

AN ABSTRACT OF THE THESIS OF

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Title: A SYSTEMS APPROACH TO PELAGIC ECOSYSTEM
DYNAMICS IN AN ESTUARINE ENVIRONMENT

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Herbert C. Currier, Jr.

Phytoplankton dynamics in Auke Bay, Alaska, were studied during summer, 1969. Nitrate, chlorophyll a, particulate organic carbon, phytoplankton and zooplankton species composition and hydrographic and meteorological data were collected and analyzed.

Nitrate input into Auke Bay through freshwater runoff was negligible. A bloom of Thalassiosira aestivalis formed the spring bloom in Auke Bay in 1969. No phytoplankton bloom occurred during a June period when winds were light and variable. Two major blooms of Skeletonema costatum occurred after periods when Auke Bay surface layers were mixed by wind-induced turbulence. The water column became nearly isothermal after periods of high wind mixing although a pronounced density and halal structure persisted, a consequence of input of freshwater to the bay from Auke Creek.

Examination of fecal pellets collected from the bay and results of laboratory grazing experiments suggested that Skeletonema costatum was not grazed by zooplankton living in Auke Bay.

Nonlinear ordinary differential equations were written to describe phytoplankton and nitrate dynamics in Auke Bay. The phytoplankton dynamics equation included formulations for time-varying insolation and for time-varying wind mixing coefficients. Formulations for effects of nitrate concentration on the photosynthetic assimilation number and for effects of phytoplankton standing crop on the extinction coefficient of light in the water column were included.

The nitrate dynamics equation included a formulation for effects of wind-mixing of nitrate-rich water into the euphotic zone from deeper layers of the water column, as well as a formulation for utilization of nitrate in phytoplankton growth.

Computer simulation response of the equations reproduced the bloom pattern observed in the field data with some discrepancies caused by assumptions used in model development. The phytoplankton and nitrate model response was strongly coupled to the pattern of the wind-mixing coefficient, as required by the field data. Variations in model parameters had little effect on phase relations between model response and field data but strongly affected model response magnitude.

A Systems Approach to Pelagic Ecosystem
Dynamics in an Estuarine Environment

by

Richard Lowell Iverson

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Harold O'Connors and Ms. Kathleen Welch spent many hours in a small boat, The RV FUBAR, aiding me in collecting the data on which this thesis is based. Most of the phytoplankton group at Oregon State contributed aid in untangling the logistic and analysis snarls generated by this project. The staff of the Coastal Oceanography Laboratory, National Marine Fisheries Service, Auke Bay, Alaska, were most generous in their logistic support for this project. Work

done in Auke Bay by Dr. Herbert E. Bruce laid the groundwork on which this project was based.

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A SYSTEMS APPROACH TO PELAGIC ECOSYSTEM DYNAMICS IN AN ESTUARINE ENVIRONMENT

I. GENERAL INTRODUCTION: THE SYSTEMS APPROACH IN ECOLOGY

Bertalanffy developed a concept called general systems theory in the late 1930's. The subject matter of general systems theory was to be "the formulation and derivation of those principles which are valid for systems in general" (Klir, 1969, p. 97). Several workers have attempted to develop a formal calculus for general systems theory (Zadeh and Polack, 1962; Klir, 1969) but at present, general systems theory must be considered a philosophical framework not to be confused with more pragmatic disciplines called systems engineering and systems research. An approach to quantitative ecology called systems ecology has been developed within the last decade; systems ecology is founded on techniques of systems modeling, simulation and analysis taken from systems engineering and systems research.

Rapaport (1970, p. 15) did not consider it possible to give a precise definition for "system" because "the word is understood in several different senses, all equally legitimate and sanctioned by wide usage". A definition which Rapaport (1970, p. 17) felt to be relatively unambiguous was "a system is a portion of the world which at a given time can be characterized by a given state together with a

set of rules that permit the deduction of the state from partial information. The state of a system is a set of values of certain variable quantities at the moment of time in question". Dale (1970, p. 3) considered a system to be "a collection of parts together with statements on the relations, of some kind, between these parts".

The primary emphasis in systems ecology is the construction of mathematical models for ecological systems. Models are used for computer simulation of systems dynamics or for systems analysis, two distinct endeavors which are related through the systems model (Patten, 1971). Computer simulation is either analog or digital computer solution of system equations in order to investigate effects of various formulations for physiological or ecological processes on model response. Variation of parameter values between simulation runs is a common experiment performed in computer simulation.

Dale (1970, p. 1) discussed several viewpoints on systems analysis in ecology and defined systems analysis as "the application of scientific method to complex problems, the application further distinguished by use of advanced mathematical and statistical techniques and by use of the computer". More specifically, systems analysis is the application of a body of analytical and numerical techniques in order to determine properties of systems models such as stability in the face of perturbations applied to elements of the system. While systems analysis has been successfully applied to models of physical

systems, systems analysis has not yet proved fruitful in application to models for ecological systems. This is a consequence of the nature and quality of models for ecological processes. Differential equations written to describe simple interactions of two populations of organisms are nonlinear, for example:

$$\dot{N}_1 = N_1(a_1 + b_1 N_2)$$

$$\dot{N}_2 = N_2(a_2 + b_2 N_1)$$

where \dot{N}_1 and \dot{N}_2 are time rates of change of some measure of populations N_1 and N_2 , a_1 and a_2 are coefficients of increase and b_1 and b_2 are coefficients of increase which depend on the nature of the interaction between the two populations (Volterra, 1928). More realistic equations written to describe ecological processes where many populations interact with each other and with the environment contain vastly more complicated nonlinearities. For this reason the powerful body of linear system techniques is not available for use with realistic models for ecological systems. Since systems analysis is based on the model for the system, the analysis is dependent on the quality of the model, on how well the model represents the system. Ecological processes are not very well known in the sort of detail required to write mathematical expressions which are good mechanistic representations for the processes. For these reasons and because the systems approach to ecology is still very young, systems ecology is strongly identified with development and investigation of computer simulation

models.

Bibliographies which contain titles and abstracts of mathematical models in ecology have been compiled by Newell and Newton (1968), O'Neil, Hett and Sollins (1970), and Kadlec (1971). Texts which treat mathematical ecology or systems ecology have been written by Watt (1968) and Pilou (1969) and edited by Waterman and Morowitz (1965), Watt (1966) and Patten (1971).

This thesis consists of two sections. The first section is a classical treatment of the phytoplankton ecology of a small embayment in a large fjord-estuarine system, Auke Bay, near Juneau, Alaska. A mathematical model for summer phytoplankton dynamics in the bay is developed in the second section. Properties of the model are investigated through computer simulation.

Since models should not be constructed indiscriminantly without real necessity or real purpose (Kac, 1969), there should be some justification for time and effort involved in model development. The scientific method is generation and testing hypotheses about phenomena. A hypothesis can be purely verbal. However, if the hypothesis is stated in a quantitative manner, it is amenable to a more demanding test by comparison of measures. In addition, the quantitative statement provides a clear description of the level of knowledge about the phenomenon. From a more pragmatic viewpoint, a model for phytoplankton dynamics can form the basis for management decisions

concerning the use of a body of water for which the model has been validated. For example, potential consequences of introduction of growth stimulating or inhibiting substances into the body of water could be studied through computer simulation of equations containing formulation for effects of the substances on phytoplankton growth.

SUMMER PHYTOPLANKTON BLOOMS IN AUKE BAY, ALASKA,
DRIVEN BY WIND-MIXING OF THE WATER COLUMN

Introduction

The classical pattern of phytoplankton growth in temperate ocean waters begins with a spring bloom following stabilization of the water column by absorption of solar radiation in the upper 100 meters (Raymont, 1963). During the summer, a strongly developed thermocline prevents transfer of nutrients into the upper lighted layers of the water column, the euphotic zone, hence standing crop of phytoplankton is generally low with some minor blooms occurring. Cooling of surface layers coupled with wind-mixing caused by fall storms results in nutrient input into the euphotic zone with concomitant phytoplankton blooms during the fall. The fall blooms are usually of lower magnitude and shorter duration than the spring bloom. A well-mixed water column and low solar insolation during the winter prevents blooms from developing although phytoplankton growth can occur during the winter (Ryther and Hulburt, 1960). This pattern is shown in seasonal changes in phytoplankton in Husan Harbor, Korea (Riley and VonArx, 1949) where midwinter minima and spring maxima were considered to be controlled primarily by radiation while time, duration and relative magnitude of summer and autumn phytoplankton blooms were attributed to changes in nutrient concentrations in the euphotic zone.

Stability of the surface layers of the water column as a prerequisite for onset of spring phytoplankton blooms was first suggested by Atkins (1928) to explain yearly variations in time of occurrence of the spring bloom in the ocean (Gran and Braarud, 1935). Pifer (1933), Gran and Braarud (1935), Iselin (1939) and Riley (1942) used the concept to explain onset of spring blooms in diverse regions. Sverdrup (1953) presented a mathematical formulation for effects of the surface mixed-layer depth on phytoplankton growth and showed that the formulation explained onset of a spring bloom in the Norwegian Sea. Steele (1966) and Parsons and LeBrasseur (1968) showed that Sverdrup's formulation accounted for the observed northward sweep of spring phytoplankton blooms in the North Atlantic and North Pacific Oceans, respectively. Smayda (1957) demonstrated that in the relatively shallow Narragansett Bay, tidal mixing prevented development of a stable water column, hence stability was not an important factor controlling phytoplankton blooms. Stability of waters outside the bay acted to contain phytoplankton populations within the bay hence enabled blooms to develop. Gilmartin (1964) found that seasonal variability in stability of the water column in a British Columbia fjord was the primary factor controlling phytoplankton production in the fjord.

I was interested in studying phytoplankton growth during the summer period in a location where the water column was highly stable. By sampling several times a week, rather than several times a month

which is a typical sampling interval reported in the literature, I hoped to discover the cause of summer phytoplankton blooms under conditions of continually high water column stability. Auke Bay was well suited for such a study as it is a small embayment in a large fjord-estuarine system in Southeast Alaska (near Juneau). Auke Bay is about 110 km from the ocean and is relatively isolated from oceanic effects and from major currents within the estuarine system. The Auke Bay Coastal Oceanographic Center, National Marine Fisheries Service, located on Auke Bay, provided convenient access to the bay.

Bruce (1969) has described physiographic and physical and chemical oceanographic features of Auke Bay (map 1). Auke Bay has an area about 11 km² and is deep enough (mean depth about 40 meters) so that tidal effects (spring tide range 6 meters) do not destroy water column stability during the summer. Bruce described major features of phytoplankton blooms in the bay and determined that availability of nitrate-nitrogen limited phytoplankton growth in the bay during the summer.

Methods

Temperature, Salinity and Sigma-T

Temperature and salinity were measured with a Beckman Model Rs5-3 in situ salinometer (CT) equipped with a thermister thermometer. The instrument was specified accurate to ± 0.3% for salinity

and $\pm 0.5^{\circ}\text{C}$ for temperature. The salinometer was periodically calibrated with standard sea water. Sigma-t values were obtained from tables (Keala, 1965). The extremes of the ranges of instrument accuracy at 29.5‰ salinity and 8.5°C gave a range in sigma-t of ± 2 percent of the mean.

Light

Solar insolation was measured with a Belfort recording pyrheliometer accurate to ± 5 percent. Daily records were gravimetrically integrated.

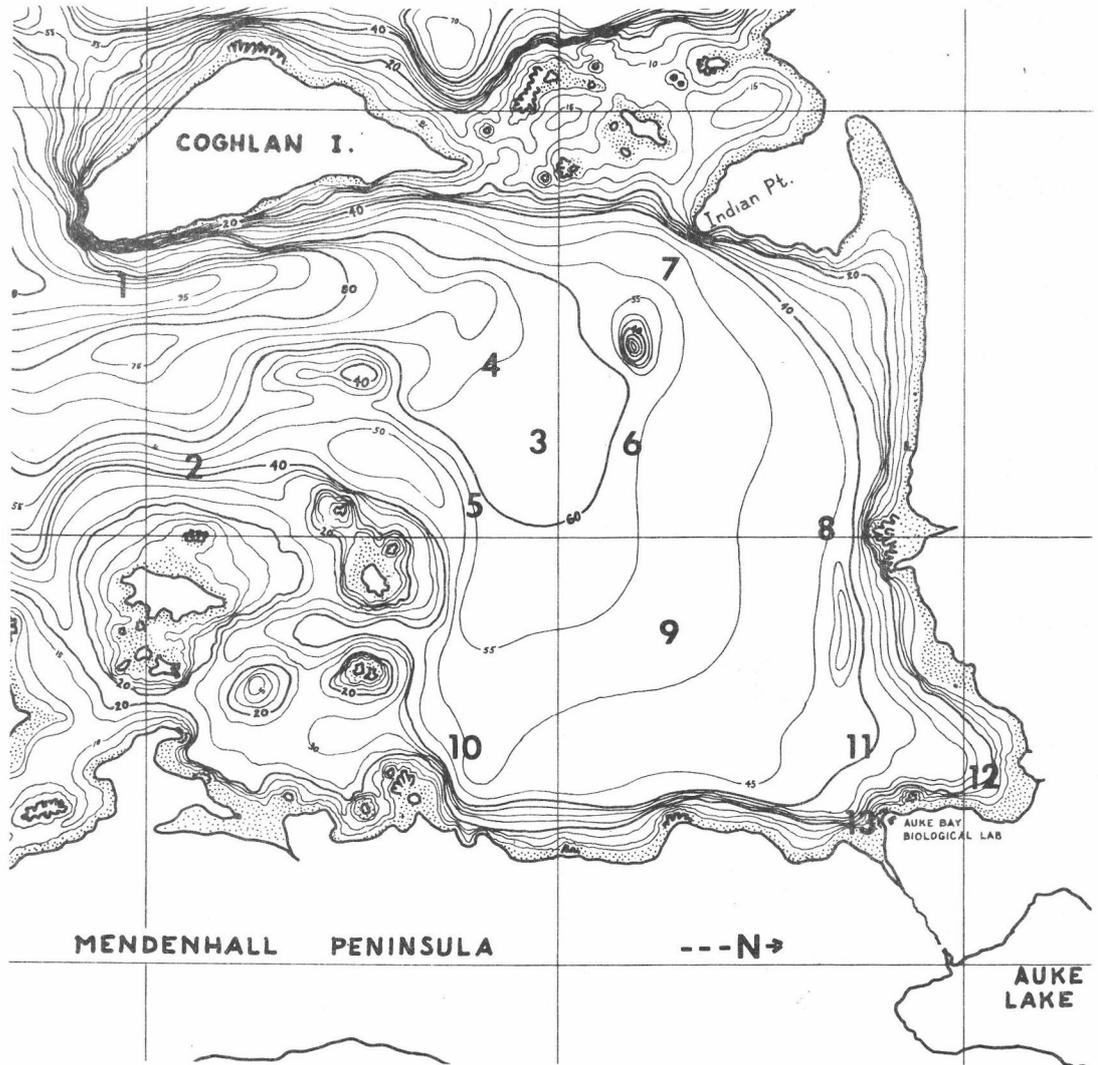
Submarine light intensity was measured with a Clarke photometer. Secchi depth measurements were obtained with a 25 cm, white Secchi disc.

Wind

Wind speed and direction were obtained from WBAN-10 forms compiled by the U.S. National Weather Service at the Juneau Municipal Airport.

Currents

Currents passing Auke Bay Monitor station (ABM) (map 1, station 3) from 9 June until 28 June were measured with Braincon type 381 current meters suspended at 2 and 12 meters. Histogram film



MAP I

records for the 20 minute sample intervals were digitized by Braincon Corporation and analyzed with the assistance of the coastal currents group at Oregon State University.

Nitrate-Nitrogen

Water samples for determination of nitrate concentration were taken with Van Dorn sampling bottles, frozen, then air-freighted to OSU for analysis. Nitrate concentrations were determined with a Technicon Autoanalyzer[®] by the method of Armstrong given by Hager, Gordon and Park (1968).

