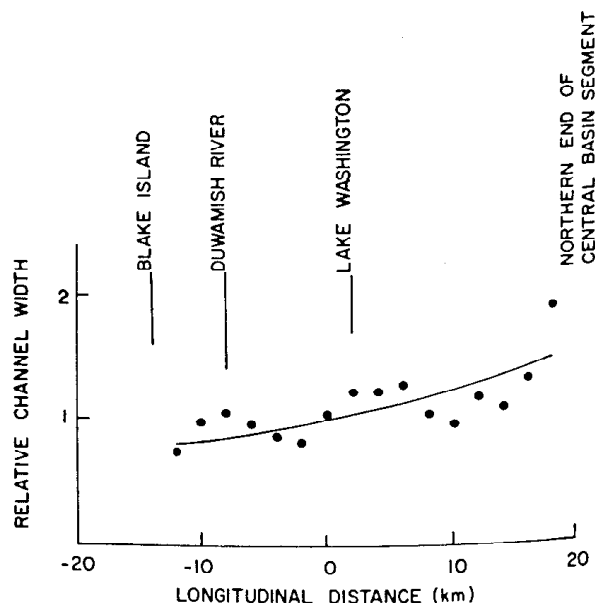

Fig. 9. Relative width of main channel as function of distance along axis of the central basin segment. Data and graph normalized by midsegment value b_0

of the coastline, as a rough approximation, the 50-m depth curves were assumed to delineate the main channel, except near the Point Jefferson promontory and in Elliott Bay and the Port Madison embayment. Not all of the water in these coastal indentations participates directly in the main channel circulation and, as a consequence, only a part of the embayments were included as part of the main channel. Fig. 9 shows a plot of cross-channel distances at 2-km intervals along the segment axis. The solid curve in the figure is an exponential function of the form $b = b_O \exp(\beta x)$ which represents a "smoothed" increase of channel width in the seaward direction; b_O is the effective main channel width at Station 1 (5 km).

Freshwater introduced into the central basin segment at its southern end consists of runoff from the Puyallup River drainage basin and the drainage basins south of the Tacoma Narrows. In addition, the central basin receives freshwater directly from the Duwamish and Lake Washington drainage basins, and distributed runoff from coastal land along the length of the segment. Daily gaging station data (U.S. Geological Survey, Water Resources Division) for the spring months of 1966 and 1967 were used as described below to estimate the temporal variations of the cumulative fresh-water runoff rate, R (m³/sec) in the central basin. Three-day averages of the hydrographs were performed to simulate the smoothing effect of mixing in the vicinity of the river mouths.

Freshwater introduced into the inlets south of the Tacoma Narrows is frequently detained in embayments by winds for 1 week or longer. Also, some fraction of the Nisqually River basin discharge experiences a delay in its passage northward through the Tacoma Narrows. In order to simulate these effects, the runoff rates from the southern drainage basins were moved forward (i.e., delayed) 6 days in time, except for the Nisqually River basin runoff which was moved forward 3 days on the basis of advice by C.A. Barnes (personal communication). Finally, the gaged discharge from each of the drainage basins was corrected to account for ungaged area. The time variation of the cumulative runoff rate at Station 1 is displayed in Fig. 10. The longitudinal distribution of cumulative runoff R, shown in Fig. 11, was assumed proportional to cumulative drainage basin area. The solid curve is a function of the form $R = R_O \exp(\alpha x)$ and is intended to indicate (very approximately) the longitudinal variation of cumulative runoff rate. The curve in the figure is normalized to the cumulative runoff rate at Station 1 (Fig. 11).

The main channel of the central Puget Sound basin exemplifies fjord-type circulation and hydrography, particularly during the spring and early summer months when the runoff intensity is of the order of hundreds of cubic meters per second. In the absence of turbulence measurements in Puget Sound (and hence direct descriptions of the turbulent transport of momentum and salt), we have drawn upon estimates of turbulent processes in other deep, stratified inlets (Winter, 1973).
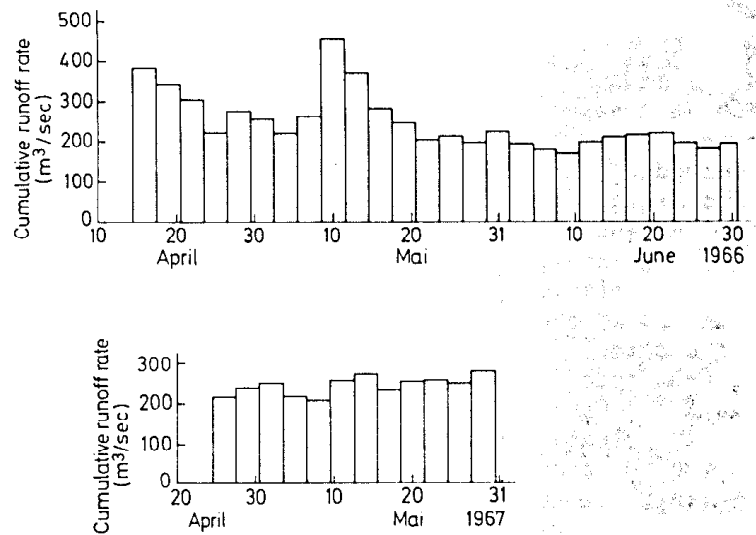

Fig. 10. Cumulative runoff rate near Station 1 during observation periods, 1966 and 1967
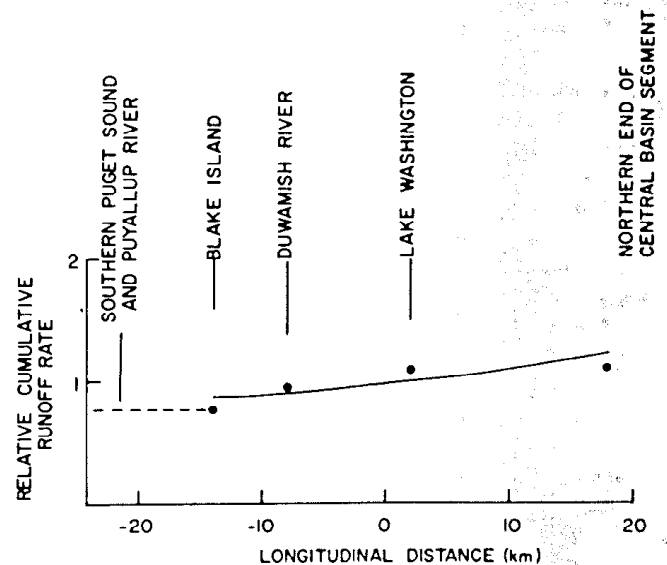
Fig. 11. Smoothed variation of relative cumulative runoff rate along axis of the central basin segment. Dashed line: runoff from southern Sound and Puyallup River entering central basin segment near Blake Island. Data and graph normalized by midsegment value R_O

Probably, tides play a more important role than winds or river discharge in providing energy for turbulent mixing in the central basin. For Canadian fjords, Trites (1955) suggested that changes in mixing intensity may be related to changes in the mean tidal velocity or its gradient in some non-linear fashion (for example, to its square). Average values of the vertical eddy diffusion coefficient K_z in the surface zones of several inlets were estimated to be in the range of 1 to 10 cm²/sec. We made herein the simple working assumption that the day-to-day change in the mean intensity of turbulent salt flux was proportional

to the square of the maximum tidal range, with an average value of about 2 cm^2/sec between spring and neap tides. Comparisons of calculations based on this assumption and hydrographic data from the field tend to support the notion of a general dependence of mixing processes on tides, although the exact nature of the dependence is probably not adequately represented. Moreover, several working assumptions and parameter assignments in the circulation analysis were inspired by observations in other fjords; therefore, our circulation description cannot be anything more than a rough approximation of the true state of affairs in Puget Sound.

Turbulent entrainment of salt water from the intrusion zone at depth in most fjords causes the salinity of the fresher surface zone to increase in the seaward direction. In the case of the central basin of Puget Sound, the seaward increase in salinity at the surface, S_S, is rather slight and is sometimes obscured by the presence of partially unmixed lenses of freshwater which originate from river mouths, following freshets. At other times, exceedingly large amounts of freshwater are introduced to the central basin from Possession Sound in the north (Fig. 1) following episodes of snow melt in the mountains. On these occasions, the longitudinal distribution of freshwater runoff may increase fast enough in the seaward direction to produce a southerly-directed pressure head near the surface in the central basin, resulting in a temporary reversal of the direction of mean surface current. Persistent northerly winds of moderate strength can also give rise to a southerly-directed mean current in a shallow layer at the surface. Apart from these exceptional circumstances, however, the salinity S_S over the segment will be determined ultimately by mixing of fresh-water runoff at the river mouths in the major embayments, and by the cumulative runoff rate, R_O. In practice, the latter can be regarded as the principal factor determining the fractional salinity excursion or "dilution factor":

$$\sigma_O = (S_\infty - S_S) / S_\infty, \qquad (1)$$

where S_∞ is the salinity at depth in the incursion zone. Thus, in the first approximation, the "dilution factor" σ_O can be expected to vary in time primarily in response to temporal changes in R_O, and secondarily to changes in wind-induced mixing, turbulence at depth, and mode of introduction of the runoff. Fig. 12 shows observed values of σ_O at Station 1 plotted against R_O for the 1966 observation period. The figure also depicts the function

$$\sigma_O = (R_O - 120)/2800, \qquad (2)$$

which represents (approximately) the tendency of the dilution factor to increase, on the average, to larger values as the runoff intensity increases. A linear regression analysis of all the exhibited data gave slightly different constants than those in Eq. (2). However, the dashed line representing Eq. (2) in Fig. 12, by deliberately overestimating
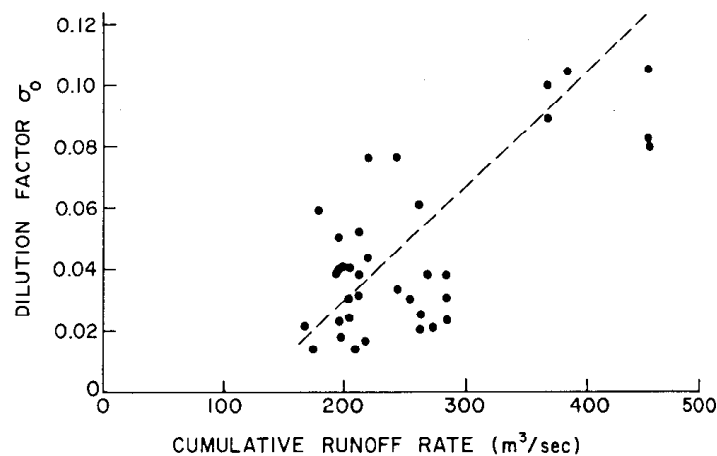

Fig. 12. Values of dilution factor [Eq. (1)] calculated from 1966 field data versus cumulative runoff rate at Station 1

σ_O for the 3 highest runoff days ($R_O = 455$ m^3/sec), produces a better overall representation of the dilution factor on days of low-to-moderate runoff. Part of the scatter of the measured points about the line is associated with observational uncertainty, and part is due to the influence of the other contributing factors listed above.

A study of the salinity changes at depth at Station 1 showed that, between the lower boundary of the euphotic zone (which varies from 15 to 30 m) and the sill depth (50 m), the seasonal increase in salinity was fairly small over the observation periods, being somewhat less than 0.5 ‰. In the simulation study of phytoplankton growth, which is described in the next section, the lower boundary, L, of the model zone is 30 m. This value was chosen since it corresponds to the greatest euphotic zone depth and also lies within the upper portion of the saline incursion zone most of the time. For the purpose of calculating the velocity field of the gravitational convection mode, it is sufficient to assume that the salinity at sill depth (about 50 m) is constant and equal to the approximate seasonal averages of 29.4 and 29.25 in 1966 and 1967, respectively. If S_∞ is assigned these values, and if R_O is identified with the cumulative runoff intensities displayed in Fig. 10, then the surface salinity S_S can be estimated from runoff by using Eqs. (1) and (2). As might be expected, a comparison between S_S calculated in this manner and the observed surface salinity would show the correspondence to be somewhat poor at times because, as mentioned earlier, wind and tides, as well as runoff, help to determine the surface salinity.