Chlorophyll a

Water samples taken with Van Dorn bottles were filtered through Millipore[®] AA 0.8 μ filters. A small amount of $MgCO_3$ was added to each of the filters which were then frozen and sent to OSU for analysis. Chlorophyll a was determined by the method of Strickland and Parsons (1965).

Phytoplankton Productivity

Phytoplankton productivity was measured with an in situ light-dark bottle technique. Glass screw-top bottles containing 180 ml of water and 2 μ Ci of ^{14}C and $NaHCO_3$ were incubated at the depth from which the sample was taken for three hours from 1000 to 1300.

Phytoplankton Enumeration

Phytoplankton species identification and cell numbers were determined microscopically with a Fuchs-Rosenthal counting chamber. Minimum population size detectable with the technique was 1×10^4 cells per liter in unconcentrated Van Dorn bottle samples.

Particulate Carbon and Nitrogen

Water samples taken with Van Dorn bottles were filtered through Whatman GF/A glass fiber filters. The filters were dried at 60°C , then processed with an F&M Model 185 carbon, nitrogen, hydrogen gas chromatographic analyzer.

Zooplankton

The composition, abundance and distribution of Auke Bay summer zooplankton were determined qualitatively from 14 June to 2 July from net tows; quantitative samples were taken from 2 July to 11 August. The quantitative sampling device was a volume-calibrated Clarke-Bumpus (CB) plankton sampler fitted with a number six mesh-size net. The sampler was towed at a slow speed to minimize wire angle. The station ABM was sampled on a routine basis with oblique tows from 15 meters to the surface.

Zooplankton species counts were made on subsamples from each formalin-preserved CB collection. Subsamples were measured with a graduated cylinder and represented about three percent of the total volume of the well-mixed sample.

On 2, 6 and 8 August, Van Dorn bottle water samples were filtered through Millipore® filters. Copepod fecal pellets were removed from the filters, transferred to cover glasses, broken apart and embedded in hyrax for microscopic examination for evidence of food organisms.

Results and Discussion

Sampling in Auke Bay

Surveys of Auke Bay were conducted in order to determine the spatial variability of density, chlorophyll a, phytoplankton productivity, zooplankton numbers and nitrate-nitrogen. Profiles for sigma-t (Figure 1) computed from data taken at stations 1, 3, 7 and 11 (map 1) at high tide on 22 August showed that density structure was very uniform over the bay at that time. Despite a possible + 2 percent error in sigma-t which could occur under combination of extremes in error of the CT device, the profile pattern does not suggest error; rather, the sequence suggests that the water column became slightly less dense down to 21 meters from Coughlan Island to the east end of the

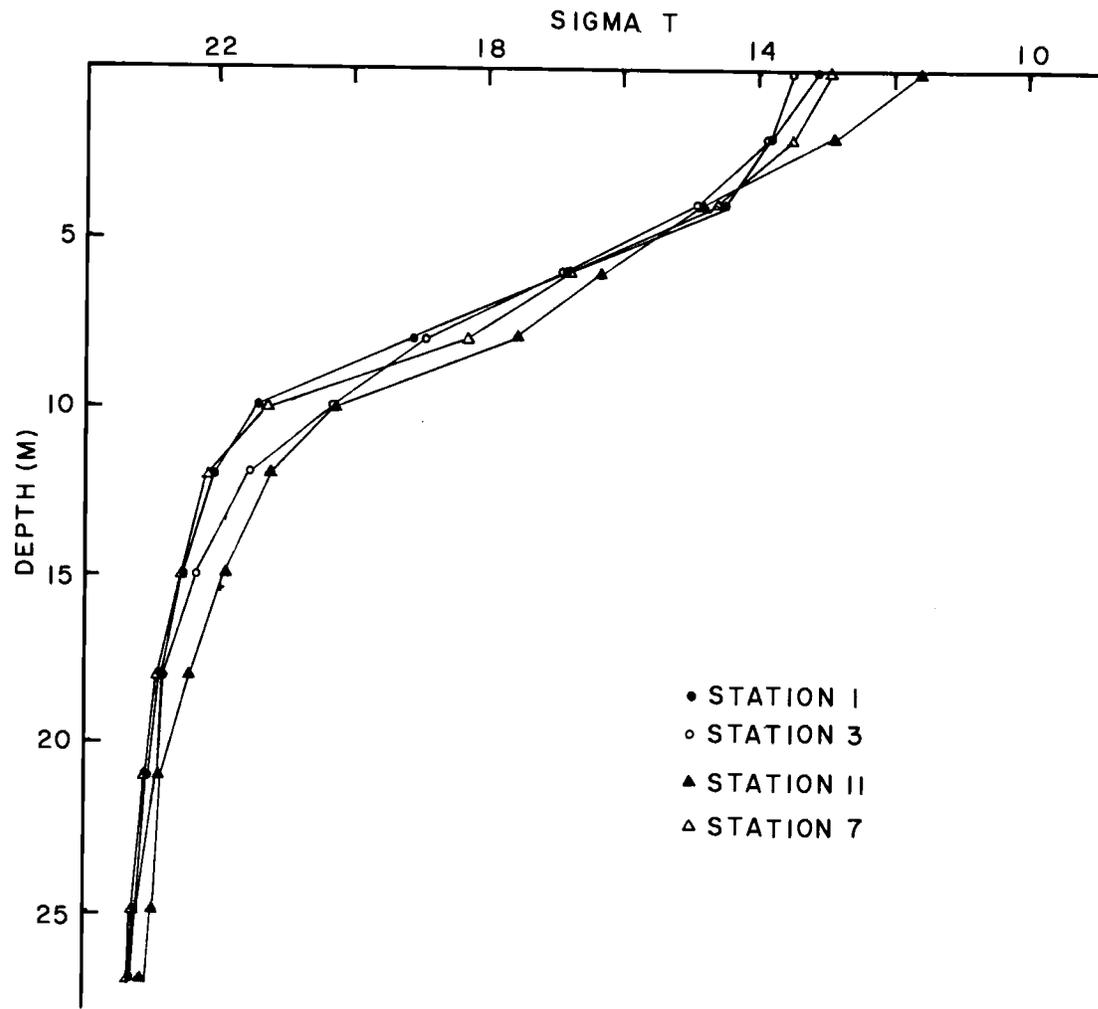


Figure 1. Sigma-t profiles for Auke Bay stations (map 1) on 22 August at high tide.

bay, a result of freshwater discharge into the bay from Auke Creek. Sigma-t variability was within experimental error below 21 meters. Sigma-t was lower in the upper two meters at station 11 than at the other stations since station 11 was located in the path that creek water took as it moved out along the north edge of the bay.

Differences in chlorophyll a among stations on 22 August (Table 1) were not significant at the 1 percent level under analysis of variance. Ninety-five percent confidence limits for chlorophyll a on 22 August were ± 58 percent of the mean (8 stations, $n = 2$). On 5 July, differences in chlorophyll a among stations 3, 4, 5 and 6 (map 1) were not significant at the 1 percent level. Ninety-five percent confidence limits were ± 35 percent of the mean (4 stations, $n = 6$).

Zooplankton counts for samples taken at each of the 11 stations on 22 August are presented in Table 2. There was considerable variability in numbers of different groups of the zooplankton over the 11 stations (Figure 2). Zooplankton were not randomly distributed among the stations under the χ^2 test. If a normal distribution was assumed for the counts, 95 percent confidence limits were ± 87 percent, a value which lies within the range ± 25 percent to ± 450 percent found by other workers (Wiebe and Howard, 1968).

Nitrate-nitrogen values appeared to be similar at 1 meter over the bay on 22 August (Table 1). Data were not sufficient for analysis of variance for nitrate-nitrogen or for phytoplankton productivity.

Table 1. Patchiness experiment 6908-22 sample depth 1 meter.

| Station Number | Temp. °C. | S ‰ | mg Chl. a m^{-3} | mg c $m^{-3}hr^{-1}$ | μg at NO_3-N L^{-1} |
|----------------|-----------|-------|---|------------------------|------------------------------|
| 1 | 9.46 | 16.83 | 3.18 | | |
| | | | 3.09 | | |
| | | | \bar{x} 3.14 | 2.43 | 4.09 |
| 2 | 9.48 | 16.86 | 3.01 | | |
| | | | 3.79 | | |
| | | | \bar{x} 3.40 | 3.14 | 4.40 |
| 3 | 9.68 | 17.62 | 3.07 | | |
| | | | 3.42 | | |
| | | | \bar{x} 3.25 | 3.32 | 4.25 |
| 7 | 9.59 | 17.06 | 3.72 | | |
| | | | 2.91 | | |
| | | | \bar{x} 3.31 | 2.43 | 4.40 |
| 8 | 9.62 | 16.83 | 3.20 | | |
| | | | 3.27 | | |
| | | | \bar{x} 3.24 | 3.66 | 4.65 |
| 9 | 9.63 | 17.34 | 2.84 | | |
| | | | 2.58 | | |
| | | | \bar{x} 2.71 | 4.27 | 4.56 |
| 10 | 9.74 | 18.23 | 3.11 | | |
| | | | 3.81 | | |
| | | | \bar{x} 3.46 | 5.50 | 4.80 |
| 11 | 9.83 | 15.38 | 2.14 | | |
| | | | 2.91 | | |
| | | | $\pm 0.5^\circ C$ $\pm 0.3\text{‰}$ 2.52 | 2.79 | 4.69 |

Table 2. Patchiness experiment 6907-14.

| | Station Number | | | | | | | | | | |
|---------------------------------|----------------|-----|-----|------|------|------|-----|------|------|------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| <u>Evadne nordmanni</u> | 690 | 331 | 176 | 330 | 518 | 288 | 151 | 253 | 1875 | 1000 | 498 |
| <u>Podon leukarti</u> | 54 | 116 | 46 | 46 | 48 | 67 | 34 | 59 | 80 | 81 | 20 |
| <u>Centropages abdominallis</u> | 166 | 57 | 42 | 80 | 70 | 96 | 51 | 45 | 64 | 84 | 20 |
| <u>Acartia longerimus</u> | | | | | | | | | | | |
| and | 217 | 26 | 153 | 199 | 230 | 48 | 62 | 27 | 194 | 288 | 69 |
| <u>Acartia clausii</u> | | | | | | | | | | | |
| <u>Oithona helgolandicus</u> | 147 | 86 | 111 | 89 | 177 | 154 | 107 | 45 | 105 | 257 | 168 |
| <u>Calanus finmarchicus</u> | 16 | 0 | 4 | 34 | 21 | 28 | 17 | 4 | 24 | 56 | 20 |
| Copepodites, all sp. | 1485 | 620 | 717 | 1112 | 1279 | 1378 | 920 | 1040 | 1369 | 1525 | 1563 |
| Barnacle nauplii | 23 | 29 | 4 | 30 | 16 | 0 | 0 | 18 | 40 | 63 | 30 |
| <u>Oikopleura</u> sp. | | | | | | | | | | | |
| and | 35 | 0 | 11 | 25 | 160 | 14 | 17 | 4 | 16 | 31 | 20 |
| <u>Fritilaria</u> sp. | | | | | | | | | | | |
| <u>Euphausiid furcilia</u> | 19 | 11 | 11 | 17 | 0 | 24 | 12 | 9 | 16 | 6 | 5 |

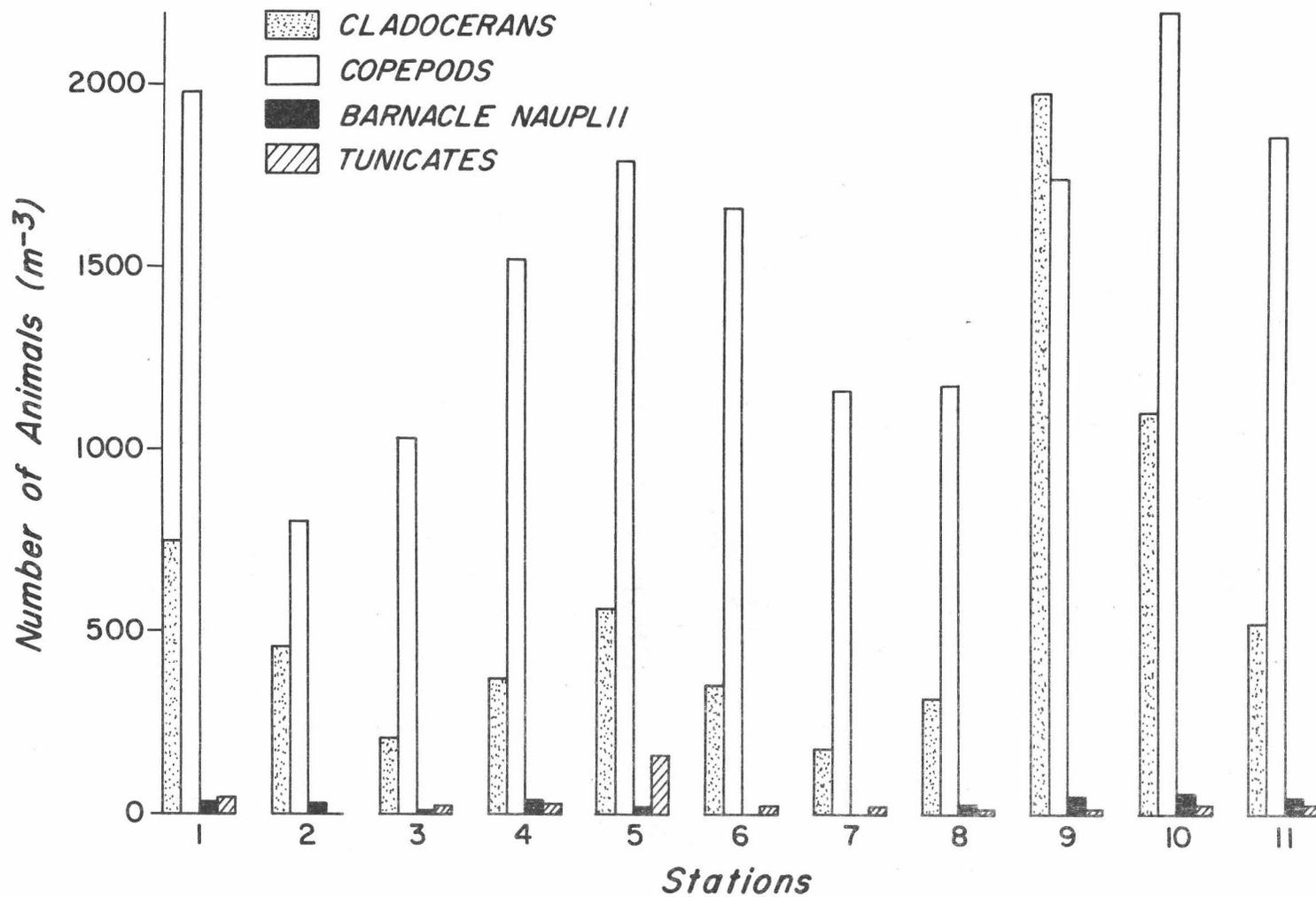


Figure 2. Zooplankton numbers for Auke Bay stations (map 1) on 22 August at high tide.

Auke Bay Monitor (ABM) (Station 3, map 1) is considered to be representative of the bay as a whole when chlorophyll a and nitrate-nitrogen are sampled. There is no representative station for zooplankton numbers. Since the properties (with the exception of zooplankton) appeared to be homogeneously distributed over the area of the bay on 22 August (and on 5 July for chlorophyll a), effects of tidal cycles were ignored in field sampling. A standard sampling time was chosen to be 0900 Pacific Daylight Time since diel variation in chlorophyll a is known to occur in natural phytoplankton communities (Glooschenko, Curl and Small, 1972).

Hydrography

Density in the Auke Bay water column was largely a function of salinity (Figure 3) with temperature effects secondary (Figure 4). Auke Bay showed both thermal and halal stratification over most of the summer (for example, Figure 5). After periods of high winds, thermal structure was greatly modified although density structure remained stratified. The water column was positively stable throughout the summer under Sverdrup, Johnson and Fleming's (1942, p. 417) stability definition:

$$E = 10^{-3} \frac{d\sigma_t}{dz}$$

where z was depth. Values for stability computed with a finite

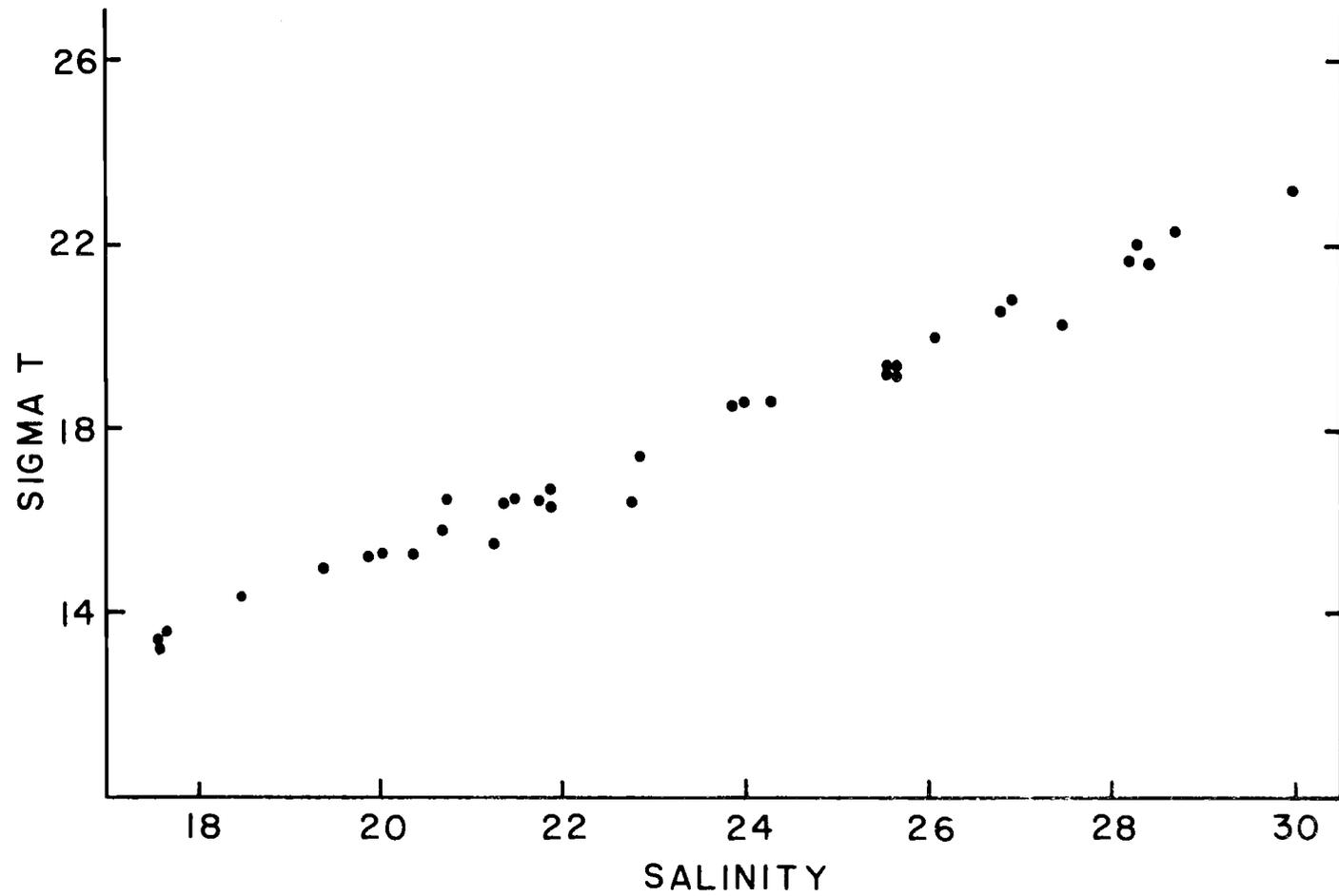


Figure 3. Salinity at 5 meters at Auke Bay Monitor (station 3, map 1) over summer, 1969.

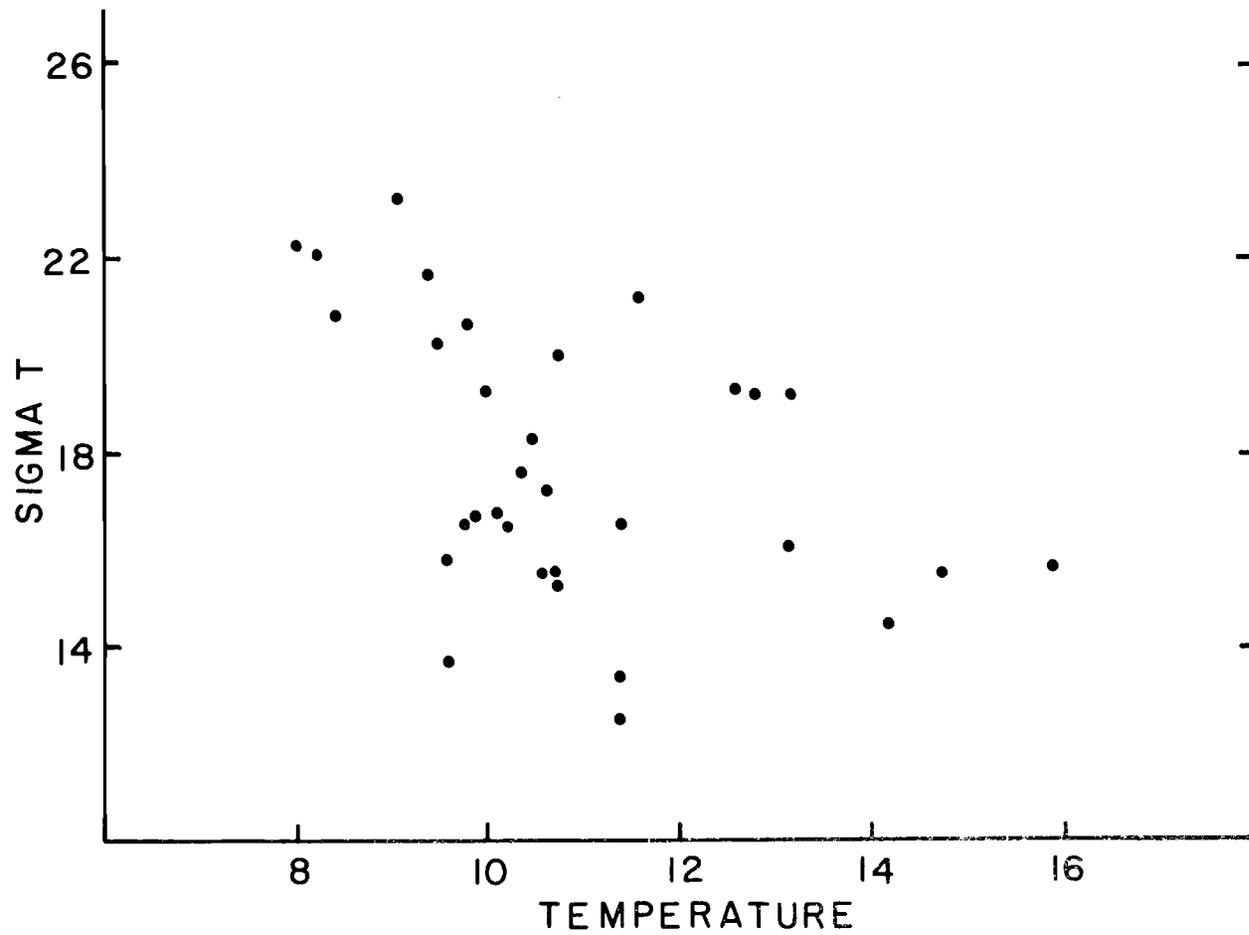


Figure 4. Temperature at 5 meters at Auke Bay Monitor (station 3, map 1) over summer, 1969.

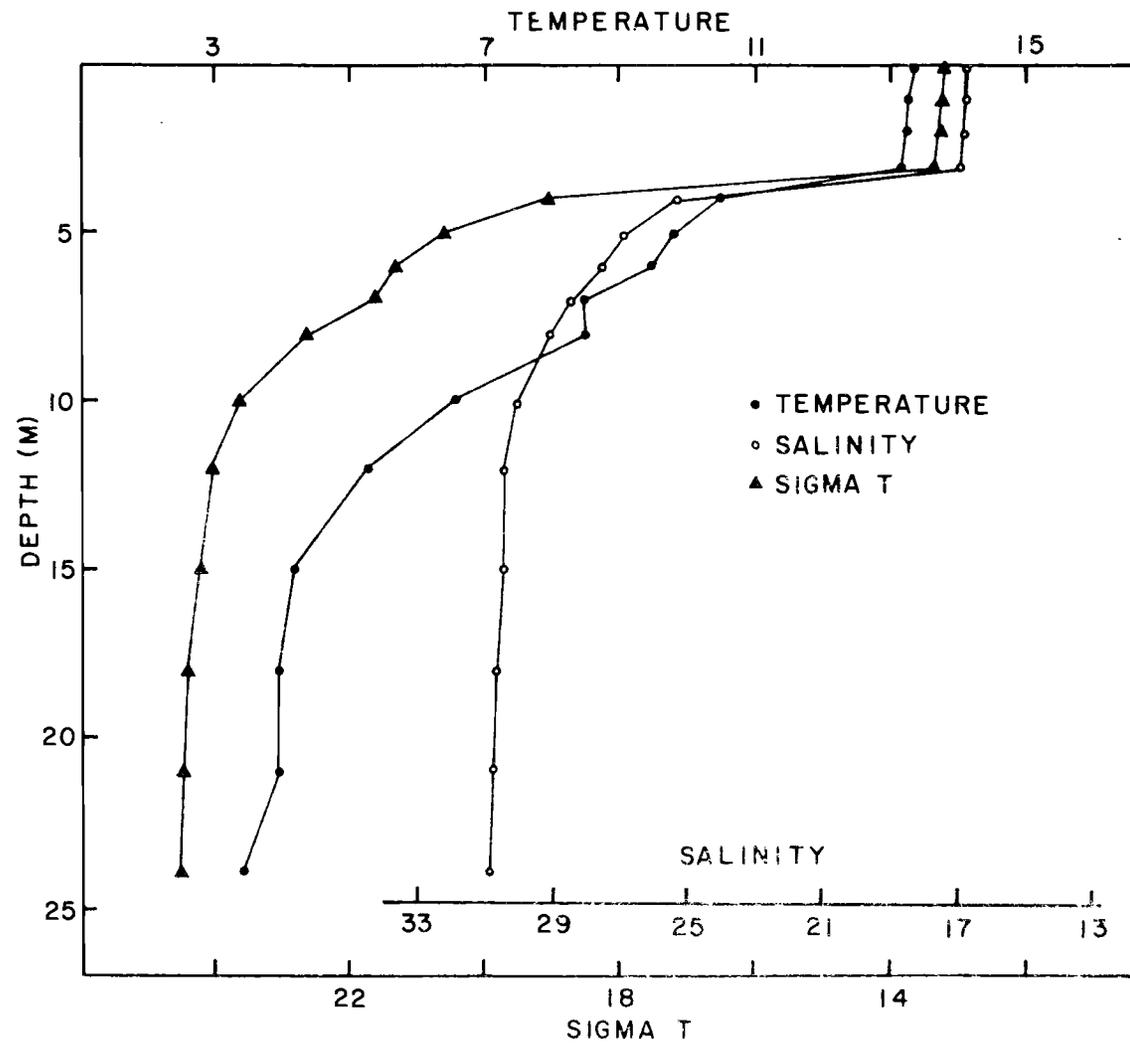


Figure 5. Temperature, salinity and sigma-t at ABM 30 May.

approximation for E (Table 3) indicated high positive stability in the upper 10 to 15 meters throughout the summer. High positive values are an expression of a large density gradient and are interpreted to mean a tendency for a parcel of water to move back to its position in the water column when displaced from that position.

Table 3. Stability values.

| Depth (m) | $10^8 E$ | | | | | | | | | |
|-----------|----------|------|------|------|------|------|------|------|-----|------|
| | 5-23 | 5-30 | 6-20 | 6-30 | 7-7 | 7-14 | 7-23 | 7-28 | 8-4 | 8-22 |
| 0 | 1008 | 1560 | 2530 | 700 | 1600 | 470 | 213 | 1130 | 970 | 890 |
| 5 | 225 | 595 | 254 | 2100 | 455 | 940 | 1570 | 320 | 770 | 910 |
| 10 | 52 | 131 | 158 | 180 | 180 | 420 | 295 | 610 | 372 | 290 |
| 15 | 50 | 43 | 47 | 200 | 57 | 250 | 170 | 340 | 43 | 75 |
| 21 | 16 | 38 | 27 | 225 | 68 | 110 | 105 | 230 | 47 | 78 |

Tidal-induced turbulence was not sufficient to destroy near-surface density structure since a well-stratified condition persisted in the upper 10 meters of Auke Bay from 16 June (Figure 7) through 30 June (Figure 8), a period when winds were less than 4 m/sec and variable.

Faller (1969) suggested the primary mechanism by which the thermocline is eroded in the oceans is Langmuir circulation, which can develop if a wind is sufficient to raise capillary waves (wind speed greater than 2 to 3 m/sec). Motion due to surface waves results in turbulence which increases thermocline depth. According to Phillips (1966, p. 242), if a wind of sufficient strength blows for much longer than one day, the motion in the mixed layer (defined by thermocline

depth for the open ocean) becomes steady with mixed layer depth:

$$d_m = \frac{(\tau/\rho)^{1/2}}{\Omega \sin \lambda}$$

where τ is wind stress, ρ is water density, Ω is angular rotation of the earth, λ is latitude. Neumann and Pierson (1966, p. 209) have suggested

$$\tau = 9 \times 10^{-4} w^{3/2}$$

where w is wind speed (m/sec). At Auke Bay, 58 north latitude, when the mean wind speed was 2.18 m/sec from 26 June to 30 June, d_m is calculated to be 8 meters. The depth at which the temperature gradient is maximum is the depth of the thermocline (Pickard, 1963, p. 33). A more formal definition (Hutchinson, 1957, p. 428) is the depth of the thermocline is the plane where

$$\frac{d^2T}{dz^2} = 0$$

On this basis, the thermocline depth on 30 June was 6 meters (Figure 8), a value approximated by theory. For 6 m/sec wind d_m is about 70 meters, suggesting that Auke Bay could mix to the bottom over much of its area during periods of high winds. An isothermal condition would exist in the water column after wind-mixing. The water column would be isohalal after wind-mixing unless large quantities of fresh water were discharged into the bay.