The aforementioned hydrographic data and topographic idealizations are used to generate self-consistent quantitative estimates of large-scale gravitational convection in the central basin, for the spring months of 1966 and 1967, by means of the approximate circulation analysis of Winter (1973). Since we focus on the quasi-steady non-tidal component of the circulation in the near-
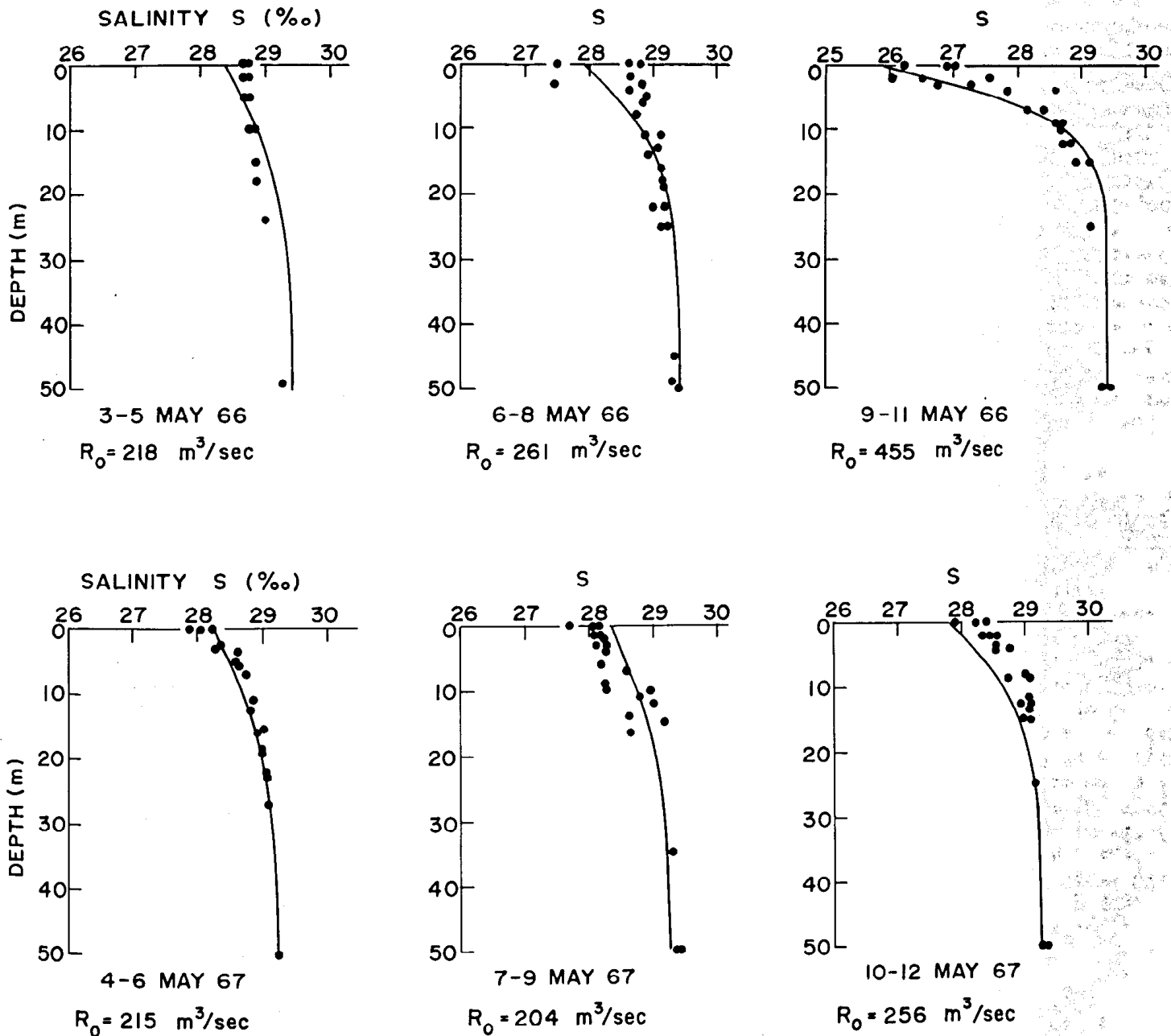
Fig. 13. Comparison of calculated and measured salinity profiles in depth at various times during 1966 and 1967 observation periods

surface flow regime, and because we are interested primarily in the interrelationship between the growth of algal populations, we forego a description of transients produced by changes in runoff and wind stress. The steady-state equations describing gravitational convection in the near-surface zone are obtained by performing a time average of the equations of motion over a tidal cycle. In addition, the relative narrowness of the segment permits the governing equations to be laterally averaged over the channel width.

Since we exclude from consideration transients associated directly with tidal motion, the cir-

culation is quasi-steady in the mean, as long as external factors, such as runoff and average surface wind stress, do not change drastically from one tidal cycle to the next. The approximate equations of motion reflect the fact that under idealized fjord conditions, changes in momentum and salt concentration produced by longitudinal mixing are small compared with variations associated with vertical mixing and advection (Rattray, 1967). The governing equations were solved approximately by the use of similarity techniques; the mixing coefficients K_z and N_z, the horizontal and vertical velocity components

u and w, respectively, and the density were expressed as products of powers of exponential functions $\xi = \exp(x)$ of the distance x along the main channel, and functions of a similarity variable $\eta = z\xi^\lambda$, λ real. In addition, longitudinal variations of cumulative freshwater runoff R and channel width b were expressed as powers of ξ, as suggested by Figs. 9 and 11. It can be shown that, when certain relationships are satisfied amongst the several powers of ξ, then the equations of motion reduce to a set of ordinary differential equations. From these equations, it is possible to obtain approximate analytic expressions for the velocity components and the density distribution which are valid in the upper regions of the flow. Thus, for an inlet segment where the conditions of similarity analysis are reasonably well satisfied, steady-state gravitational convection can be represented by an approximate, self-consistent description in which the mixing coefficients, the salinity, and the velocity field are continuous functions of x and z.

Comparisons of the calculated results with measured salinity profiles at various times during the springs of 1966 and 1967 are shown in Fig. 13. The smooth curves depict the calculated salinity profile for the second day of each 3-day period, the time interval over which the cumulative runoff rates were averaged. Salinity data for 3 days are superimposed, except in 3-day intervals for which there were fewer than 3 cruises. The data periods were chosen to cover the broad range of runoff conditions encountered during the observation periods. It should be noted that our idealized hydrodynamical analysis implies that changes in the non-tidal circulation component reflect changes only in tidal amplitude and runoff intensity. Since time-smoothed runoff data and day-to-day changes in tidal amplitude excursions constitute the input data to the analysis, the calculated density structure and velocity fields over the basin segment do not usually show large changes on consecutive days. For this reason, the calculated salinity variation on the second day of each period is representative. In most cases, fair agreement was achieved between the calculated salinity profiles and the observed salinity at Station 1.

The velocity components u and w are calculated from the same analysis (Fig. 14). We regard these calculations as a working hypothesis and the analysis as an interim theory. However, the calculated time-mean outflow at the surface agrees well with data from the few available measurements in Puget Sound made by Paquette and Barnes (1951) and by Cannon and Laird (1972). It is difficult to determine experimentally the depth at which the horizontal component of current reverses sign because the non-tidal velocities above and below that depth are small compared with tidal velocities. The calculated depth of no mean motion is somewhat more shallow than that inferred by Paquette and Barnes, but is the same order as that observed by Cannon and Laird when runoff is low or moderate (see also Winter, 1973).
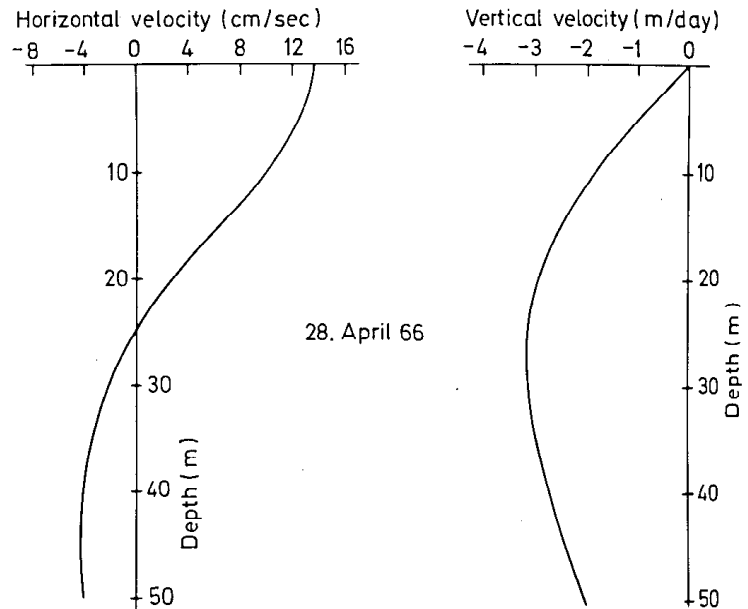

Fig. 14. Depth variation of calculated horizontal and vertical velocity components at Station 1 for period of moderate runoff intensity

Dynamic Model of Phytoplankton Production

Introduction

A convenient measure of phytoplankton standing stock is the amount, P, of chlorophyll a in a cubic meter of water. In the sequel, P is taken to be the dependent variable of a partial differential equation which expresses the time rate of change of P as the resultant of changes due to transport by turbulent mixing and advection, photosynthesis and respiration, sinking, and grazing by herbivorous zooplankton. As stated, we neglect the effects of certain short-time scale flow phenomena on algal dynamics, i.e., the response of phytoplankton to changes in hydrography and circulation which are other than long-time scale (tidal cycle). However, we retain the option of examining the response of the algal community to diurnal and day-to-day changes of available light. For this reason, we included explicitly the time variation of light intensity in the expressions for photosynthetic and respiration rates.

Under the hydrographic conditions described in the previous section, changes in momentum and salt concentration produced by longitudinal mixing are small compared with variations associated with vertical mixing and advection. We make the assumption that the turbulent transport mechanisms of suspended and dissolved substances are the same. Thus the turbulent flux of phytoplankton will be represented by the product of the eddy diffusion coefficient, K_z, and the vertical gradient of the mean algal concentration, P. Also, we assume that the advective flux of chlorophyll a can be represented adequately by the quasi-steady state velocity components u and w.

Under these assumptions, a laterally-averaged equation for the concentration of plant chlorophyll $P(x,z,t)$ can be written as

$$\frac{\partial P}{\partial t} = \frac{1}{b}\frac{\partial}{\partial z}\left(bK_z\frac{\partial P}{\partial z}\right)$$
$$- \frac{1}{b}\left(\frac{\partial buP}{\partial x} + \frac{\partial bwP}{\partial z} + \frac{\partial bw_sP}{\partial z}\right)$$
$$+ P_r(x,z,t)P - g_rH, \qquad (3)$$

where w_s is a representative vertical sinking speed of algal cells, P_r is the net specific production rate[1], g_r is the specific grazing rate, and H is the herbivore concentration. In principle, Eq. (3) is to be solved in a specified space-time domain, subject to appropriate boundary conditions and an initial condition.

The relevant space domain in the present instance is defined by

$$\{ 0 \le z \le L; \quad -10 \text{ km} \le x \le +20 \text{ km} \},$$

where L is 30 m. The bounds on x correspond to the mid-channel distances from Station 1 to Blake Island and the southern tip of Whidbey Island, respectively. The time domain is April 15 through June 30 for spring of 1966 and April 25 through May 30 for spring of 1967. The starting dates are chosen so as to be near the beginning of daily observations and to lie well within a time period when algal blooms were absent.