Auke Bay was well-stratified on 30 May with a 3 meter mixed layer depth (Figure 5). After two days of 7 m/sec winds and one day

of 4 m/sec wind, with rain throughout the period, the temperature structure had de-stratified (Figure 6). Salinity structure remained stratified but salinity had decreased throughout the water column. Freshwater entered Auke Bay at several points with Auke Creek as the predominant source of freshwater. The Mendenhall River was observed to flow across the surface of the bay on several occasions but was not observed in the bay from 30 May to 2 June. Auke Creek discharge was $24,910 \text{ m}^3$ from 30 May to 2 June (personal communication from the U.S. Department of the Interior Geological Survey, Juneau, Alaska). If Auke Creek discharge is assumed to spread evenly over Auke Bay during periods of high discharge, and if total salt in the water column was assumed to be NaCl, the expected effect of dilution of the Auke Bay water column by an equivalent 2.6 meter head (where all the discharged freshwater was assumed to be present in the bay at one time) can be calculated. A change in total salt down to 27 meters was calculated to be from 788 gm to 725 gm. A change in total salt from 788 gm to 734 gm was measured during the period. For the period 7 July to 14 July, when winds were greater than 6 m/sec, Auke Creek discharged $71,000 \text{ m}^3$ of freshwater into Auke Bay. Change in total salt due to dilution of the water column by a 6.4 meter equivalent head was calculated to be from 827 gm to 667 gm. Measured change was from 827 gm to 670 gm. Interpretation of calculations for this period are complicated by the presence of Mendenhall River Water in

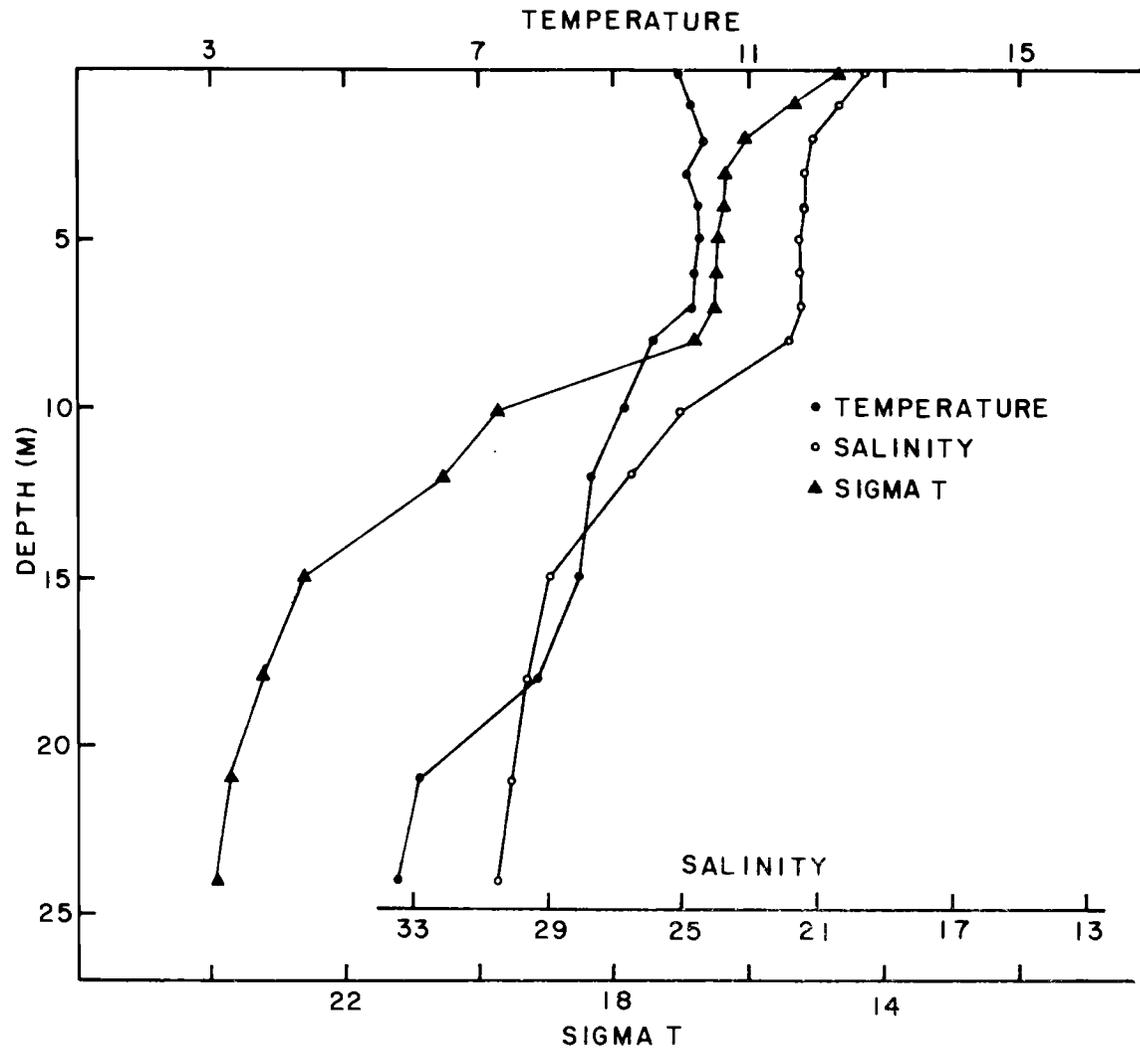


Figure 6. Temperature, salinity and sigma-t at ABM 2 June.

Auke Bay.

A definite hydrographic pattern was observed in Auke Bay over the summer. Salinity, temperature and sigma-t showed stratified structure during periods when wind speed was less than 4 m/sec. After periods during which wind speeds were greater than 4 m/sec, the thermocline deepened with nearly an isothermal condition observed on 14 July (Figure 9). Salinity decreased at any given depth after periods of high winds accompanied by rain but salinity profiles exhibited stratification, a consequence of mixing of freshwater down into the Auke Bay water column.

Currents

Current speed data were obtained at ABM during the June period of light winds (mean speed 2.8 m/sec) when the bay was strongly stratified (Figures 7 and 8). Progressive vector diagrams (Figure 10) show considerable meandering with the trend toward the south at 2 meters and toward the west at 12 meters. Mean speeds were 6.5 cm/sec at 2 meters and 4.0 cm/sec at 12 meters. Threshold for Braincon type 381 current meters is about 2.7 cm/sec (National Oceanographic Instrument Center, 1970). Tidal ellipses were not observed in the progressive vector diagrams. This could be the result of a 6 meter scope in the meter-string mooring line necessary to maintain the meters at the same depth relative to the surface over the tidal cycle.

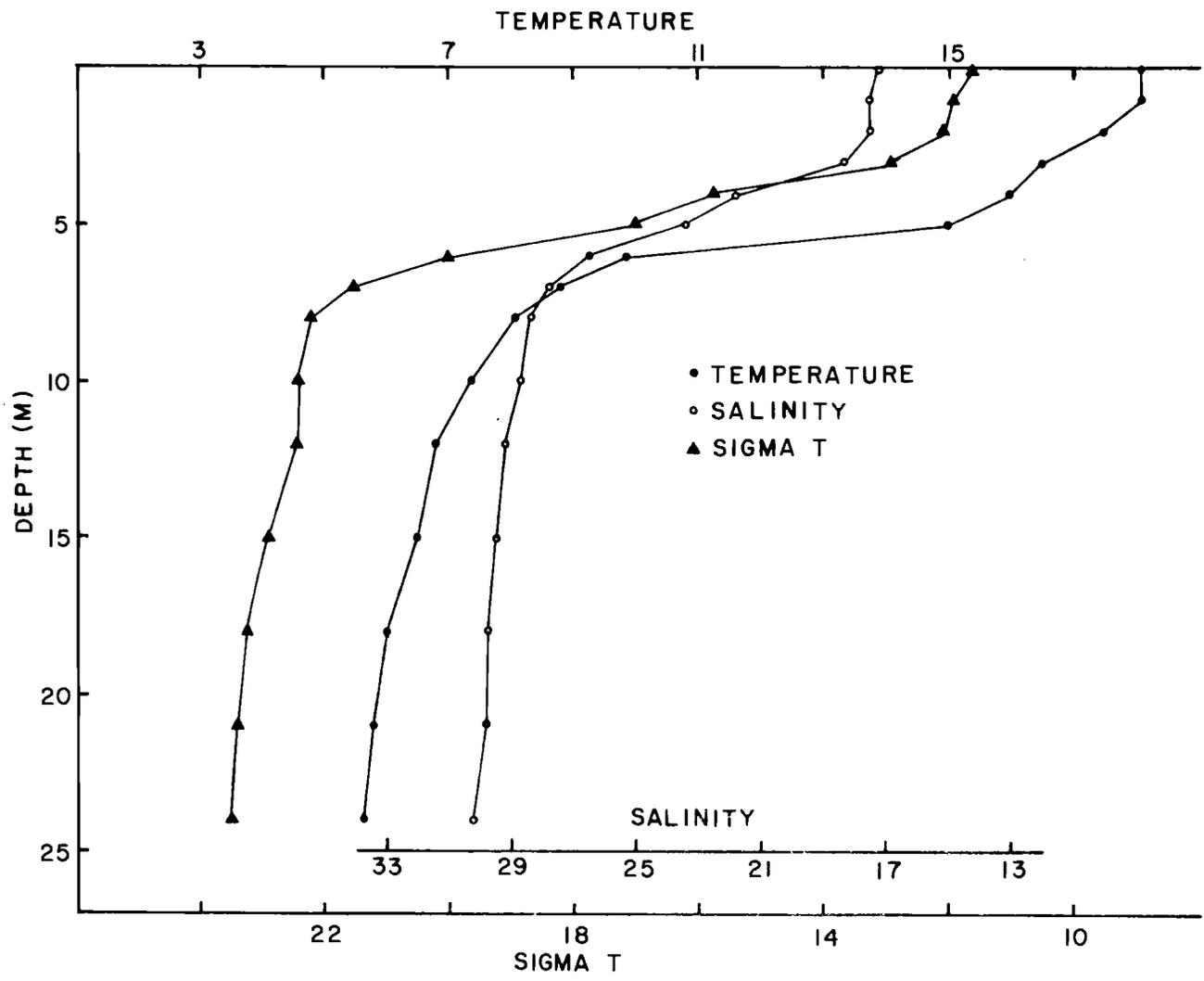


Figure 7 Temperature, salinity and sigma-t at ABM 16 June.

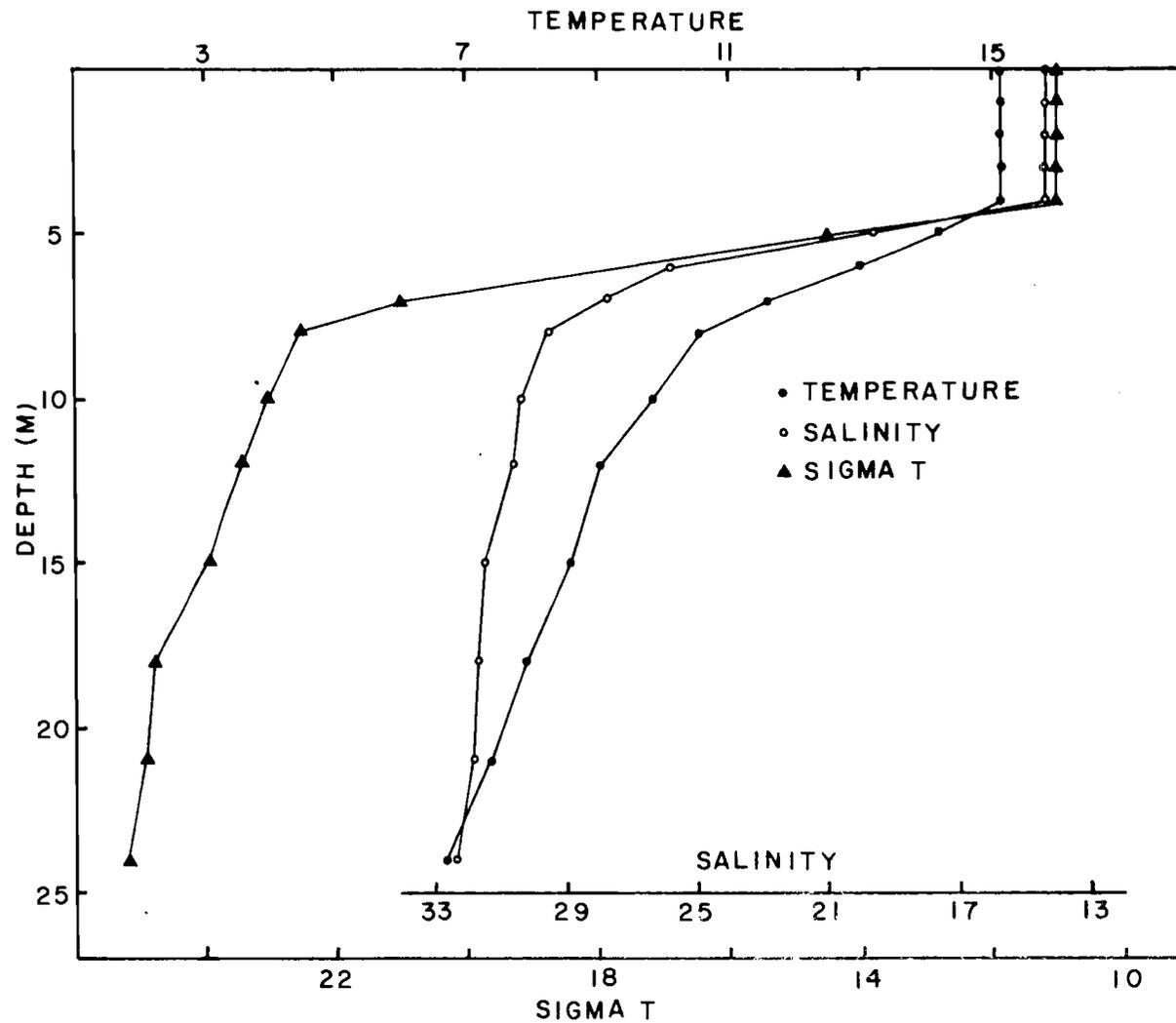


Figure 8. Temperature, salinity and sigma-t at ABM 30 June.

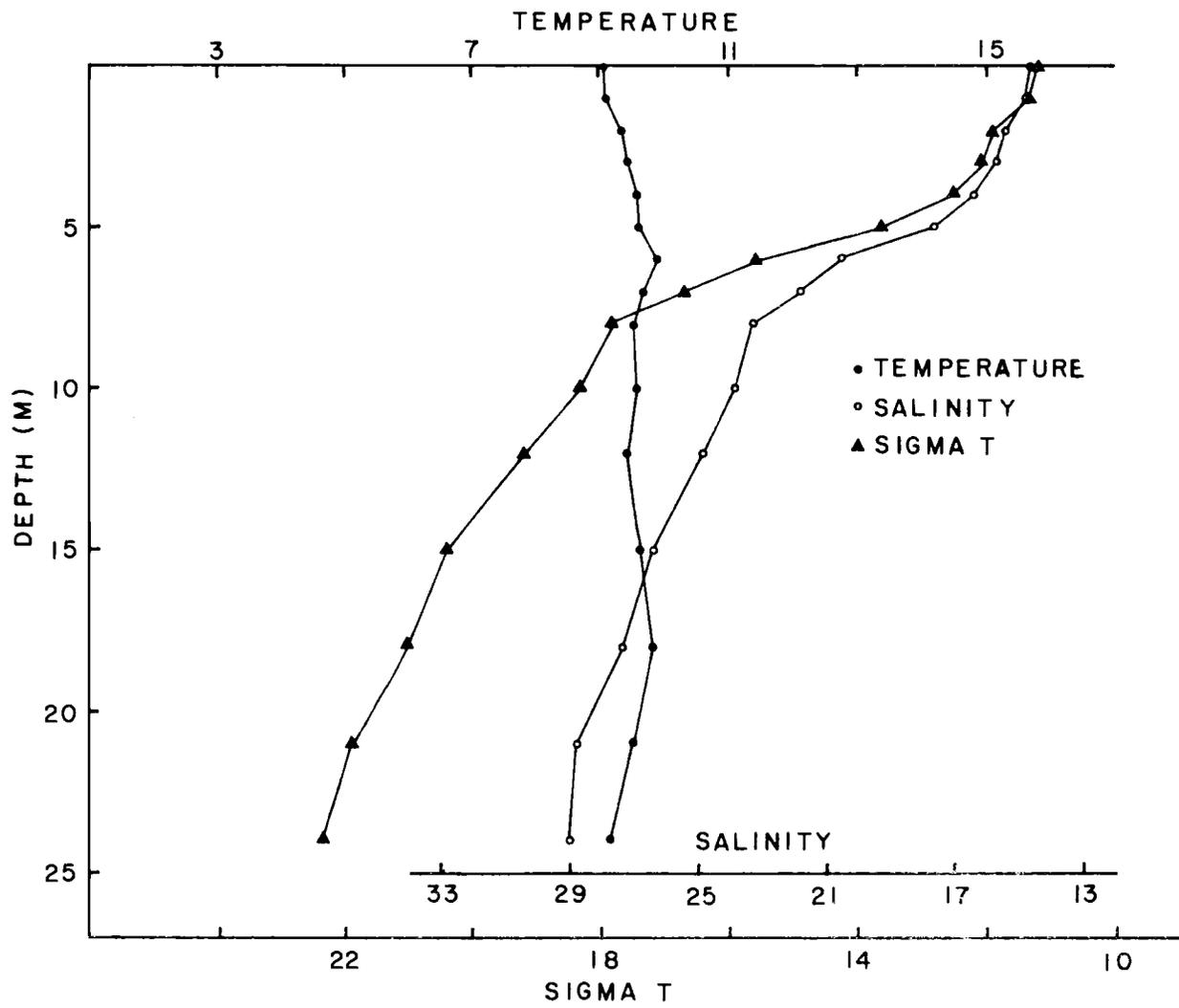


Figure 9. Temperature, salinity and sigma-t at ABM 14 June.