The boundary condition at the free surface requires that the flux of phytoplankton is zero:

$$-K_z\frac{\partial P}{\partial z} + w_sP = 0. \qquad (4)$$

The appropriate boundary condition at depth is suggested by the observation that a low-level concentration of phytoplankton is maintained by the transport of cells into the basin with the salt water intrusion. The deep chlorophyll concentration was assigned an average value for the observation period:

$$P \doteq 1.5 \text{ mg chlorophyll } a/\text{m}^3 \text{ at } z = 30 \text{ m}. \qquad (5)$$

In reality, the chlorophyll concentration at depth was observed to vary from about 0.25 to 2.0 mg chlorophyll a/m^3 over the time periods of interest. An undetermined fraction of the pigment at depth consists, however, of chlorophyll breakdown products and, therefore, does not contribute to P, which represents only chlorophyll in viable cells. Moreover, during 1966 and the latter part

of the 1967 observation period, the chlorophyll concentrations at depth appear to peak several days after the onset of vigorous growth in the surface zone. This is the result of partial mixing of productive surface waters with denser, deeper landward-moving waters near the northern sill. In view of the fact that such potentially important factors operating at depth are not included in Eq. (5), we do not expect the model to reproduce algal concentrations near and below the bottom of the euphotic zone. However, the main features of the bloom dynamics nearer the surface should not be drastically affected if an average condition at depth is used.

Boundary conditions at $x = -10$ km and $+20$ km could be specified on the basis of observations (e.g. Munson, 1970) that longitudinal gradients at the ends of the central basin segment are small, on the average. Hence, as a rough approximation, it might be appropriate to apply zero horizontal flux conditions on P at the ends of the segment: Munson's survey suggested that the growth and decline of phytoplankton in the central basin is characteristically a widespread occurrence and does not represent propagation of algae from one or two sites of intense flowering. Pigment variations in the longitudinal direction often appear to be local phenomena, and are rather indefinitely related to several environmental factors, including tides, runoff, and wind. On the average, therefore, it may be assumed that at any point within the domain of interest, the time rate of change of P associated with longitudinal gradients in cell concentration is small compared with rates of change due to other processes, such as vertical mixing, net photosynthesis, and grazing. We have performed a numerical study of the three-dimensional (x,z,t) problem. As expected, a slight relative increase in pigment was predicted in the down-inlet direction, but the chlorophyll distributions with depth were similar at all stations along the inlet axis. Since calculated phytoplankton concentrations at the central station differed by only a few percent from those predicted by the simpler, more economical two-dimensional model, the latter was subsequently used in the investigation.

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[1] Because the hydrodynamic equations were averaged both over the channel width and over a tidal cycle, it is inconsistent to introduce K_z and velocities u and w as coefficients in equation (3) if $P_r(x,z,t)$ is to vary throughout the day. Some additional comment is in order, since this approximation is frequently encountered in practice. Suppose that some appropriate expression of conservation of phytoplankton, valid over a relatively short-time scale, is subject to the same averaging operations as were applied to the circulation equations. Then the laterally averaged, time-mean net production term could not be written as P_rP, where each factor represents the appropriate mean, unless rather special conditions were satisfied. Nevertheless, it cannot be denied that the concept of a specific production rate, P_r, has been useful, and that the product P_rP has provided a convenient and reasonably accurate measure of algal density changes due to metabolic processes under a wide variety of conditions. For example, Steele (1962) proposed a specific production rate to describe empirically marine productivity on a time scale considerably longer than a single day. Later workers have found this representation and modifications of it to be equally useful in describing daily or hourly variations in primary production (e.g. Vollenweider, 1966; DiToro *et al.*, 1970). In this same spirit, we favor pragmatism over rigor and, in the present work, have expressed density changes due to diurnal variations in algal metabolism by the product P_rP.

When the x derivative of P is assumed negligible throughout the length of the inlet segment, the original three-dimensional problem is transformed to a two-dimensional one, the relevant coordinates being z and t:

$$\frac{\partial P}{\partial t} \doteq \frac{\partial}{\partial z}\left(K_z \frac{\partial P}{\partial z}\right)$$
$$- \left(w + w_s\right)\frac{\partial P}{\partial z} + P_r P - g_r H, \quad (6)$$

where we have assumed w_s to be independent of depth and have used the laterally-averaged equation of continuity,

$$\frac{\partial bu}{\partial x} + \frac{\partial bw}{\partial z} = 0.$$

Boundary conditions (4) and (5) are still applicable. Eq. (6) is to be solved for the two springtime intervals of 75 days and 35 days in 1966 and 1967, respectively. Initial conditions for the two periods are the observed vertical profiles of chlorophyll a at Station 1 on April 15, 1966, and April 25, 1967. The starting profiles actually used in the computations were adjusted at depth to pass smoothly through the seasonal average concentration of 1.5 mg chlorophyll a/m^3.

The coefficients K_z and w in Eq. (6) are obtained from the results of the circulation analysis summarized in the previous section. For the purpose of calculating the dynamical response of phytoplankton to changes in circulation, the salinity distribution and the nontidal flow field were calculated daily in response to (usually modest) changes in cumulative runoff rate and in the intensity of turbulent mixing (as related to tides).

Net Specific Production Rate

The net specific production rate P_r in Eq. (6) is a complicated and not fully understood function of several environmental variables and physiological parameters. Therefore, we employed rather traditional descriptions of photosynthesis. In making parameter assignments, we were guided by studies in other laboratories or bodies of water, as well as the results of our own field measurements.

Since the total range of water temperature was less than 4.5°C in both study periods, the effect of temperature on algal metabolism was neglected. The dependence of the net-specific algal production rate P_r on underwater light flux $i = i(z,t)$ (cal/cm²sec) and nitrate concentrations N (µg-at/1) was expressed in the form

$$P_r = (p_{max}/F)\left[\phi(i,N,P; z,t)/\phi_{max}\right], \phi < \phi_{max}$$
$$= (p_{max}/F), \text{ otherwise} \quad (7)$$

where p_{max} is the maximum specific photosynthetic rate (mg C assimilated/mg chlorophyll a/h), and F is the algal carbon-to-chlorophyll ratio. The function ϕ was expressed in the form

$$\phi = f(i)g(N) - r(z,t), \quad (8)$$

where the auxiliary functions $f(i)$ and $g(N)$ represent the dependence of gross production on light

intensity and nutrient concentration, respectively, and r represents the dependence of the algal respiration rate on depth and time. The function ϕ attains its maximum value ϕ_{max} on those days when there is sufficient sunlight to produce photo-inhibition near the surface during at least part of the day. By definition, the total (time-integrated) insolation on such days will equal or exceed a certain light saturation value I_{max} (cal/cm²); the determination of this parameter and its functional role in the expression for ϕ will be made clear below. Since ϕ_{max} depends upon the functional forms of f, g, and r, its evaluation is postponed to the subsection on respiration. First, we shall briefly discuss the dependence of photosynthesis on nutrient concentration.

Nutrient Limitation Factor. Nitrate was considered as the only limiting nutrient ion during the periods of observation. We adopted the Michaelis-Menten expression for $g(N)$, modified by the inclusion of a time lag τ to allow for the fact that the instantaneous growth rate of the plankton community depends upon the past external nutrient environment (Caperon, 1969; Caperon and Meyer, 1972):

$$g(N) = \frac{N(t - \tau)}{N(t - \tau) + K_s} \cdot \quad (9)$$

The value of the "half-saturation" constant K_s was taken to be 1.0 µg-at/1 in accord with estimates for temperate-zone marine phytoplankton by MacIsaac and Dugdale (1969). The introduction of a time lag, τ, interpreted as the effective time interval between the onset of nitrate deprivation and the observed decline in specific production, may appear arbitrary. Our value exceeds by a factor of 5 that proposed by Caperon (1969) to account for observed transients in cell concentrations in a pulsed chemostat. However, the local field studies (Munson, 1970) strongly suggest the existence of a time lag and, further, indicate that 72 h may be reasonable here. Also, Antia *et al.* (1963) observed on an enclosed, semi-natural plankton bloom in the Strait of Georgia that the growth rates of several algal species were unaltered for 1 or more days beyond the onset of nitrate exhaustion. A similar uncoupling of nitrate and carbon uptake was discussed by MacIsaac and Dugdale (1972).

Underwater Light Intensity. In the discussion of the light factor $f(i)$ which follows, the symbol I_s will be used to denote the above-surface radiative flux, integrated over the daylight hours, as measured by a total energy detector (Fig. 3). The temporal variation of light intensity just below the surface during the daylight hours is taken to be adequately represented by the "standard light day" proposed by Vollenweider (1966). Thus, for a day of t_d hours duration, the instantaneous flux $i_o(t)$ immediately below the water surface is given by

$$i_o(t) = (\mu I_s/t_d)\left[1-\cos(2\pi t/t_d)\right], \qquad (10)$$

where time t is measured in hours from sunrise and μ is a correction factor (equal to 0.4) to account for reflection losses at the surface, and scattering and absorption in the upper few centimeters of the water column. The light energy available for phytoplankton growth is directly proportional to the photosynthetically active fraction of the radiative intensity at depth z and time t. Depth variations in the spectral distribution of underwater radiation are neglected, so that the photosynthetically availabe light depends only upon $i_o(t)$ and a frequency-independent extinction coefficient $k_e(z,t)$. In fjord waters the extinction coefficient is critically dependent upon the concentrations of suspended terrigenous sediment and algal cells, particularly during seasonal episodes of vigorous production (e.g. Pickard, 1961). In the calculations for Puget Sound, we represented k_e by a semi-empirical relation in which the effects of both the aforementioned factors were included. Specifically, it was assumed that the contributions to extinction by dissolved substances, inorganic particulates, and phytoplankton are additive in the sense that

$$k_e(z,t) = k_1 + (1/z)\int_0^z \left[k_2'C(z,t)+k_3P(z,t)\right]dz, \qquad (11)$$

where $C(z,t)$ is the concentration of silt and k_1, k_2' and k_3 are constants. Since terrigenous sediment is introduced by runoff, we assumed that the silt concentration was proportional to the fresh-water fraction at any given depth. In other words, the function $C(z,t)$ in Eq. (11) was computed from a relation which involves the salinity $S(z,t)$, the latter being calculated from the approximate hydrodynamic analysis described in the previous section:

$$C(z,t)\alpha\left[S_\infty - S(x=0,z,t)\right]/S_\infty \equiv \sigma_o\sum(z,t). \qquad (12)$$

This last equation constitutes a definition of the fractional salinity defect $\sum$, where σ_o is the (nondimensional) dilution factor. When Eq. (12) is introduced into Eq. (11), the constant $k_2'\sigma_o$ can be redefined as k_2, and the instantaneous light flux i at depth z can be expressed as

$$i(z,t) = i_o(t)\ exp\ \{ -k_1z - \int_0^z\left[\ k_2\sum(z,t)\right.$$
$$\left. + k_3P(z,t)\ \right]dz\ \}, \qquad (13)$$

where $i_o(t)$ is given by Eq. (10).

The constants k_1, k_2 and k_3 must be determined from measurements in the field. The optical properties of Puget Sound waters were studied in some detail by Utterback and Miller (1937) and are summarized, along with more recent findings, in an oceanographic survey of Puget Sound (University of Washington, 1954). Following the latter reference, the period of optimal transpareicy of local waters is the fall of the year, when freshwater runoff is minimal and biological activity is low; extinction coefficients measured in the late autumn (University of Washington, 1954) suggest a value for k_1 of about 0.1, consistent with Secchi disk depths of about 50 feet (about 17 m)

when concentrations of silt and phytoplankton are low. Estimates of appropriate values for k_2 and k_3 were obtained from our own Secchi disk measurements in the central basin. We used data from days when either the salinity was low or the chlorophyll concentration was high, but not when both conditions prevailed. Approximate values of 1.2 and 0.03 were obtained for k_2 and k_3, respectively. Undoubtedly, improved values for the constants could be ascertained by a more careful treatment of the historical data. However, the additional time and effort would more profitably be devoted to a study of scattering and absorption of light in fjord waters using modern instrumentation and more sophisticated methods of analysis.