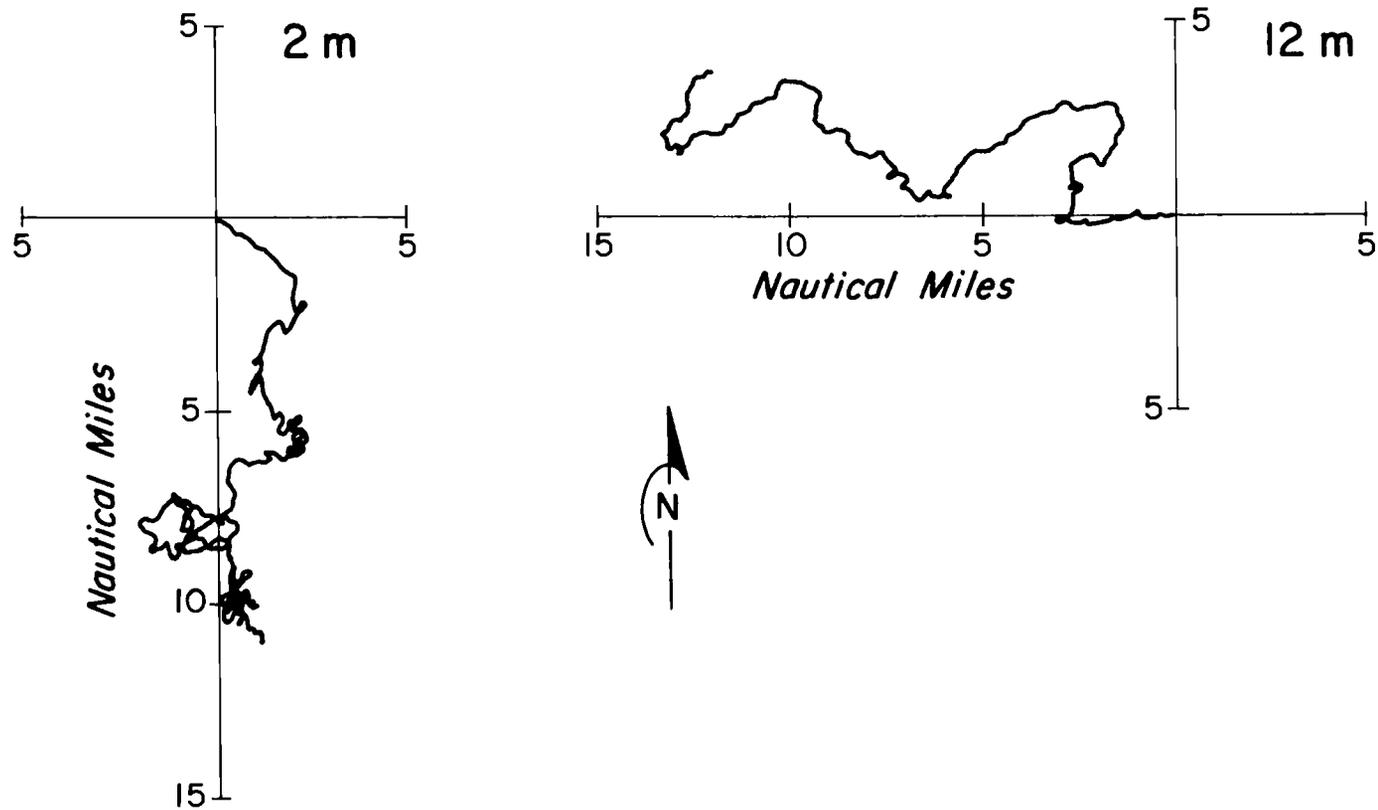


Figure 10. Progressive vector diagrams of current meter records at ABM during June.

Since measurement of current speed and direction at one point is not sufficient to define the current field, the general circulation pattern in Auke Bay can only be inferred from general principles. During periods when Auke Creek was discharging freshwater into Auke Bay, surface color changes and flotsam were observed near the north edge of the bay. Auke Creek water appeared to accompany a drift of Auke Bay surface water in a counter-clockwise manner as expected at these latitudes. ABM was located approximately in the center of the gyral drift. Transport cannot be estimated from one-point current meter measurements but must be low at ABM, at least in the upper 12 meters.

Wind

Except for several days (30 May, 31 May and 3 June) during which wind speed was greater than 7 m/sec, wind speed was less than 4 m/sec until 8 July (Figure 11). After a week-long period during the first of July when winds were not less than 5 m/sec, winds were high and variable until the end of the study period. Winds above 4 m/sec blew from the south, along the main fetch into Auke Bay.

Light

Total daily insolation was variable throughout the summer with a tendency toward high (600ly/day) values during the first part of the

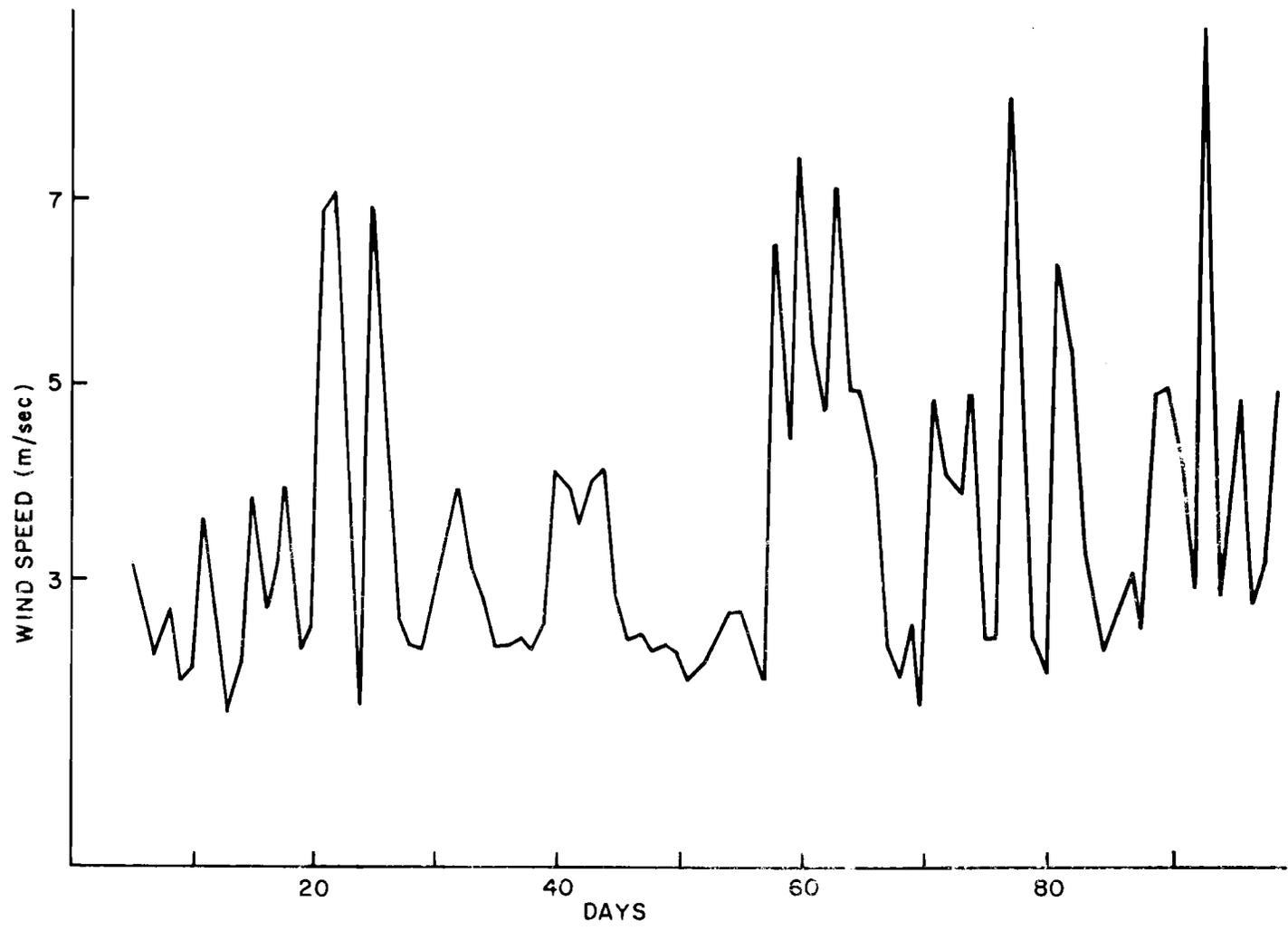


Figure 11. Daily mean wind speed over summer 1969 at the Juneau Municipal Airport.

summer. A period of low insolation (about 200 ly/day) occurred during the first part of July (Figure 12).

Several times during the summer (20 June, 9, 11 and 14 July) when the wind had a strong southeast set, the Mendenhall River was observed to flow over the surface of Auke Bay. Comparison of a submarine photometer profile for bay water with a profile taken through the layer of river water into the bay water as the river was encroaching on the bay (9 July) suggests the upper 2 meters of the bay were immediately affected by the high glacial flour load of the river (Figure 13).

Extinction coefficients of light varied over the summer in a pattern which reflected phytoplankton standing chlorophyll a (Figure 14).

Phytoplankton

A phytoplankton bloom composed of a population of Thalassiosira aestivalis and a population of Chaetoceros compressus were present in late May at the start of the study. Bruce (1969) observed that Thalassiosira nordenskioldii formed the spring bloom in Auke Bay in 1967 and that either T. nordenskioldii or Thalassiosira aestivalis had formed the spring bloom during several preceding years (personal communication). The chlorophyll a maximum which was observed at the start of the study was therefore associated with the spring phytoplankton bloom in Auke Bay.

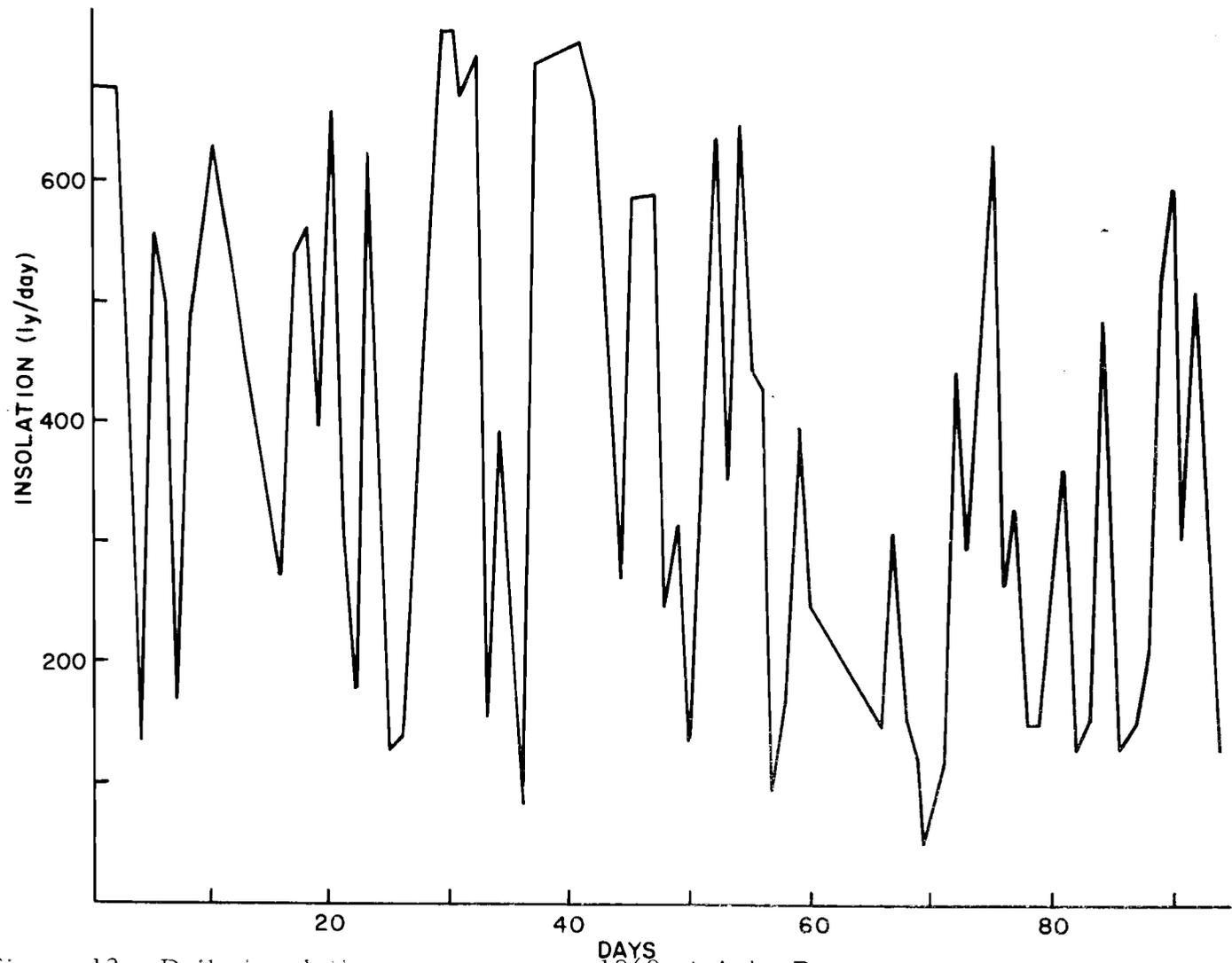


Figure 12. Daily insolation over summer 1969 at Auke Bay.

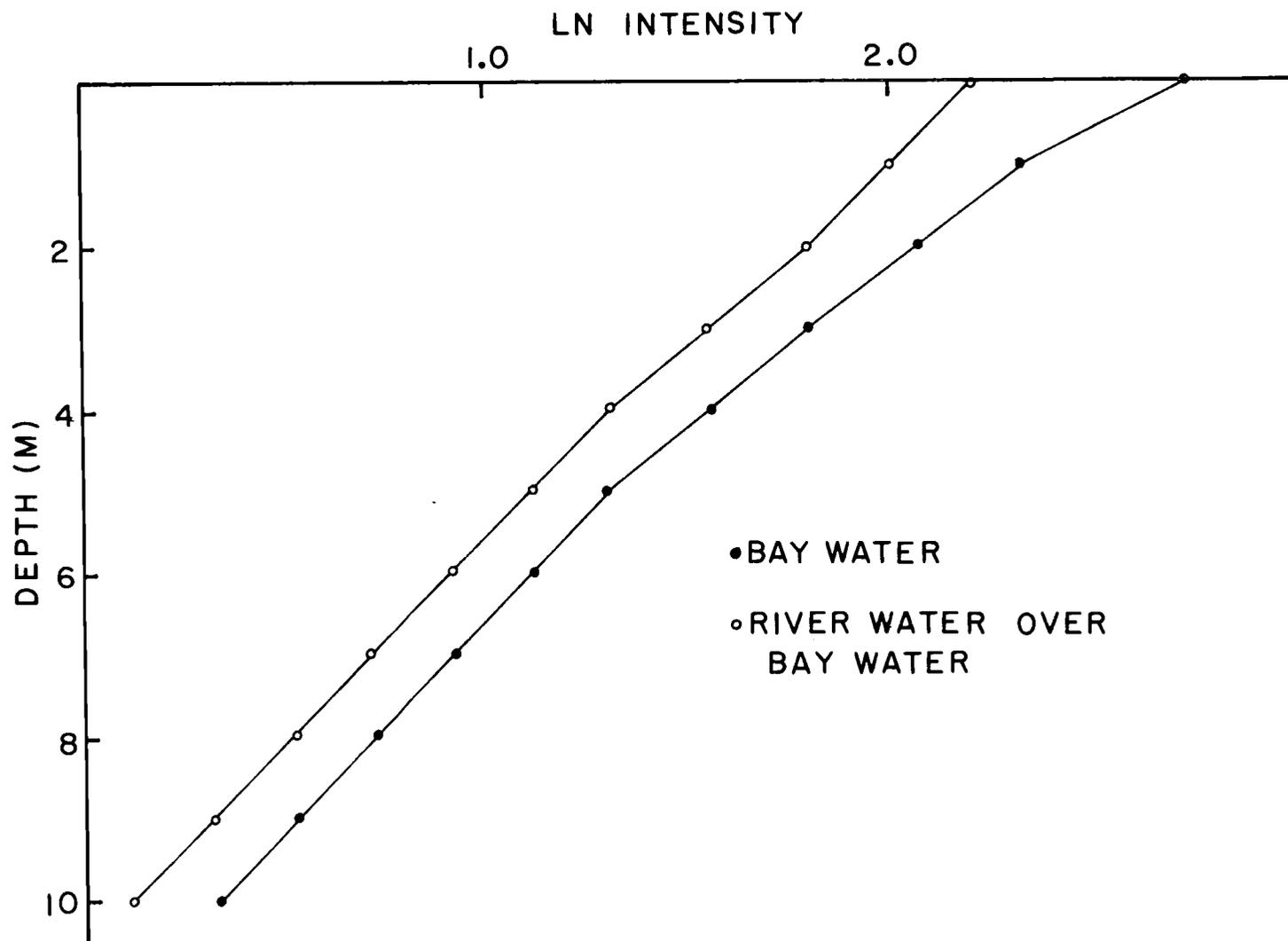


Figure 13. Submarine photometer profiles (log-transformed) through Auke Bay water alone and through Auke Bay water covered with Mendenhall River water.

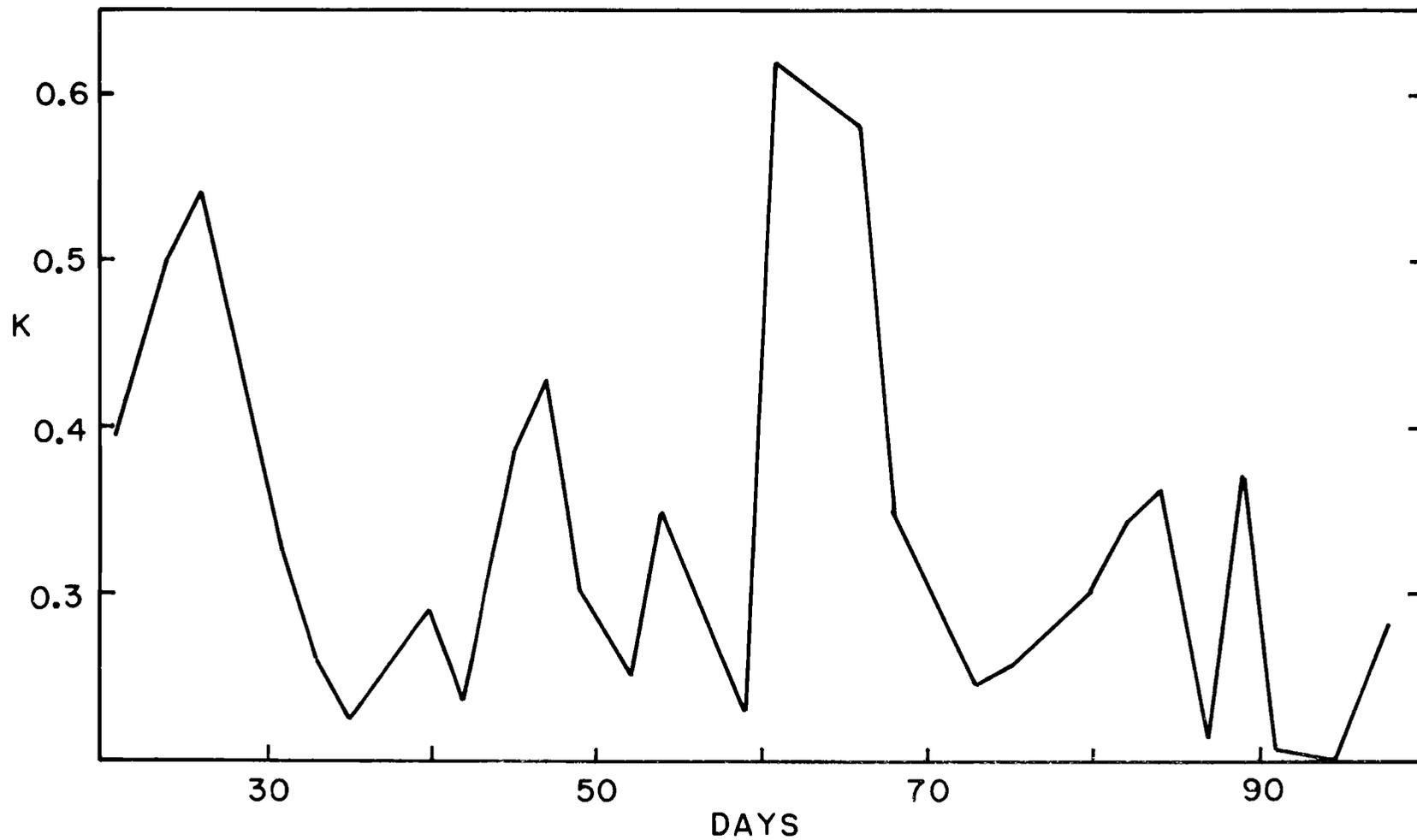


Figure 14. Extinction coefficient of light, k , over summer 1969 in Auke Bay.

From 20 May through 23 June, diatom populations were smaller than could be detected with the microscopic counting technique. Small, unidentified flagellates as well as several species of dinoflagellates (Peridinium sp. and Ceratium sp.) were observed during this period. From 25 June until the end of the study, Skeletonema costatum formed greater than 90 percent of the numbers of the phytoplankton in Auke Bay. Thalassionema nitzschiodes and Leptocylindricus danicus were usually present in samples taken during this period. From time to time, species such as Ditylum brightwellii, Chaetoceros decipiens, Chaetoceros debilis, Chaetoceros didymus and Distephanous speculum appeared in the samples.

Vertical profiles of chlorophyll a and phytoplankton productivity bracketing the major summer Skeletonema costatum bloom are given in Figures 15 through 17. Maximum S. costatum numbers were about 6 million/liter at 2 meters on 2 July (Figure 15). Maximum Thalassionema nitzschiodes numbers were about 0.6 million/liter at 4 meters. Total chlorophyll a was 58 mg/m² with unidentified flagellates forming the 6 meter chlorophyll a maximum. Productivity was maximum at 5 meters where few flagellates were observed. On 9 July, total chlorophyll a had reached a peak value of 144 mg/m² with maximum Skeletonema costatum numbers about 17 million/liter at 7 meters where no flagellates were observed. Thalassionema nitzschiodes numbers were about 0.03 million/liter throughout the water column.

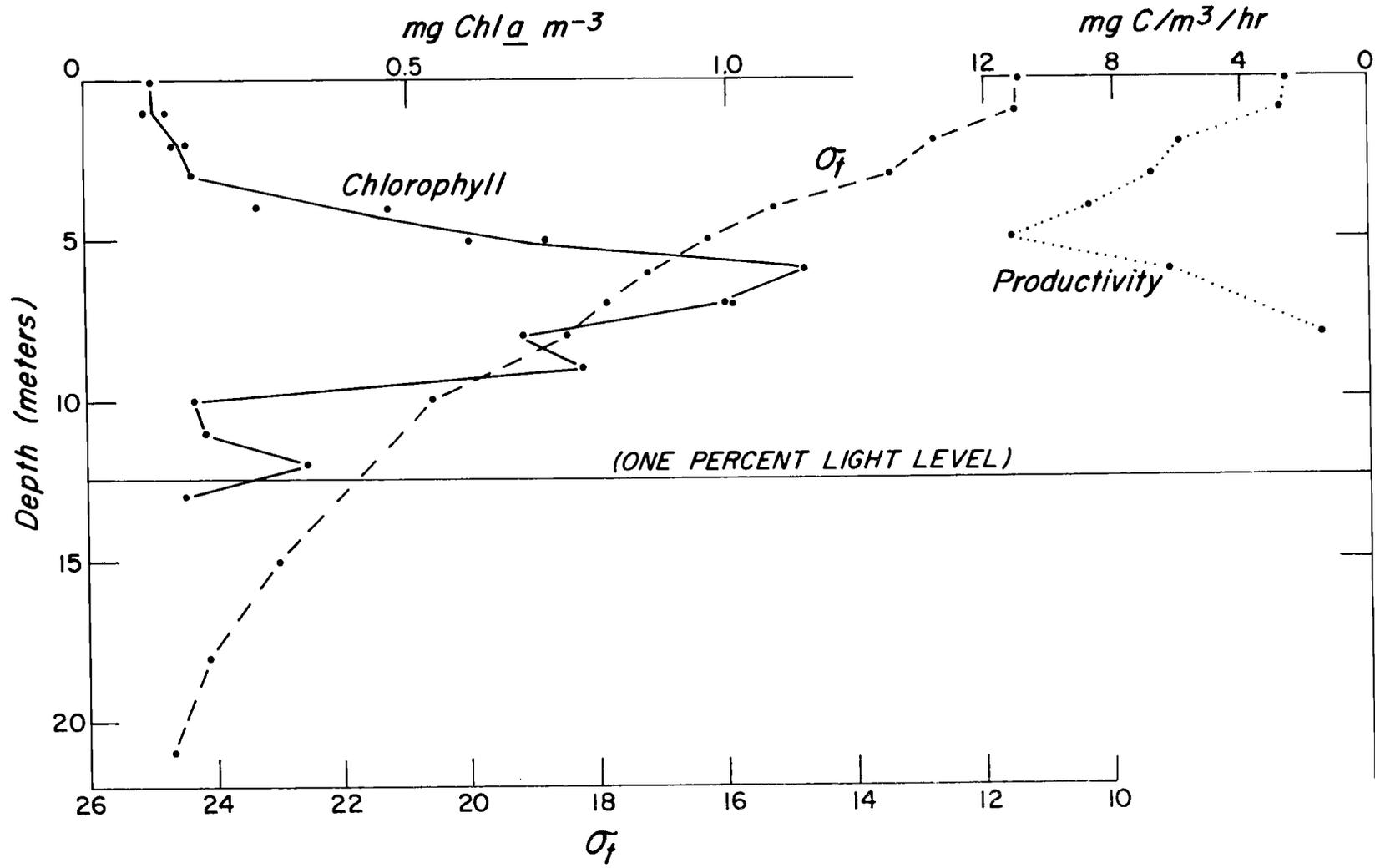


Figure 15. Profiles of chlorophyll a, density and phytoplankton productivity at ABM on 2 July.

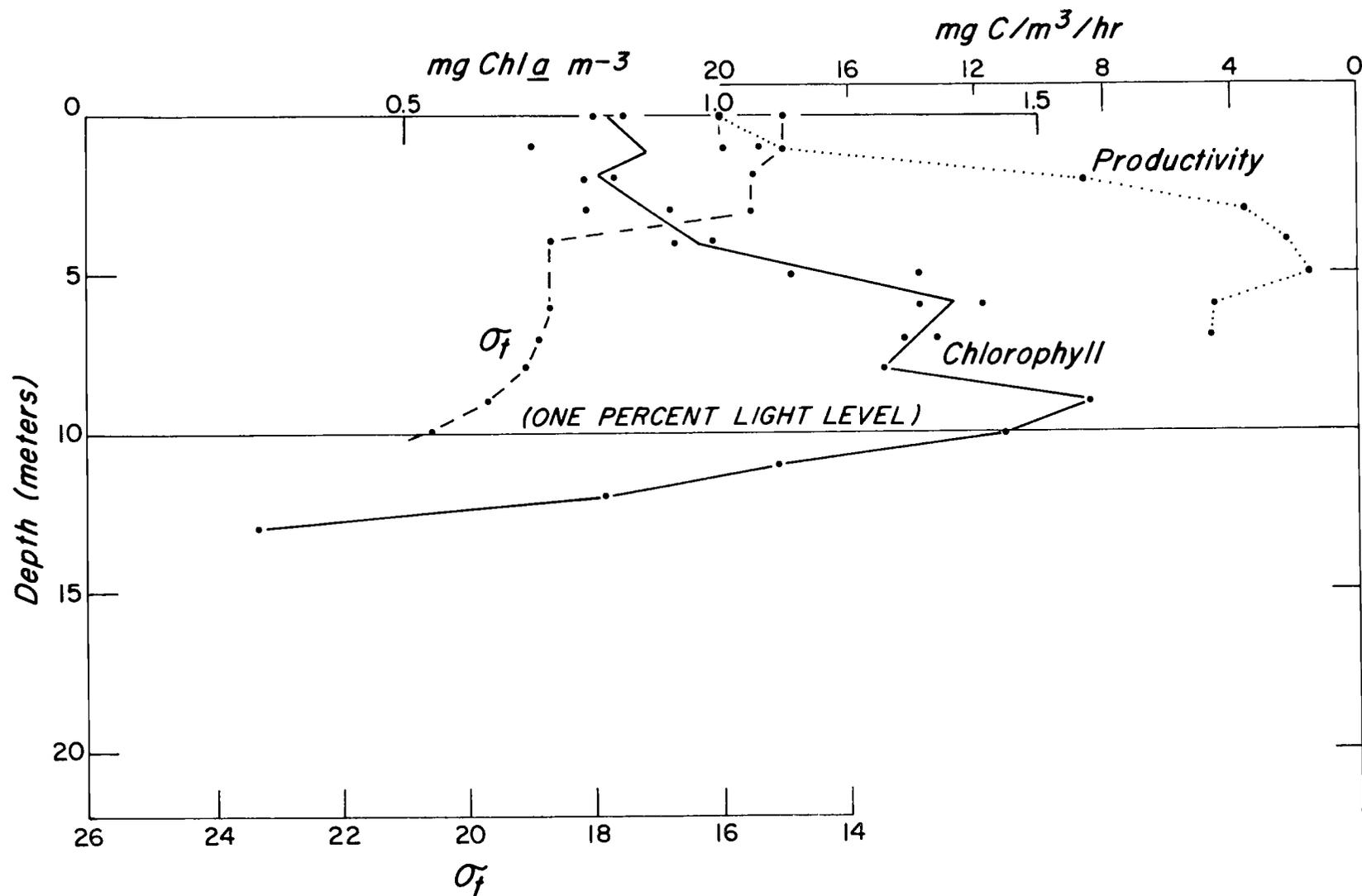


Figure 16. Profiles of chlorophyll *a*, density and phytoplankton productivity at ABM on 9 July.