Light Factor. By way of recapitulation, Eq. (10) gives the time variation of sub-surface light intensity $i_o(t)$ over the day when the total above-surface insolation is I_s. Eq. (13) can be used to calculate the light intensity $i(z,t)$ at depth z when the subsurface intensity $i_o(t)$ has been determined and the fractional salinity defect and the phytoplankton concentration are known. Under the assumptions stated earlier, light saturation will occur during some part of a day that is t_d hours long when the total above-surface insolation exceeds I_{max} (and nutrients are in adequate supply); i.e., when the average integrated sub-surface radiative flux is greater than $(\mu\ I_{max}/t_d) = i_m$. In consequence of this observation and the fact that under low-to-moderate illumination, photosynthesis is observed to proceed at a rate proportional to the light flux, it is convenient to define the auxiliary function $f(i)$ as

$$f(i) = i(z,t)/i_m. \qquad (14)$$

Unfortunately, we have too few data to allow a direct determination of I_{max}. It has been shown (e.g. Talling, 1957; Steemann Nielsen and Hansen, 1961; Macan, 1970) that the quantity I_{max} for plankton varies as a result of physiological adaptation to changing environmental conditions, e.g. water temperature and available light. As already mentioned, the excursion of water temperature during our study periods was not large enough to require a consideration of the temperature effect on algal metabolism. Therefore, we simply assumed that the algal community would adapt to the average light conditions of the season and that I_{max} would be somewhat greater than the mean daily light intensity during the periods of study. More precisely, I_{max} was estimated by first calculating the average of the daily insolation values and then making the assumption that I_{max} would exceed the mean by an amount equal to the standard deviation. The estimates for I_{max} so obtained were close to 550 cal/cm^2 per day (i.e., about 275 cal/cm^2 photosynthetically available light) for each of the two study periods. This value is consistent with our insolation values (Fig. 3) on those days in 1966 when photoinhibition was suggested by the specific productivity values near the surface (Fig. 8).

Maximum Specific Productivity. The values adopted for p_{max} were the approximate seasonal averages inferred from the rates of carbon uptake observed at the 100 and 50% light depths. During the first 30 days of the 1966 study period, the value of p_{max} was 4.0 mg C/mg chlorophyll *a*/h, declined to 3.0 during the next week, and remained at that level for the rest of the period. Throughout the entire 1967 study period, p_{max} was taken to be 4.0 mg C/mg chlorophyll *a*/h. Although the experimental data on carbon uptake are thereby regarded as representing gross photosynthesis, there is little to be gained by attempting to correct them in view of the low accuracy of the techniques used for measuring productivity.

Carbon-to-Chlorophyll Ratio. The carbon-to-chlorophyll ratio, F, was assumed to remain constant with depth and time. This is consistent with our neglect of temperature effects and with the fact that we did not observe light adaptation with depth. Although we infer a slight seasonal change of p_{max} in 1966, we neglect the fact that this change probably would have been reflected in a changed carbon-to-chlorophyll ratio. Increases of the carbon-to-chlorophyll ratio could also be expected to accompany the decline of growth rate associated with low nitrate concentrations. However, such a relationship was not introduced into our computations in contrast, for example, to Steele (1962) and Riley (1965), since our data were insufficient to prescribe appropriate functions that were consistent with our other assumptions (cf. Eppley, 1972).

The somewhat low value of $F=15$ used herein was chosen on the basis of a re-evaluation of experiments with semi-natural plankton, such as those reported by Antia *et al.* (1963), and new field data of our own from open ocean waters. Moreover, plots of cell-carbon estimates versus chlorophyll for some of the 1967 data (Booth, 1969) suggest a ratio well below 25, which was the value proposed by Antia *et al.* (1963).

Our specification of the parameters p_{max}, I_{max}, and F implies that the depth variation of gross production is associated with the relative change of light intensity with depth. As stated before, our data do not suggest the occurrence of marked light adaptation. We recognize, however, that the field observations were not acquired in a manner suitable for detecting small changes in adaptation. We also note that the assumption of constant p_{max}, I_{max}, and F, during 1967, led to a seasonally increasing specific daily increment of algal mass because of the increasing day length; this was not the case in 1966 because of the decrease of p_{max}.

Respiration. We make two important assumptions concerning algal respiration: (1) the respiration rate decreases with increasing depth; (2) photorespiration can lead to different respiration rates during daytime and nighttime hours.

Near the surface, algal respiration was assumed to be adequately represented by the measurements of Steemann Nielsen and Hansen (1959b). Their procedure involved exposure of natural plankton to graded light intensities and extrapolation of the rates of carbon-14 uptake to zero illumination. By this means, Steemann Nielsen and Hansen (1959b; see also Steemann Nielsen, 1963) obtained an average respiration rate equal to approximately 8% of p_{max}/F, which we accepted for the surface during daytime hours. With F equal to 15 and a seasonal average p_{max} of 3.5, the corresponding respiration rate is 0.0187 mg C/mg C/h.

On this basis, we can assign a value to ϕ_{max}. On a day when the total insolation is I_s the product $f(i)g(N)$ can attain a maximum value of $2I_s/I_m$ just below the surface where $r(0,t)$ is equal to 0.08 ϕ_{max}. Since photoinhibition occurs at midday immediately below the surface when I_s is just equal to I_m, we have $\phi_{max} = 2/(1 + 0.08) = 1.85185$.

The choice of respiration rate at depth presented considerable difficulties: in algae exhibiting photorespiration (cf. Goldsworthy, 1970) the rate is related to light intensity at some low illumination; at even lower illumination, the rate of dark respiration is reduced below that prevailing in algae held for some hours in complete darkness (cf. Hoch *et al.*, 1963); thus, when there is photorespiration, a basic assumption of the procedure of Steemann Nielsen and Hansen (1959b) for estimating respiration would not hold. Further, somewhere below the average compensation depth, the respiratory rate of phytoplankton would approach that of algae kept for long periods in the dark, regardless of whether or not photorespiration was present. Therefore, it seemed reasonable to introduce a decrease in the specific respiration rate with depth. Specifically, we assumed an exponential decrease from the specific rate prevailing at the surface to that prevailing all the time below the 1% light depth. The assumed dependence of the respiration rate on depth is functionally similar to that of the photosynthetic rate at low light intensities. We recognize that the uncoupling of the respiratory rate from p_{max} is unconventional; however, a formulation which is physiologically sound in every respect (and which includes the role of light quality) is not yet possible for field situations.

Algal respiration at night is described herein by a constant rate of carbon loss, although some variation with time should be expected during the night. Some workers have considered the rate to decrease exponentially with time (e.g. Genevois, 1927; French *et al.*, 1934; Taylor, 1951). In contrast, Webster and Frenkel (1953) have reported a constant algal respiration during the first 4 h in the dark. In any case, after 36 to 48 h in the dark at about 25°C, respiration rates were 1/3 to 1/5 of the initial values in species studied by Myers (1947), Webster and Frenkel (1953), and Kratz and Myers (1955). From these and similar

data, we are unable to choose a unique function which describes the temporal rate of change of respiration. Therefore, we simply assumed a time-invariant (average) respiration rate to prevail during the nighttime. We considered that Ryther and Guillard (1962) had found an average value of 0.2 mg C/mg chlorophyll *a*/h from 24-h experiments with temperature-adapted algae at temperatures of concern to us. Because their rates must have been somewhat higher during the first 8 to 10 h, we arbitrarily selected an average value of 0.25 mg C/mg chlorophyll *a*/h which, after division by F, is approximately 90% of our daytime rate.

For the algae below the 1% light depth, respiration rates might be estimated on the basis of studies such as that of Hellebust and Terborgh (1967). However, as stated earlier in connection with the chlorophyll density at depth [Eq. (5)], we do not expect to reproduce in detail the variations of pigment concentrations near and below the bottom of the euphotic zone. Consequently, we assumed simply that below the 1% light depth the rate of net production (gross production minus respiration), averaged over a 24-h period, is equal to zero. We should point out, however, that in the absence of light adaptation it may be preferable to set the rate of net production equal to zero where the 24-h average light intensity attains a certain value. However, field data must be taken which would allow a direct estimate of that value to be made.

The foregoing description of respiration is summarized by the expression for respiration rate which is used in connection with Eq. (8). Denote the 1% light depth by z_1; a consideration of the forms of Eqs. (7) and (8), together with the assumptions stated above, leads to an expression of the form,

$$r(z,t)/\phi_{max} = 0.08 \; h(t) \; exp\,(-\gamma z/z_1),$$

$$\text{for } z < z_1, \tag{15}$$

where $h(t)$ is equal to 1 during the daytime and is reduced to 0.9 during the nighttime hours. When $z > z_1$, P_r is set equal to zero. The factor γ is estimated by first substituting $r(z_1,t)$ into Eq. (8) for ϕ, specialized to $z = z_1$. The resulting expression can be simplified by setting the Michaelis-Menten factor equal to unity. The expression for ϕ is then integrated over 24 h and the integral set equal to zero since, by assumption, the net daily production is zero at the 1% light depth. If I_s is specified, the resulting equation determines γ since all other parameters except γ are known. When I_s is of the same order as I_{max}, then γ turns out to be about 3.1 and this is the value used in the calculations described here. In the computations, the depth z_1 was calculated on a daily basis to allow for the effect of changing water transparency.

Sinking of Algal Cells

A comprehensive review of studies of the sinking characteristics of algal cells has been published by Smayda (1970), including sinking rates measured in laboratory cultures as well as those inferred from field measurements performed under a variety of conditions. The range of values is very large. In general, sinking speeds measured in actively growing cultures tend to be rather low; approximately 85% of chain-forming species and about 75% of the solitary species sink at speeds of less than 1 m/day. Cells of the same species may sink several times faster in a senescent culture. Sinking rates found in the field are generally higher than those found in laboratory studies, the average value being about 5 m/day (e.g. Margalef, 1961). However, these speeds are usually determined indirectly from temporal changes in the observed depth of the maximum of the algal concentration, and the estimated rates are, therefore, subject to bias from other processes which determine the distribution of cells, such as circulation, photosynthesis and grazing. Since we have not ascertained whether this bias will lead to high or low apparent sinking rates, we have given somewhat less weight to evidence from the field in estimating the appropriate sinking speed of algae in Puget Sound. In addition to differences in cell size and shape, turbulence and advection probably produce in the surface zone a mixture of cells which is somewhat heterogeneous with respect to levels of physiological activity. We assumed a constant sinking speed of 0.5 m/day throughout the upper circulation zone when nutrients were in adequate supply. However, during those episodes when cellular activity was expected to decline due to prolonged nitrate depletion, the sinking speed was increased to 2 m/day throughout the zone. Thus, the coefficient w_s in Eq. (6) was calculated from

$$w_s = 2.0 \text{ m/day, if } N \leq 2.5 \text{ µg-at/l}$$

$$= 0.5 \text{ m/day, otherwise,} \tag{16}$$

where N is the time-delayed nutrient concentration in the surface zone.

Zooplankton Grazing

A single grazing function, independent of size of the grazers, was applied to the herbivorous zooplankton. The dependence of grazing rate on food concentration is described by Ivlev's relation (cf. Parsons *et al.*, 1967)

$$g_r = g_{max} \; [1 - exp(-k_a P)], \tag{17}$$

where g_r is the ration at food concentration P, g_{max} is the maximum ration, and k_a is an appropriate species-dependent constant. The dominant herbivores in the net samples of 1966 were small adult copepods, copepodites, and furcilia larvae of euphausiids, mostly of 5 to 10 µg C weight. Therefore, parameter assignments were made on the basis of work by Evans (cited by Frost, 1974) who studied local *Pseudocalanus* sp. females of 7 to 10 µg C weight, which fed on the rather large diatom *Thalassiosira fluviatilis* at a temperature of 12°C. The value of g_{max} was approximately equal to 0.018 mg C/mg of animal carbon/h. When P is about 8 mg chlorophyll *a*/m³, the grazing rate

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attains a value equal approximately to 90% g_{max} and, on this basis, k_a was estimated to be approximately 0.27 (m^3/mg chlorophyll a). On those days for which estimates of herbivores are available, the vertical distributions of grazers above and below the 1% light depth were assumed constant with depth and equal to the depth-mean values within each zone. On days for which no direct observations are available, concentration estimates were generated by interpolation. Finally, because the supply of ammonium ion is considered to be unimportant in comparison with the demand for nitrogen compounds, a term for nitrogen regeneration by zooplankton is not included in the model.

Discussion of Model

Introduction

The distribution of phytoplankton in space and time at Station 1 is described approximately by Eq. (6) which is of the form of a nonlinear partial differential equation of a parabolic type. We seek solutions in the depth domain $0 \leq z \leq 30$ m and over time intervals of 75 days and 35 days duration in 1966 and 1967, respectively. The approximate initial conditions for the two periods are derived from observed concentrations of chlorophyll a near the surface and the seasonal average of chlorophyll a at depth. The boundary conditions applied at the surface and at depth are given by Eqs. (4) and (5), respectively.

The relationships amongst the various components of the model are depicted in Fig. 15. The hydrographic and climatic inputs, which include runoff intensity, tidal range, and insolation, are supplied on a daily basis. Observed nitrate distributions and estimated herbivore concentrations are also provided each day and, therefore, these variables act as "forcing functions" in much the same way as the environmental inputs. The several model parameters, such as p_{max}, I_{max}, K_z, g_r, S_∞, algal density at depth, etc., play a somewhat different role, inasmuch as they are of the nature of input constants, most of which are fixed throughout the course of a calculation. The feedback shown in the model diagram between the phytoplankton concentration submodel and the submodel for underwater light intensity is a consequence of the effect of self-shading on water transparency. Feedback also occurs between the phytoplankton submodel and the grazing submodel due to the dependence of the herbivore ration upon food concentration.

A detailed discussion of the numerical solution of the model equations is outside the scope of the present report. Briefly stated, the space derivatives in Eqs. (4) and (6) were rewritten in centered finite difference form and the time derivative in Eq. (6) was expressed as a forward difference. The boundary conditions (4) and (5) were incorporated in a standard way (cf. Ames, 1965). The resulting terms on the right-hand side of Eq. (6) were evaluated midway between time steps n and $n+1$. The corresponding evaluations of
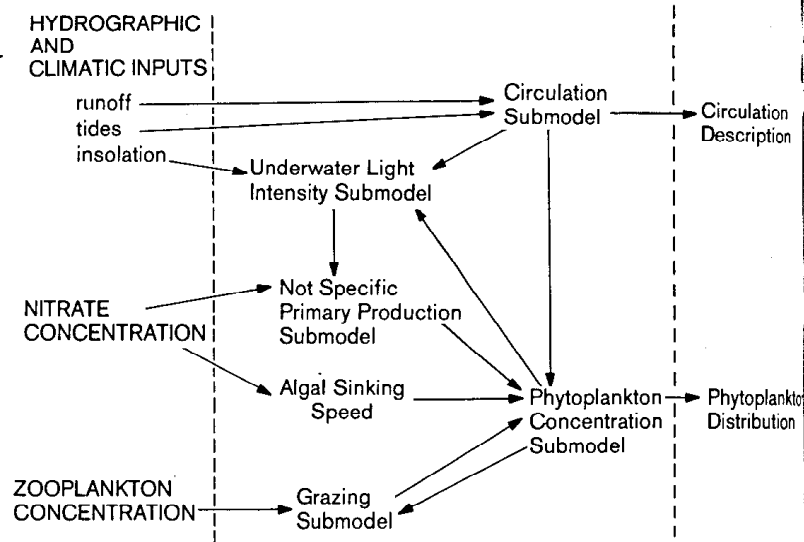

Fig. 15. Flow diagram of numerical model showing relationship amongst the several components of the model

the undifferentiated terms which are nonlinear in P and the integral of $k_3 P(z,t)$ appearing in Eq. (13) were accomplished by iterating on each time-step until a prescribed accuracy criterion was satisfied (fractional change less than 0.01%).

The basic time unit was taken to be one day and the time step Δt used in the calculations was equal to 1/50 which corresponds to about $\frac{1}{2}$ h in real time. The space increment used (Δz) gave a resolution of 0.5 m in real depth. Since K_z varies about fourfold in all over the two study periods (the mean is approximately 2 cm^2/sec), the stated choices for the space and time increments imply that the numerical parameter $\rho = (\Delta z)^2/2K_z\Delta t$ is in the range of about 0.8 to 3.5. The numerical integration procedure was always stable, of course, since an implicit method was used. The question of accuracy was examined by performing numerical experiments with smaller Δz and with values of Δt determined from the condition that $\rho = 1/2$. Assuming that the results so obtained were indeed accurate (as experience would suggest), we compared the output with our earlier computations and found that the results for P never differed by more than a few percent even over a fairly long time interval. By means of the procedure just described, the numerical problem is reduced to solving a tridiagonal system, and this is readily accomplished by Gaussian elimination. At the beginning of each day of the calculation, output was printed from the circulation analysis. At midday, the extinction function [Eq. (11)] was used to calculate the apparent Secchi disk depth. Next, the computed noontime chlorophyll concentration was integrated from the surface to the calculated Secchi disk depth and both variables were printed out, along with the depth distribution of chlorophyll a. All the numerical calculations were performed on the CDC 6400 computer at the University of Washington.

Numerical Results

Standard Runs. The numerical integrations carried out with the functional forms and parameter values given in the preceding section are referred to subsequently as "standard runs". Before examining the results, however, we wish to mention that because the model in its present form does not include explicitly the effects of sustained winds, it was necessary to perform the 1966 computation in two stages. In an open inlet, such as Puget Sound, occasional episodes of strong, persistent winds will drastically retard or accelerate seaward advection in the upper zone, simultaneously altering its density structure and

phytoplankton content. Such an occurrence is exemplified by the abrupt changes of surface salinity around mid-May, 1966 (Fig. 6): beginning on 12 May, an episode of high runoff due to snow melt was followed immediately by sustained strong southerly winds which rapidly moved the relatively fresh surface water to the north and, at the same time, removed from the central basin the algal blooms which had previously been extant in the surface zone. The reduction of the fresh-water fraction in the surface zone was accompanied by upwelling of saline water from depth and the occurrence of low rates of specific algal production (Fig. 8). Therefore, the calculation for 1966, which began on April 15, was terminated on
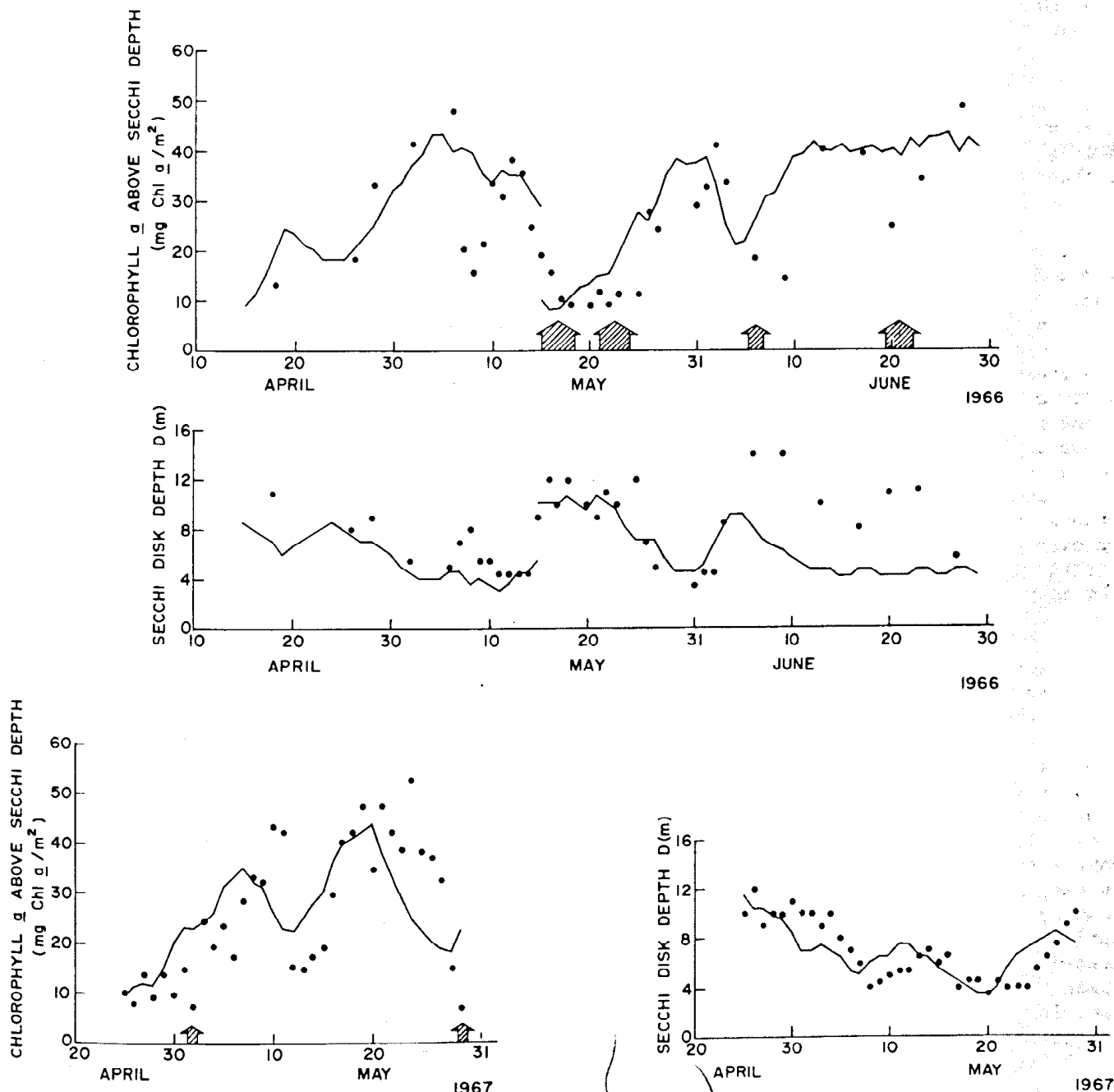

Fig. 16. Comparison of measured and calculated integrated chlorophyll *a* from surface to Secchi disk depth and Secchi disk depth at Station 1, April to June 1966, and April and May, 1967. Arrows: endings of periods of rapidly rising salinity in brackish zone

15 May, which was the third consecutive day on which the average wind speed was near or exceeded 10 knots. The algal density was reset at 1.0 mg chlorophyll a/m^3 near the surface, in accord with observation, and the computation continued without further interruption to the end of June. Although there were episodes of winds during the 1967 period, they were of shorter duration and lesser intensity and, as a consequence, the entire calculation for 1967 was performed without interruption.

The day-to-day variations of the computed Secchi disk depth and the integrated chlorophyll values of the standard computer runs are shown together with the observed values for the spring-time periods of 1966 and 1967 in Fig. 16. Comparison of the computed and observed results indicates that the model reproduces satisfactorily not only the general pigment level but also many of the details of the springtime phytoplankton dynamics in both years. Moreover, we will show below that reasons are apparent for the periods of marked divergence between calculated and observed values.