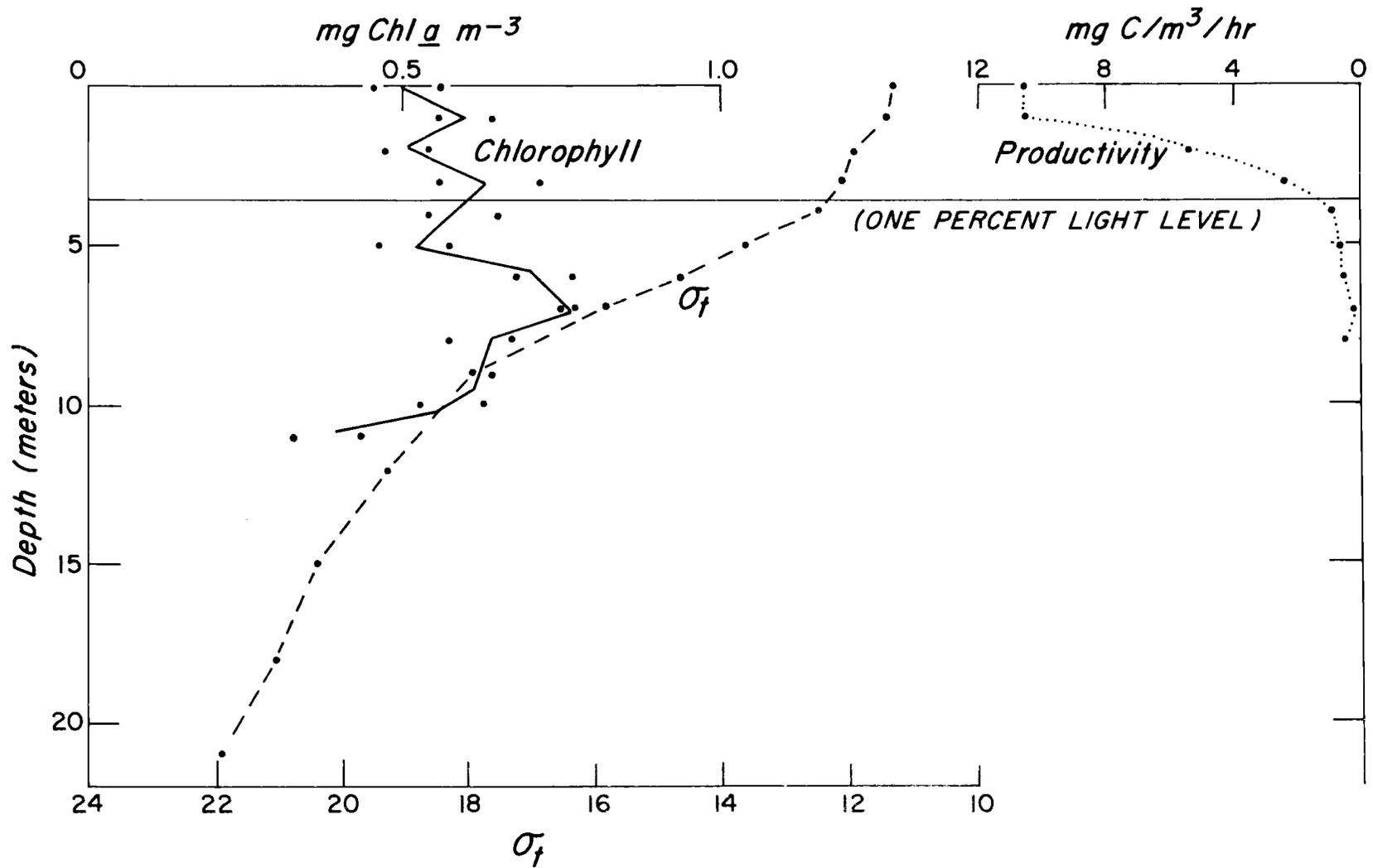


Figure 17. Profiles of chlorophyll a, density and phytoplankton productivity at ABM on 14 July.

Productivity was maximum at the surface on this low-light day (142 ly/day) (Figure 16). The bloom had declined by 14 July with total chlorophyll a at 74 mg/m². Skeletonema costatum numbers were about 6 million/liter at 4 meters while Thalassionema nitzschiodes numbers were about 0.05 million/liter. Productivity was maximum at the surface since light was low (127 ly/day) (Figure 17).

There were large differences in numbers of diatoms at different depths in the water column. Skeletonema costatum numbers varied by about a factor of two within several meters (Table 4) on 9 July while rarer species showed greater variability.

Table 4. Diatom numbers (millions per liter) on 9 July at ABM.

| Depth meters | <u>Skeletonema</u> <u>costatum</u> | <u>Thalassionema</u> <u>nitzschiodes</u> | <u>Nitzschia</u> sp. | <u>Leptocylindricus</u> <u>danicus</u> |
|-----------------|---------------------------------------|---|-------------------------|---|
| 0 | 11.4 | 0.06 | 0.04 | 0.13 |
| 1 | 11.5 | 0.14 | 0.11 | 0.00 |
| 2 | 13.7 | 0.00 | 0.20 | 0.00 |
| 3 | 8.33 | 0.07 | 0.00 | 0.00 |
| 4 | 7.84 | 0.03 | 0.00 | 0.00 |
| 5 | 12.2 | 0.03 | 0.29 | 0.00 |
| 6 | 16.4 | 0.00 | 0.00 | 0.04 |
| 7 | 17.5 | 0.07 | 0.29 | 0.22 |
| 9 | 13.6 | 0.22 | 0.22 | 0.00 |

Depth of the one percent light level varied from about 18 meters during periods when phytoplankton populations were low to about 10 meters on 9 July when phytoplankton were at a summer maximum. Mendenhall River water was observed to overflow Auke Bay on 14 July and the high glacial flour load was responsible for the 4 meter one percent light depth. (Figure 17).

Nitrate

Surface nitrate had been exhausted when sampling started. Nitrate concentration was less than $0.5 \mu\text{g-at/l}$, (μ mole) in the upper 5 meters of Auke Bay over most of the summer (Figure 18). A short period (three days) of high winds (greater than 7 m/sec) the last of May (Figure 11) mixed nitrate-rich water up into the euphotic zone raising the nitrate concentration at 0, 5 and 10 meters and decreasing nitrate concentration at 27 meters. Nitrate concentration increased at 10 meters during early June, perhaps as a result of diffusion processes beneath the mixed layer and decreased during the latter part of June. The decrease in nitrate concentration may have been caused by growth of large populations of flagellates observed during that period. Variability in nitrate concentration at 10 meters during the last part of July and during August was the result of interaction between wind-mixing effects and growth of the Skeletonema costatum population during that period.

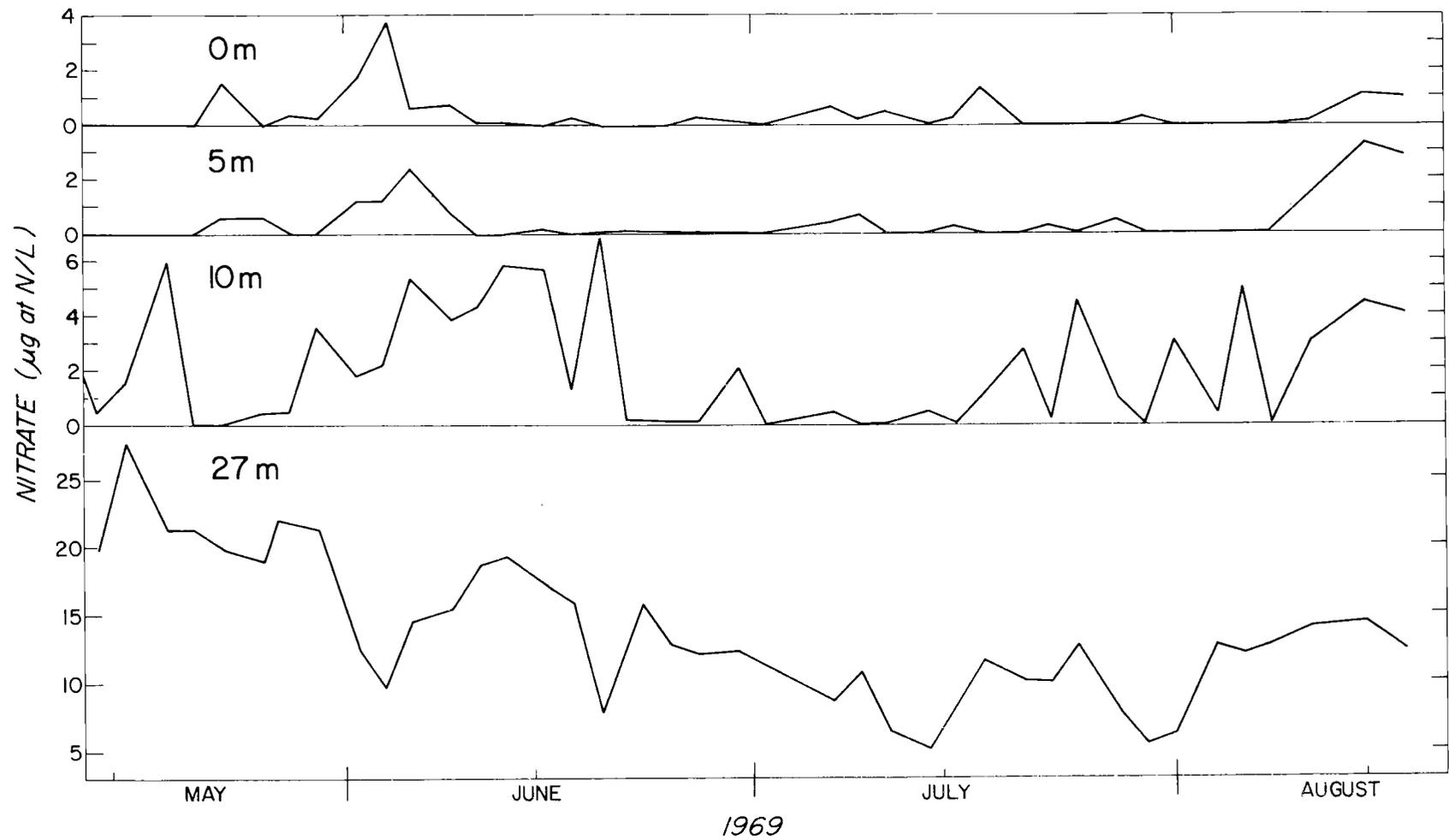


Figure 18. Nitrate-nitrogen at 0, 5, 10 and 27 meters at ABM over summer, 1969.

At 27 meters, nitrate showed a general decrease over the summer. An accelerated decrease occurred during the first few days of June after a period of strong wind-mixing of the Auke Bay water column. The process by which nitrate concentration increased at 27 meters after the period of wind-mixing is not yet understood. The phenomenon of decrease following periods of wind mixing was observed during mid-June and during the middle and end of July.

Nitrate concentration in surface waters around the bay was not significantly different from concentration at ABM over the summer. Lindstrom and Welch (1969) found nitrate concentrations in the surface layers of Auke Lake to be similar to nitrate concentrations at ABM (0.1 to 0.3 μ mole over most of the summer). Nitrate concentrations in the Mendenhall River were about 0.1 μ mole. Freshwater discharge did not appear to contribute significant amounts of nitrate to Auke Bay.

Nitrogen and Phytoplankton Growth

There are several possible sources for nitrogen which phytoplankton can use in growth. Nitrate, nitrite and ammonia are available inorganic forms while some amino acids can support phytoplankton growth (Bruce, 1969). There are several possible mechanisms by which the various forms of nitrogen could enter the Auke Bay euphotic zone in quantities sufficient to support phytoplankton blooms. All of the forms could enter the Bay through freshwater discharge, through

tidal induced vertical mixing or through vertical wind-mixing effects. Ammonia could be excreted by zooplankton or perhaps could be formed in situ by bacterial regeneration of detrital matter. Amino acids could be excreted by phytoplankton or perhaps by zooplankton. Fresh-water discharge into Auke Bay did not carry significant quantities of nitrate into the bay. Since the pattern of phytoplankton productivity was nearly similar over the bay after a period of runoff (Table 1), other sources of nitrogen were not carried into the bay in significant quantities. Since no phytoplankton blooms occurred during the June period when the water column was well-stratified and when winds were light and variable, tidal induced turbulence did not carry significant quantities of nitrate into the euphotic zone. Harris (1959) stated that an inverse relationship between phytoplankton standing stock and ammonia concentration was the first indication that had been found of a cause for oscillations in the size of phytoplankton populations in Long Island Sound during the summer. Dugdale and Goering (1967) showed that ammonia excreted by zooplankton can provide perhaps 1 percent of daily ammonia uptake by phytoplankton in the Sargasso Sea. Martin (1968) showed that zooplankton provide only a small fraction of the required nitrogen during periods of phytoplankton abundance but can be an important source of nitrogen when phytoplankton populations are low and nitrogen is scarce. According to Johannes (1968, p. 203),

"It has been demonstrated beyond reasonable doubt that most of the nitrogen and phosphorous incorporated into aquatic plants and animals is usually regenerated by processes other than direct bacterial action." While Johannes' statement may hold for processes within the euphotic zone, it is not clear that the statement holds for processes occurring in major oceanic water masses below the euphotic zone (Vacarro, 1965). The remaining alternative for a nitrogen source for Auke Bay summer phytoplankton blooms is organic nitrogen compounds excreted by phytoplankton or zooplankton. Approximately 60 days elapsed between the initial Thalassiosira aestivalis bloom and the midsummer Skeletonema costatum bloom. We have no measurements of amino acids in Auke Bay for 1969. If phytoplankton carbon is estimated from chlorophyll a (see section Estimation of Standing Phytoplankton Carbon, p. 81) and if mean carbon to nitrogen ratio for Auke Bay, 6.7, is applied to integral values for euphotic zone phytoplankton standing carbon, the initial Thalassiosira aestivalis maximum contained 0.121 gm N/m² while the midsummer Skeletonema costatum maximum contained 0.98 gm N/m². It is highly unlikely that 80 percent of the Thalassiosira aestivalis standing nitrogen could have been excreted in the euphotic zone and contained there with no effects on phytoplankton growth for 60 days. Populations of flagellates and dinoflagellates were observed in the bay during June. Populations of diatoms were not large enough to be seen with the microscopic counting technique

but were seen in net tow samples. Skeletonema costatum cells appeared in microscopically analyzed samples on 23 June, about two weeks before the midsummer S. costatum maximum which occurred after a period of high winds. Wind-mixing of nitrate-nitrogen into the euphotic zone from deeper layers of the water column is the only reasonable mechanism whereby enough nitrogen could be made available for support of the S. costatum maximum which was observed in Auke Bay on 9 July.

Zooplankton

Species which formed the Auke Bay zooplankton community are (with rarely collected species omitted): (1) Cladocerans: Evadne nordmanni, Podon leukarti; (2) Copepods: Centropages abdominalis, Pseudocalanus minutus, Acartia clausii, Acartia longerimus, Oithona helgolandicus, Calanus finmarchicus; (3) Barnacle nauplii (unidentified); (4) Tunicates: Oikopleura sp., Fritilaria sp.; (5) Euphausiid furcilia.

Copepods were not present in the upper 15 meters of the water column in any quantity until the second week of June when a large mass of eggs accompanied by a large number of nauplii and metanauplii was observed in the upper several meters of the bay. By 25 June, adults and copepodites were more abundant than more immature forms. From 2 July until 22 August, copepods were numerically the most abundant group in the zooplankton (Figure 19).