Unfortunately, we lack the supplementary field measurements that would be needed to establish rigorous error estimates for the data points in Figs. 7 and 16. A statistical analysis of replicate samples acquired during 1964 at and near Station 1 indicated that the confidence interval (P = 0.05) for individual chlorophyll values was about 30% during vigorous growth. Because several depths are involved in the evaluation of integrated pigment values in Figs. 7 and 16, the confidence intervals for these latter values would range from about 50 to 200%. Thus, it would not be particularly fruitful to interpret the data in Figs. 7 and 16 simply as random fluctuations about a seasonal mean. On the contrary, a consideration of the available evidence strongly suggests that the observed variations in pigment concentration represent a dynamic response to changes in the environment. For example, as mentioned earlier, the surveys of near-surface pigment concentrations by Hirota (1967) and Munson (1970) indicate that low and high pigment values are not randomly distributed, but rather are associated with general, widespread quiescent episodes and algal blooms, respectively. As will be seen below, an assessment of the chlorophyll observations by means of a deterministric model is reasonably straightforward and unambiguous.

There are several episodes during both study periods when the measured values of integrated chlorophyll fall considerably above or below those predicted by the model. In some instances, we can identify possible reasons for the difference. For example, the values of maximum specific productivity measured in 1967 suggest a seasonal increase in p_{max} of about 50% despite the large amount of scatter in the data points. If this trend represents the true state of affairs, then the assumed value of p_{max} overestimates the production during the first 10 days and later underestimates it, near the onset of nitrate depletion

at the end of the period. In fact, the discrepancy between calculation and measurement in 1967 often reflects this type of bias in the prediction (cf. Fig. 20).

A different sort of situation arises on those days when markedly low natural chlorophyll densities coincide with periods of somewhat lower water density gradients in the upper 50 m (associated with rising surface salinities). The ends of periods of rapidly rising surface salinity (arrows in Fig. 16) were estimated from the plots of density differences in Fig. 5. With the exception of mid-May 1966, the estimates of specific production rates are not consistently lower during these events and, consequently, the discrepancy between measured and predicted chlorophyll concentrations is more probably caused by inadequate model representation of horizontal advection effects, rather than improper description of photosynthesis (e.g. light adaptation).

Another type of problem is posed by the occasional discrepancies between the observed and computed Secchi disk depths after 27 May, 1966, and 8 and 23 May, 1967. An overestimate of water transparency will lead to an overestimate of subsurface light available for photosynthesis and, hence, to increased phytoplankton production. This would seem to be the case during the first-mentioned interval in 1966, when algal proliferation is observed to begin later than predicted, possibly because the model inadequately represented the sediment load prevailing in the upper part of the water column during the last week of May, 1966. By contrast, water transparency during the latter part of 1967 is consistently overestimated during intervals when algal standing stock is rather high, which suggests that the parameter p_{max} may actually have been greater than was assumed, as mentioned above.

A critical examination of the periods during which the standard run succeeds and fails leads us to conclude that much of the apparent patchiness near Station 1 would not be properly described as random fluctuation, since it is explicable to some degree and can be partially accounted for by hydrographic effects.

Calculated and observed depth distributions of chlorophyll before, during, and after the first intense algal bloom in 1966 are compared in Fig. 17. It is evident that the near-surface concentrations are fairly well represented, although the predicted profile is smoother than that inferred from the observations. It is also apparent that the model fails to reproduce concentrations near and below the euphotic zone when the bloom is in progress. This particular shortcoming was anticipated in our earlier discussion of boundary condition in Eq. (5), for the reasons cited there. In addition, minimal phytoplankton concentrations are predicted by the model below the halocline in the region around 20 m depth, possibly as a result of low net *in situ* production, combined with an underestimate of mixing, resulting in insufficient downward transport of near-surface algal material and upwelled seed stock from depth.
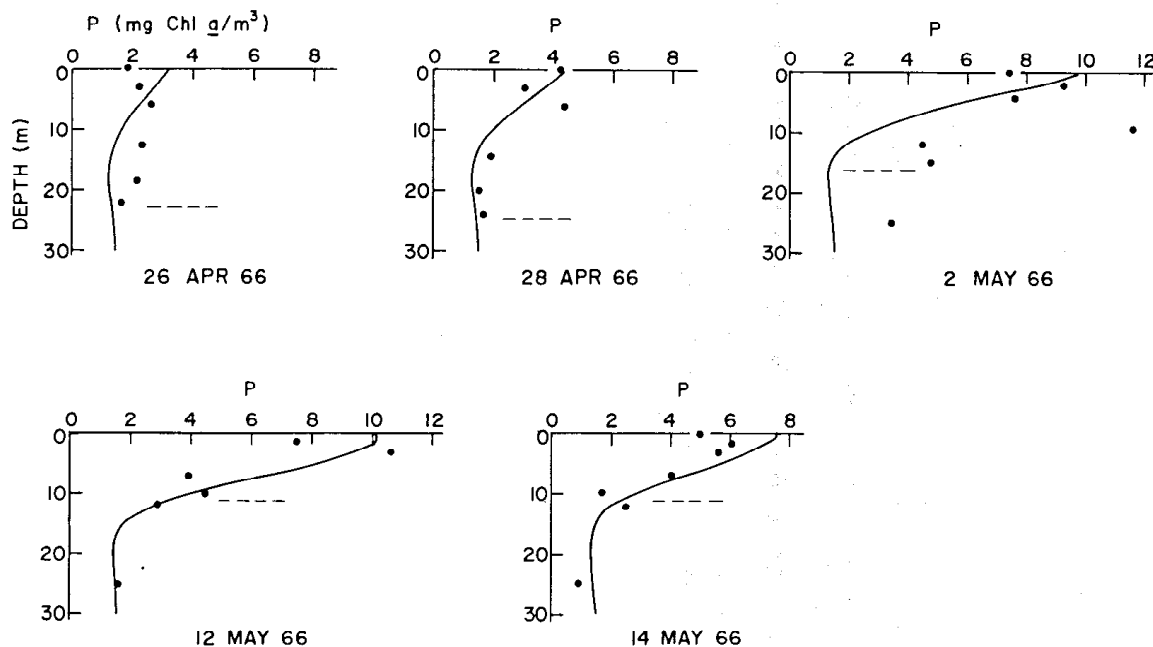
Fig. 17. Comparison of measured and calculated chlorophyll *a* concentrations as functions of depth at Station 1 before, during, and after algal bloom in 1966. Dashed lines: estimates of 1% light depths

Numerical Experiments. In order to evaluate the relative importance of the several processes governing primary production, as well as to elucidate further the causes of the disparities between observed and predicted parameters, we have performed a number of numerical experiments with the model. In the remainder of this section, we present some of the results of numerical experimentation with the biological submodels. As pointed out earlier, the term in Eq. (6) which describes the specific algal growth rate was formulated in a conventional manner and it is, therefore, unnecessary to extend the discussion already provided in the last section. In our opinion, the choice between our representation of P_r and other functions describing the net specific growth rate cannot be made on the basis of historical data like ours. Instead, it would require a new laboratory or field program specifically designed for the purpose. Since the same argument holds for the other biological functions, we forego experimentation with functional forms, except for that describing respiration. We concern ourselves instead with parameters in these functions, most of which were chosen on the basis of literature studies. The results of numerical experimentation will indicate the sensitivity of the model to these coefficients and constitute thereby an elaboration of the standard run. Moreover, they may indicate which biological measurements require emphasis in future field work and which biological processes should be intensively studied in the laboratory. In the experimentation, we varied only one factor at a time and did not analyze the results of various combinations of parameters. Finally, we confined the study to gross effects and did not search for the "best fit" with statistical analyses of manipulated data.

The conclusions of this experimentation should be of general applicability because of the largely conventional choice of the biological functions.

Nutrient Dependence. Fig. 18 demonstrates the effect of nutrient depletion on algal growth over the 1967 study period. During both years the inclusion of nitrate limitation appears to have two effects: (1) the rapid development of algal blooms is generally delayed by about 2 days, although the dates of maximum standing stock are unchanged; (2) specific production and standing stock are significantly reduced during periods of sustained low nitrate concentration. The first of these effects is unimportant since it represents the cumulative effect of a slightly lower gross production due to the fact that the values of the Michaelis-Menten factor $g(N)$ are usually somewhat between 0.9 and 1.0 when nutrients are plentiful. The second effect is genuine and of potential importance inasmuch as nutrient limitation occasionally overrides all other factors that normally control the population level.

Although the inclusion of a time-lag effect proved useful, additional experiments both in the laboratory and in the field are needed to elucidate the processes which it actually represents. Our choice of τ equal to 72 h was influenced by field observations and is considerably greater than values suggested by pulsed chemostat experiments (Caperon, 1969). The use of a time lag shorter than 72 h would have decreased the difference between the solid and broken lines in Fig. 18 during the period prior to 20 May, but the improvement would be superficial, as pointed out above. During the last 10 days of May, 1967, when there was an extended period of low nitrate content, the dis-
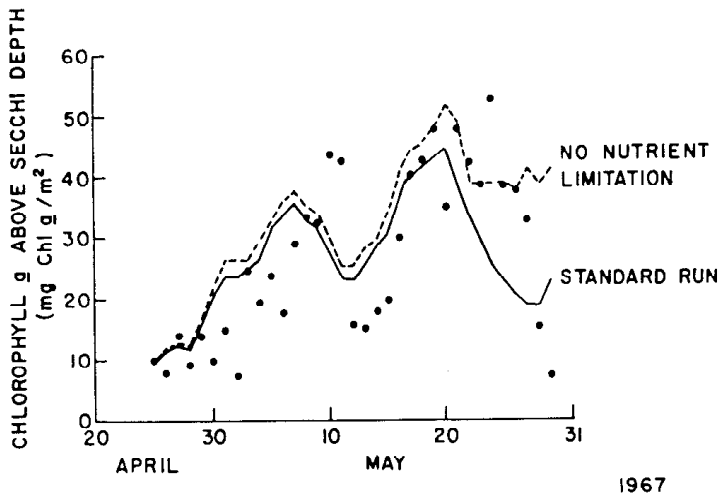
Fig. 18. Effect on algal standing stock of removing nutrient limitation during 1967 study period
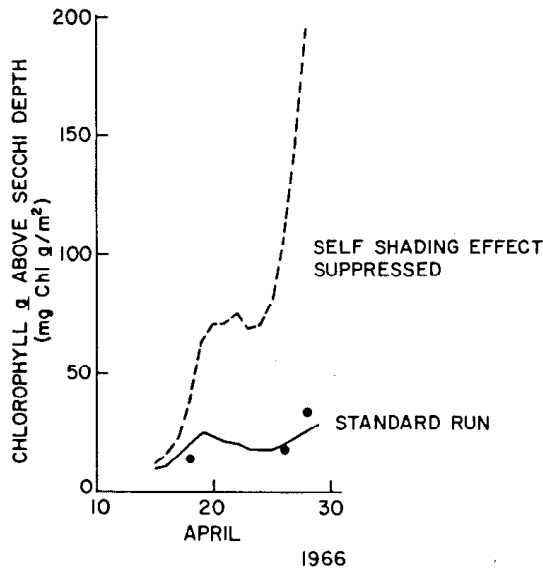

Fig. 19. Illustration of importance of self-shading in curtailing algal growth during last 2 weeks of April, 1966
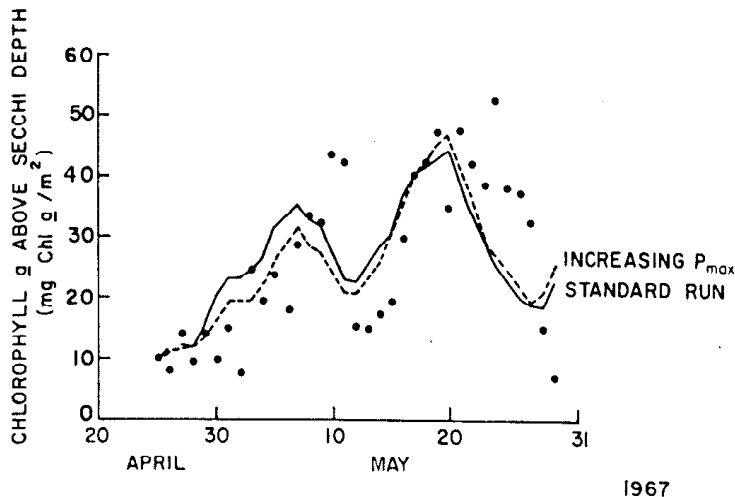

Fig. 20. Effect on algal standing stock of linear increase in p_{max} from 3 to 5 mg C/mg chlorophyll a/h during 1967 study period

crepancy between prediction and observation would have been enhanced.

Extinction Coefficient. It was suggested earlier that the constants in Eq. (13) could probably be improved by a more careful treatment of the historical data, but that the effort would be more profitably spent on field studies using modern instruments. For that reason, we include here only part of a calculation in which k_3 was set equal to zero in order to suppress the effect of self-shading. The result (Fig. 19) is an intense proliferation of algae in the near-surface zone following just a few consecutive days of favorable light. This is contrary to the field observations and underlines the necessity of incorporating self-shading into models of this type (cf. Riley, 1965, in contrast with Steele, 1958).

Maximum Specific Productivity. Nearly all parameters adopted for the standard runs were chosen either from the literature or were based on Puget Sound field work which was essentially independent of the present study. The reason for this constraint was to avoid bias in comparing computed results with data and in evaluating the effectiveness of the modeling technique. The one important exception was the assignment of p_{max} from carbon-uptake rates measured during the cruise sequence. We have already described the difficulty of interpreting the cruise measurements and deciding upon a suitable estimate for p_{max}. The selection of the appropriate value for I_{max} was less difficult because the choice was ultimately based on an interpretation of relatively dependable insolation data. Of course, it may be argued that the basis for our choice of I_{max} was incorrect, but that is a separate question.

The sensitivity of chlorophyll levels to parameters describing algal metabolic processes is illustrated in Fig. 20, which shows the results of allowing p_{max} to increase linearly from 3 to 5 during May, 1967. The results are not as striking as one might expect from Eq. (6), in part because of the self-shading effect and the larger absolute losses from an increased population when sinking rates and turbulence remain the same. The greatest divergence between the two runs depicted in Fig. 20 would be expected at the beginning and the end of the period, when the difference between the constant p_{max} of the standard run and the run with seasonally changing p_{max} were greatest. Some days with low incident radiation during the last days of April (Fig. 3), however, and nutrient limitation during the last 10 days of May (cf. Fig. 18) prevented the development of a marked divergence in the computed algal stocks. It should be intuitively obvious, however, that a different combination of environmental factors could lead in a few days' time to a pronounced surge of algal concentration. For example, several days of consistently high solar radiation combined with low

surface salinity and sufficient nutrients could produce an algal population adapted to high light intensity, whose p_{max} was enhanced by a temperature increase of 3° to $5C^\circ$, and which was subject to low rate of loss by turbulent mixing.

We note that standard runs (Fig. 16) seldom lead to chlorophyll values higher than those observed which suggests that, on the average, the calculated algal concentrations are slightly too low. In addition, it will be shown below that the grazing losses must have been underestimated in the standard runs, so that it seems likely that we underestimated the algal growth rate, as well (i.e., p_{max}). We cannot offer a simple explanation as to why the field data on carbon uptake may have yielded rates which are too low. Variable losses of ^{14}C from filters stored over desiccant may contribute to the low values (Wallen and Geen, 1968). Another possible source of bias could have been the use of neutral density filters without correction for color in the simulated *in situ* experiments. As shown by Kiefer and Strickland (1970), accurate simulation of photosynthetic rates can be achieved under neutral-density filters provided the underwater attenuation of irradiance is measured in the green. This requirement was approximately satisfied in our experiments, since the attenuation coefficient was estimated with a Secchi disk that appeared blue-green or green when submerged. Nevertheless, if a bias were to exist, it would indeed lead to an underestimate of p_{max}.

Our experience leads us to reiterate strongly the statement by Steemann Nielsen and Hansen (1961) that, in studies of this kind, an effort must be made to obtain directly the values for p_{max} and I_{max} appropriate to a particular algal community, rather than use a standard curve or attempt to infer these parameters from measurements of simulated *in situ* productivity. Also, in order to improve model reliability, it will be necessary to gain a better understanding of the close association between the maximum specific productivity of a phytoplankton community, its carbon-to-chlorophyll ratio and respiration rate, and the relationship of these parameters to supplies of essential nutrients and to water temperature.

Respiration. Discussion is in order regarding two special attributes of our description of algal respiration: (1) the decrease of the specific respiratory rate with increasing depth; (2) the distinction between daytime and nighttime respiration. Both features assume importance when the specific rates at the surface are as high as approximately 0.018 mg C/mg C/h. This value results largely from the fact that a low carbon-to-chlorophyll ratio is applied to experiments by Ryther and Guillard (1962) which express respiration per pigment unit; this leads to 24-h losses of almost one-third of gross photosynthesis.
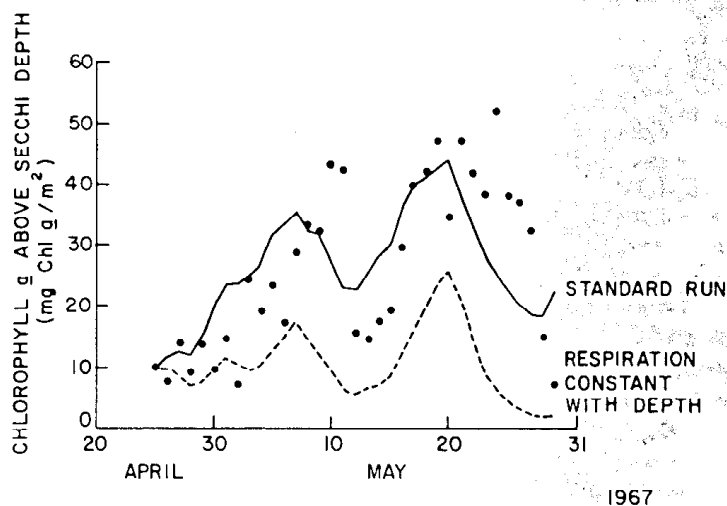

Fig. 21. Effect of a respiration rate which is equal to its surface value at all depths during 1967 study period

The importance of describing correctly the vertical variation of algal respiration is illustrated by a numerical experiment which assumes an absence of depth dependence (Fig. 21). It predicts a marked decrease of integrated concentrations of chlorophyll in the euphotic zone and a dramatic decline in pigment concentrations in the lower part of the illuminated layers (not shown). Since neither response is observed in the field under favorable growth conditions, our formulation in the standard run is supported.

Among earlier workers who included respiration explicitly into models, McAllister (1969), in his study of primary and secondary production from time series, calculated depth-integrated production using average values for the euphotic zone. He found that, in order to obtain positive grazing rates (i.e., to provide a ration to the herbivores) it was necessary to reduce the hourly phytoplankton respiration rate from 0.01 (a value suggested by perusal of the literature) to 0.005 mg C/mg C/h. Similarly, other quantitative treatments of phytoplankton distribution, which modeled average concentrations over the euphotic zone, used lower rates than the surface rate employed herein (e.g. 0.0015 mg C/mg C/h in Steele, 1958; 0.003 in Parsons and Anderson, 1970). Although we have not routinely calculated the average value of our respiration rate over the euphotic zone, rough estimates of that quantity show that it is of the same order of magnitude as the values just cited (i.e., about 0.006 mg C/mg C/h).

In contrast with the importance of depth variation, the incorporation into the model of photorespiration turned out to be immaterial because the low p_{max} chosen led to daytime rates which were only slightly higher than the nighttime rates.

In conclusion, it is apparent that an accurate and reliable description of respiration has eluded

us in this study. It is our opinion that nothing
short of new measurements will suffice to answer
the crucial questions concerning algal respira-
tion.

Sinking Rate. The sinking rate of phytoplankton
is among the variables which cannot be routinely
measured in the field. As stated, we based our
choice of 0.5 m/day on laboratory studies. By
contrast, other models of phytoplankton growth
in offshore waters and the open sea have employed
rates which are higher by at least a factor of 5
(Steele, 1958; Riley, 1965).

The consequences of changing the sinking rate
to zero and to 3 m/day are depicted in Fig. 22.
Evidently, the assumption of neutral buoyancy
does not affect the integrated chlorophyll con-
centration greatly, when compared with the stan-
dard run. A sinking rate of 3 m/day, however,
removes most algae from the layer above the Secchi
disk depth. The reason for this becomes clear
upon consideration of Fig. 23, which compares the
instantaneous noontime value of phytoplankton
flux on 28 April, 1966 at several depths due to
turbulent mixing, upwelling associated with grav-
itational convection, and the sinking of algal
cells. The results are computations from the stan-
dard run; the vertical velocities are given in
Fig. 14 and the chlorophyll concentration at noon
in Fig. 17. Above the Secchi disk depth, downward
transport by sinking and turbulence exceeds the
upward flux due to upwelling, but not by so great
an amount as to nullify the effectiveness of
photosynthesis or even to prevent the occurrence
of algal blooms. However, if the sinking rate is
increased by more than a factor of 5 (to 3 m/day),
this is no longer the case and the upper part of
the euphotic zone is depleted of cells at a rate
comparable with that of growth and reproduction.

It has been suggested that the sinking term in
some models of primary productivity may actually
include losses other than sinking and that suc-
cessful model replication of observed data with
a particular sinking rate does not indicate that
the correct sinking rate has been assigned. The
criticism refers to two-layer models where the
criterion for "success" is matching the observed
average pigment concentration in the top layer,
analogous to the integrated chlorophyll concen-
tration in our model. By contrast, however, the
dependent variable in the present model is a
continuous function of depth, allowing for the
additional comparison of computed and observed
vertical distributions and, thereby, lending
greater confidence to our choice of sinking rate.

Finally, it should be pointed out that if
average sinking speeds for the algal cells in
the surface layer are low, it is also possible
that low sinking rates prevail in the upper part
of the intermediate zone, below approximately
25 m. This is most likely to be true when the net
downward flux of phytoplankton mediated by hy-
drodynamic factors is high, as illustrated in
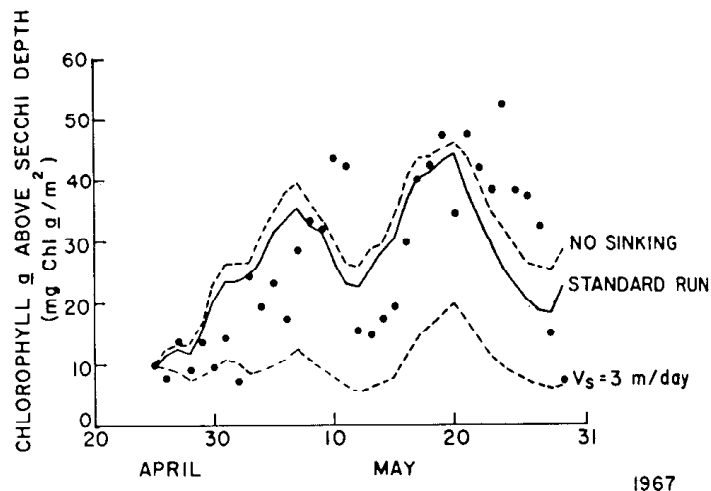Fig. 23. Because of the great vertical distance

Fig. 22. Effect of different sinking speeds on
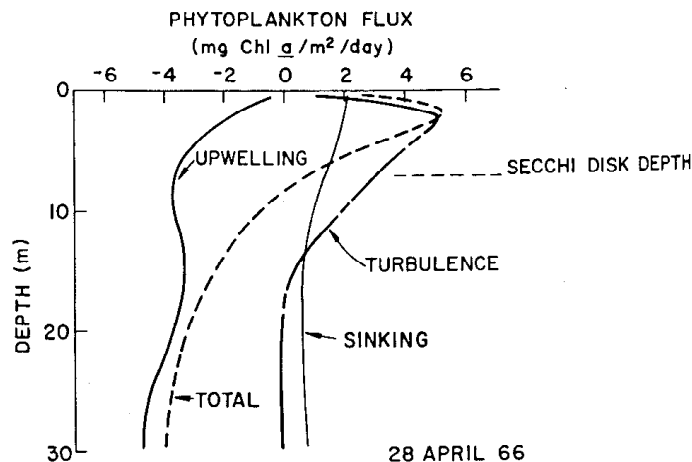algal standing stock during 1967 study period

Fig. 23. Depth variation of algal flux due to
turbulent mixing, upwelling, and sinking for
standard run at noon on 28 April, 1966

to the upper part of the deep zone (approximately
100 m) and the rapid advection of deep water from
the sill at Admiralty Inlet (only a few days), it
is likely that most of the cells found at great
depth at Station 1 are derived from processes
occurring at the sill. In contrast, the phaeo-
pigment fraction of chlorophyll observed at great
depth could originate at Station 1 near the sur-
face from zooplankton grazing and reach the deep
zone as fecal pellets which have high sinking
speeds.

Grazing Losses. The comparison of the standard
run with a calculation that omits grazing (upper
line, Fig. 24) shows that the grazing as in-
corporated in the model delays the mass develop-
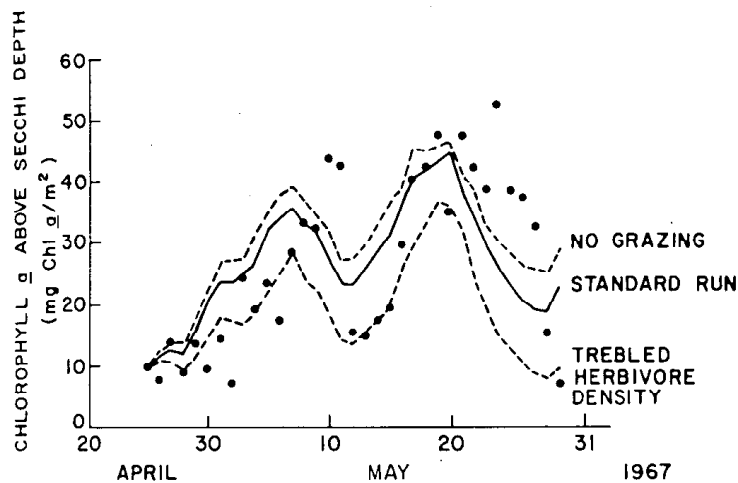ment of algae by about 2 days, but does not shift

Fig. 24. Effect of different herbivore densities on algal standing stock during 1967 study period

the time of occurrence of maximal algal concentration. The highest values of standing stock attained with grazing are not markedly lower than those with no zooplankton present. A discussion of the minor role of zooplankton, which is due to low animal concentrations, seems warranted as this is a highly unusual situation for temperate waters. The copepod concentrations in a subsidiary fjord of Puget Sound are much higher than those at Station 1 (Damkaer, 1964), as are those in the Strait of Georgia (e.g. Parsons *et al.*, 1969a, 1970), although the annual primary production is lower than that in the central basin of Seattle. Similarly, euphausiid concentrations in the central basin are lower than in subsidiary fjords of Puget Sound (W. I. Aron, personal communication; Cooney, 1971) but no explanation is readily apparent. To demonstrate that our grazing estimates for the zooplankton collected by nets are reasonable, we will first show that the grazing coefficients used were high. We will then comment on the total amount of zooplankton present.

The choice of a single grazing coefficient not only neglects differences among zooplankton species, but also ignores the role of different kinds of food within species (see Nassogne, 1970; Schindler, 1971). The maximal ration, when expressed as carbon, however, does not depend on the kind of food, as long as it is suitable (e.g. Sushchenya, 1969; Frost, 1972). The assigned maximal daily ration [Eq. (17)] is 43% of the body weight, and is comparable with the highest rates reported by Parsons and LeBrasseur (1970) for local species. However, in our case it is reached at a lower concentration of food than in their studies. The assigned value for the maximal ration is also similar to the highest found by Mullin and Brooks (1970) at 15°C for developmental stages of two copepod species which were of the same size as *Pseudocalanus* sp. females. The value is close to that obtained by Frost (1972) for local *Calanus*

sp. when size difference is taken into account by the formula of Sushchenya and Khmeleva (1967). In contrast, Parsons and LeBrasseur (1970) often found quite low grazing rates in the Strait of Georgia, British Columbia, with natural plankton as food. This suggests that local algal assemblages may be at times unsuitable for many local copepods.

With our carbon-to-chlorophyll ratio and coefficients of the Ivlev function, a ration level of 90% maximum is attained at chlorophyll concentrations of about 8 mg chlorophyll a/m^3, which is common only when blooms are in progress. Therefore, the modeling of grazing is sensitive to the slope in the Ivlev function [k_a in Eq. (17)]. Within a zooplankton species, at food concentrations below those at which the maximal ration is reached, large food particles result in higher rations than smaller ones, i.e., the initial slope of the Ivlev function is steeper (see Frost, 1972). Our value for k_a is likely to be somewhat high for *Pseudocalanus* sp. because of the food size utilized in the experiments on which we based our choice of k_a. We conclude that the modeling of grazing by the zooplankton collected by the net is unlikely to have led to an underestimate of grazing.

The second experimental run of the model (lower line, Fig. 24) represents an attempt to account for the animals too small to be retained by the sampling net. The choice of an average biomass value is based on counts of nauplii and ciliates in a few water samples taken near Station 1 in 1964 and 1966 (Hirota, 1967; J.M. Dewey, personal communication). Multiplication of the calculated biomass data by reasonable specific respiration rates (cf. Hemmingsen, 1960) suggested that ciliates could be neglected. The daily ration of nauplii was estimated from extrapolation of values by Mullin and Brooks (1970) for 15°C. The herbivore biomass entered in the experimental computation was adjusted so that a correct maximal ration would be obtained when using the same Ivlev coefficients as before. Thus, we increased the biomass by a factor of 3, with the result shown in Fig. 24. The experimental run predicts a marked reduction of algal concentrations, although the timing of the occurrence of maxima is largely unaffected. During the first half of the run, the incorporation of small zooplankton leads to a better representation of the average pigment concentration except for a few days around 10 May, 1967. The prediction for the later half of the 1967 study period is unsatisfactory. However, nutrient limitation prevailed much of the time (e.g. Fig. 18), and it is unrealistic to omit nutrient regeneration by zooplankton in any of the experimental runs shown in Fig. 24.

Our description of grazing assigns minor roles to diel migration and to large forms not collected by the net. As mentioned earlier, the evidence for diel migration into the surface layer from our own data is ambiguous. Almost no published investigation of small zooplankton collected by nets is available for fjord waters of the Pacific

Northwest during the summer or spring. A single exception is the study by Cameron (1957) in the Queen Charlotte Islands, but this does not lend itself to an assessment of the relative role of the migrator in terms of biomass. However, diel migration of a sound scattering layer consisting largely of euphausiids has been studied near our station by Cooney (1971). In summer, the layer is found in the daytime at 50 to 80 m depth and migrates at night up to at least 20 m. A high count of the dominant *Euphausia pacifica* in the surface layer at this time of the year is 10 m³. Conversion of the length of these individuals (5 to 7 mm; Cooney, 1971) into mass by the relationship of Lasker (1966) gives an estimate of 2.0 to 4.5 mg C/m³ as entering the surface layer at night. This is a negligible addition to grazing pressure, especially as the specific grazing rate must be low. Also, the maximal ration of euphausiids is attained only at very high plant concentrations (Parsons *et al.*, 1967; Parsons and LeBrasseur, 1970). Cooney's observations further suggest that, in terms of biomass, few other large organisms have been missed by our net in the surface layer.

Obviously, there still remains great uncertainty about the concentration of total zooplankton and about the appropriate way to describe its grazing effects. However, there is little doubt that small zooplankton was present in quantity during 1966 and 1967. Therefore, since the standard runs predict the right level of chlorophyll in the upper layers despite the fact that grazing losses were underestimated, it seems likely that either we have underestimated p_{max}, or other sources of loss of plant material were overestimated.

Conclusions

We have described in this paper a detailed quantitative analysis of the dynamics of spring phytoplankton blooms in the central basin of Puget Sound with the aid of a numerical model. The calculations of the standard run reproduced most of the general features of data acquired in a cruise sequence carried out during the springtime months in 1966 and 1967. The results of the standard runs and the numerical experiments with the model confirm the existence of a close relationship between the circulation and the physical and chemical properties of the water, climatic (light) conditions, and the level of primary production in Puget Sound. The model is general enough to be applicable to other temperate fjords provided that the constraints on the physical submodel are satisfied and that nutrient exhaustion is not a major feature. Incorporation of nutrient regeneration by zooplankton would be necessary in the Strait of Georgia and in fjords subsidiary to the central basin of Puget Sound where nitrate levels are low over extended periods.

This study lends further support to the notion that the estuarine mechanism supplies the euphotic zone with algal seed stock from depth and replenishes exhausted supplies of essential nutrients during vigorous flowering. A complete quantitative verification of these hypotheses is somewhat beyond the present state-of-the-art, since it would require the development of fjord circulation models which include the influence of bathymetry (especially sills) and changing hydrographic conditions in external source waters. Nevertheless, various results of the model computations, such as the flux-component profiles shown in Fig. 23, indicate that the high productivity of Puget Sound is due to strong, persistent upwelling of nutrients and algal cells from depth. It would appear that during the spring and early summer the quantity and quality of fresh-water runoff in the central basin is such as to maintain moderately intense gravitational convection without producing an excessively turbid, brackish, surface layer.

In contrast with the situation in the open sea, the mixing processes in the main channel of Puget Sound do not create a deep mixed layer within which primary production is light-limited. Instead, algal growth in the central basin is limited by a combination of hydrodynamic factors (as illustrated in Fig. 23) and modulation of the underwater light intensity by self-shading and by inorganic particulates. On occasions of sustained winds, standing stock is limited by relatively short residence times determined by horizontal advection. Evidently, the late occurrence of spring blooms in fjords like Puget Sound is not explainable in terms of the critical depth concept originally proposed by Gran and Braarud (1935) and Sverdrup (1953).

In the central basin of the Sound, several consecutive days of bright sunshine are sufficient to promote massive development of phytoplankton. Given the right combination of weather, water stratification, and flushing characteristics in the upper brackish zone, blooms might also occur earlier in the year, but apparently these instances are somewhat uncommon and have not been observed during 1964 and 1965. As noted above, horizontal advection by sustained winds will remove blooms from the central basin; prolonged nitrate depletion and a succession of cloudy days will discourage vigorous growth and will cause a bloom to decline in intensity. At the same time, however, the effects of grazing by herbivorous zooplankton and cellular sinking are of secondary importance. Because of the rather rare occurrence of nutrient limitation during the spring and the light limitation that prevails during the fall and winter months, nutrient addition from sewage treatment plants is not likely to change the level of primary production in the main channel significantly; perhaps, species composition is altered, but no direct observations are at hand. It is likely that this conclusion holds also for the summer season, in consideration of our 1964 and 1965 field investigations.

We conclude that the functions and parameters traditionally employed to describe phytoplankton metabolism are marginally adequate for use in a

short-time scale model, such as the one developed here. Certainly, our present ability to describe quantitatively the response of phytoplankton to changing environmental stimuli is much too limited to permit the construction of predictive models of algal growth which are both reliable and generally applicable to all fjords. Then, one might ask, why attempt to construct models of systems with biological components? Part of the answer is given by our own experience in attempting to model part of the Puget Sound ecosystem: in the course of the modeling effort, new relationships amongst the system components are often perceived, traditional descriptions of processes are re-evaluated from different perspectives, experimental priorities are clarified, and new experiments are frequently suggested. To the extent that these contribute to an improved understanding of the system under study, the numerical model is a legitimate investigative tool and the modeling effort is justified.

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