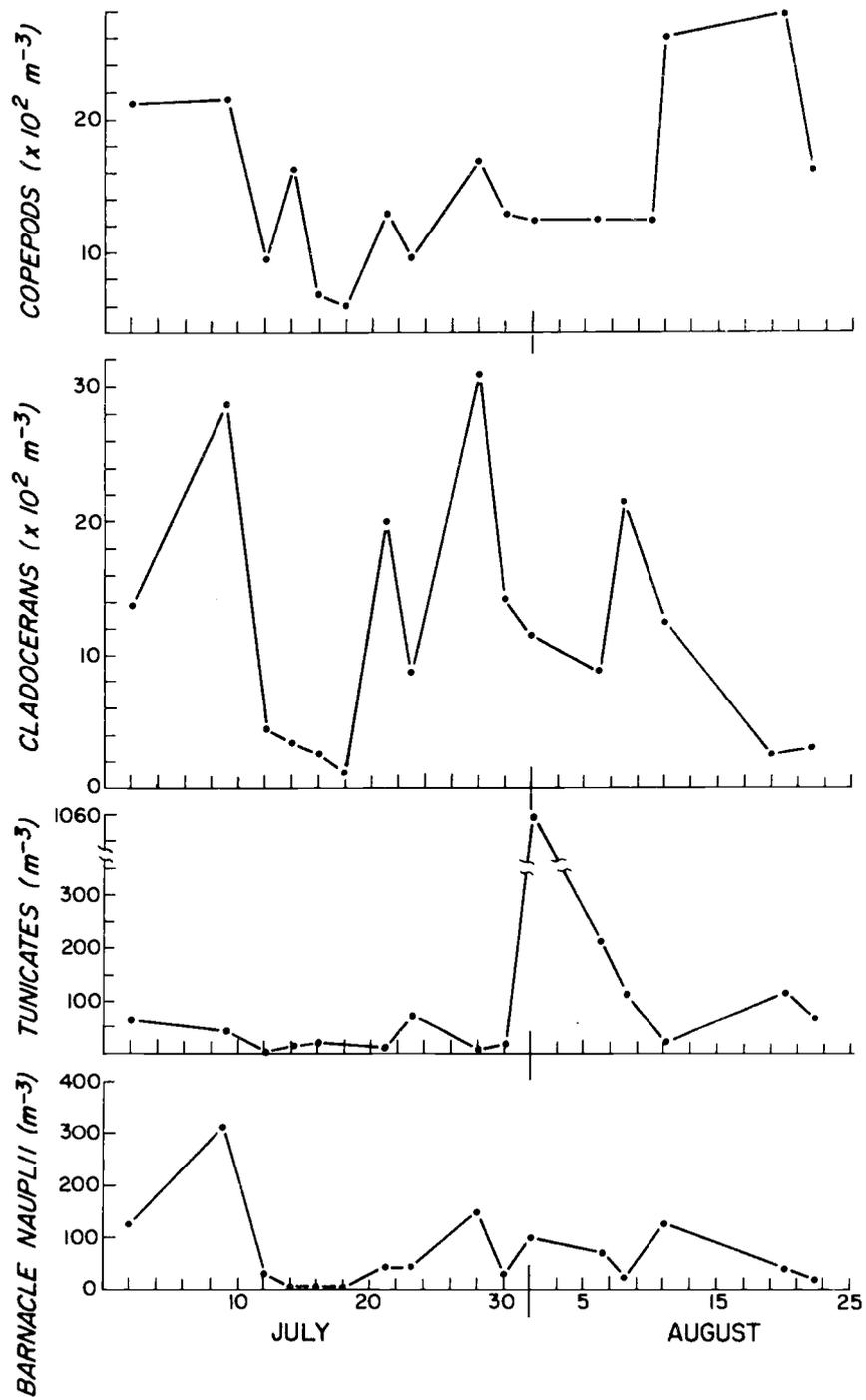


Figure 19. Total numbers of different zooplankton groups at ABM during summer 1969.

Microscopic examination of slides prepared from copepod fecal pellets revealed fragmented phytoplankton frustules and bits of dinoflagellate plates embedded in a greenish, granular matrix. For 4, 6 and 8 August, frustules of Thalassionema nitzschiodes were numerically dominant in the fecal pellets. Frustules of Cocconeis sp., Coscinodiscus sp., Navicula sp., and Thalassiosira aestivalis were observed in the fecal pellets. Frustules of Skeletonema costatum, the most abundant species in the community, were not observed in the fecal pellets. S. costatum has been reported to be a preferred food source for Acartia tonsa and Pseudocalanus sp. (Curl and McLeod, 1961). Pseudocalanus minutus has been shown to graze Skeletonema costatum (Parsons and LeBrasseur, 1970) as has Acartia tonsa (Martin, 1970).

Frustules of Skeletonema costatum are delicate compared to frustules of other diatoms observed in the fecal pellets and may have been destroyed beyond recognition in zooplankton digestion processes. Separate cultures of S. costatum and mixed Thalassiosira aestivalis and Coscinodiscus sp. were grown in enriched Auke Bay water. When Acartia clausii adults were added to the cultures, fecal pellets were produced in the flask containing the diatom mixture but were not produced in the flask containing only Skeletonema costatum.

While these simple observations are not conclusive, they suggest that Skeletonema costatum was not grazed by Acartia clausii, one

of the two species of copepods which dominated the numbers of the Auke Bay zooplankton over the summer. The other co-dominant species of zooplankton, Oithona helgolandicus, was not used in the experiments, but the absence of S. costatum frustules in fecal pellets indicates this species also did not feed on S. costatum. Parsons and LeBrasseur (1970) showed that Oithona sp. grazed Skeletonema costatum. Different sized species of copepods are known to selectively feed on different sized species of phytoplankton (Mullin, 1963; Richman and Rogers, 1969; Parsons and LeBrasseur, 1970). Copepods of the genus Acartia as well as other copepods about the same size as Acartia clausii have been shown to feed on Skeletonema costatum. The observation that Auke Bay copepods in general and Acartia clausii in particular did not appear to feed on Skeletonema costatum is unexplained. Perhaps factors other than size of phytoplankton can influence grazing selectivity of copepods.

Wind-Driven Auke Bay Summer Phytoplankton Blooms

Several features are evident in the pattern of total Auke Bay euphotic zone chlorophyll a over the summer (Figure 20). A chlorophyll a maximum occurred at the end of May shortly after the start of the study. The maximum was due to growth of Thalassiosira aestivalis, a species which had formed the spring phytoplankton bloom in Auke Bay during years previous to 1969. A June period of low

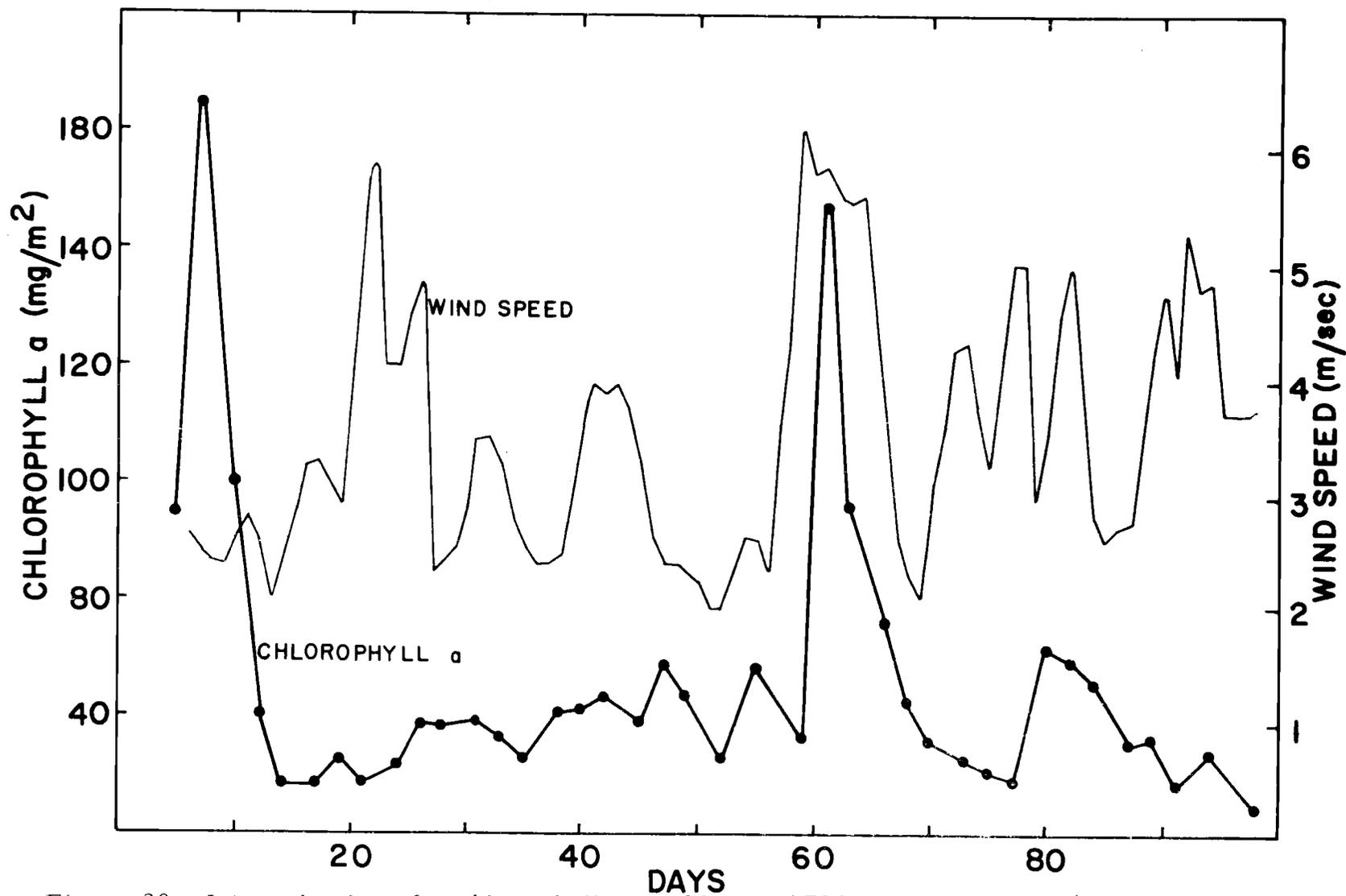


Figure 20. Integral values for chlorophyll a profiles at ABM over summer 1969. Three-day running mean of daily wind speeds at Juneau Municipal Airport during summer 1969.

standing chlorophyll a was followed by two pronounced maxima which were due to growth of Skeletonema costatum.

Nitrogen was not transported into the bay by freshwater runoff in sufficient quantities to produce the midsummer phytoplankton blooms. Tidal effects were not sufficient to mix nitrate-rich water into the euphotic zone. Auke Bay thermocline and pycnocline depths were equivalent during periods of high solar insolation and low wind speed. After periods of high winds, Auke Bay became nearly isothermal but retained pronounced density structure, the result of mixing of warm freshwater down into the water column. Oceanic thermocline theory predictions (Phillips, 1966) for thermocline depth during periods of low wind speed were in agreement with Auke Bay observations. The theory predicts that the bay could mix to the bottom during periods of high winds. Phytoplankton blooms were observed in Auke Bay only after periods (3 to 4 days) during which the three-day running mean wind speed was greater than 4 m/sec (Figure 20). From oceanic thermocline theory, a steady 4 m/sec wind speed would yield a 13.5 meter mixed-layer depth, approximately the depth to which the Auke Bay euphotic zone extended. Auke Bay can be considered a two-layered system with respect to phytoplankton photosynthesis. The water column can be divided at 12 meters (the mean summer depth of the one percent light level) into a euphotic zone where phytoplankton photosynthesis and growth occurred and an underlying aphotic zone where

no appreciable growth occurred. The thermocline depth (mixed layer depth) would be located within one of the two layers depending on wind speed. For wind speed less than 4 m/sec, the mixed layer depth would be within the euphotic zone, hence turbulence induced by wind-mixing would not extend down into the nitrate-rich aphotic zone. When winds blew greater than 4 m/sec for more than one day, the mixed layer depth would extend into the nitrate-rich aphotic zone and nitrate would be carried into the euphotic zone. High stability of the Auke Bay water column would act as a damping factor after high winds ceased and would resist continued mixing by lighter winds, hence phytoplankton populations would not be carried out of the euphotic zone and conditions would be set for a phytoplankton bloom.

Conclusions

1. The Auke Bay water column is mixed deeper than the 12 meter euphotic zone when winds blow from the south at speeds greater than 4 m/sec for more than one day. The bay could mix to the bottom over much of its area when winds blow 6 m/sec or greater. Salt balances suggest fresh Auke Creek water is mixed down into the bay when rain occurs during periods of high winds.
2. Nitrate concentrations at 27 meters decreased during periods of high winds.

3. Nitrate is not carried into Auke Bay through freshwater runoff in quantities sufficient to support phytoplankton blooms.
4. Phytoplankton blooms occurred only after periods during which winds greater than 4 m/sec blew from the south for longer than a day. Phytoplankton blooms in Auke Bay are the result of wind-mixing of nitrate from deeper layers into the Auke Bay euphotic zone.

III. COMPUTER SIMULATION MODEL FOR AUKE BAY SUMMER PHYTOPLANKTON DYNAMICS

Introduction

Modeling Plankton Dynamics for Aquatic Ecological Systems

The ecology literature contains models for ecological dynamics, some of which were written long before the discipline now called systems ecology became fashionable. Fleming (1939) wrote a model for control of diatom populations by grazing in the English Channel. Riley (1946, 1947, 1965) and Riley, Stommel and Bumpus (1949) wrote papers concerning quantitative aspects of phytoplankton and zooplankton dynamics related to environmental factors in the Atlantic Ocean. Steele (1958) modified Riley's equations and estimated equation parameters from North Sea data. Solutions for the equations fit temporal patterns of phosphate concentration and phytoplankton and zooplankton standing crops in the North Sea. Parker (1968) included an equation for feeding and growth of land-locked salmon along with equations for plankton dynamics in a lake. McAllister (1969) modeled feeding relations of zooplankton on phytoplankton. Williams (1971) included equations for plankton dynamics in a model for energy flow in a lake. Walsh and Dugdale (1971) modeled nitrogen flow in the Peruvian upwelling system. Patten (1968) reviewed the literature on mathematical models for plankton dynamics while Mann (1969) reviewed the literature on

dynamics of aquatic ecosystems.

Models are hypotheses which are posed to account for phenomena within the "realized" world. The "realized" world is the perception of the "real" world which, itself, is not completely known (W. S. Overton, lecture notes, Statistics 526, Systems Ecology). The "realized" world is in turn a model of the "real" world in the sense of the scientific paradigm of Kuhn (1962). Models can be either verbal or quantitative but in either case are abstractions of the "realized" world:

"Real" world --- "Realized" world --- Model.

According to Kac (1969, p. 695), "models are for the most part caricatures of reality. If they are good, then like good caricatures, they portray some of the features of the real(ized) world, though perhaps in distorted manner. The main role of models is not so much to explain and predict (although ultimately these are the main functions of science) as to polarize thinking and pose sharp questions."

The fundamental assumption involved in modeling, as in the scientific method, is reductionistic: complex entities can be degraded into a larger set of less complex entities which, when analyzed and recombined, account for observations about the character of the complex entity.

There are several phases involved in quantitative modeling:

(1) definition of purpose of the model, (2) definition of the systems to be modeled (hence definition of the elements and relations which will

be considered in the model out of the set of all possible elements and relation, (3) specification of the functional form for the relations and combination of the forms into equations which describe behavior of the elements, (4) solution of system equations and validation of the equations by comparison of their solutions with data, (5) investigation of properties of the validated system equations. The set of equations written to describe system dynamics is called the model. Watt (1968), Dale (1970) and Kowal (1971) provide discussions of the modeling process. The phases in the modeling process are written in sequential order; however, the phases are interrelated by the nature of the modeling strategy and are conducted, in practice, in parallel rather than in series.

Initial attempts to model plankton dynamics for Auke Bay involved development of a parameter estimation algorithm which could be used to fit a general model for plankton dynamics to field data. Steele (1958) had written two sets of ordinary differential equations, based on Riley et al.'s (1949) general equations for plankton dynamics, to describe plankton dynamics in the North Sea. When nutrient level was greater than or equal to 0.4 ug-at PO₄-P/liter, the equations were:

$$\frac{dP}{dt} = P(a_{11} - a_{12}Z - m) \quad (1)$$

$$\frac{dN}{dt} = -a_{21}P + m(a_{22} - N) \quad (2)$$

$$\frac{dZ}{dt} = a_{31}P - a_{32}Z^2 \quad (3)$$

where P was standing phytoplankton carbon, N was standing phosphate-phosphorous, Z was standing zooplankton carbon and a_{ij} were constants. When nutrient level was less than 0.4 ug-at $\text{PO}_4\text{-P/liter}$, equations (1) and (2) were modified to equations (4) and (5), respectively:

$$\frac{dP}{dt} = P(a_{41}N - a_{42} - a_{43}Z - m) \quad (4)$$

$$\frac{dN}{dt} = P(a_{51} - a_{52}N) + m(a_{22} - N) \quad (5)$$

Steele varied m twice over a 100-day simulated summer growth period for the North Sea.

A pseudo-gradient least squares parameter search routine was used successfully to fit equations (3), (4) and (5) to Steele's data with m allowed to vary ten times over the 100-day simulated growth season (Curl and Saugen, 1969). Equations (3), (4) and (5) could not be fit to data from Auke Bay with the parameter search routine. This was a consequence of the form of the Auke Bay data compared with Steele's North Sea data. Steele's set of differential equations adequately described monthly variations (Steele's sample interval) in North Sea plankton but could not describe daily variations in Auke Bay plankton (sample interval was three times each week).

Success in development of a model for Auke Bay phytoplankton dynamics resulted only after a modeling strategy was adopted. The strategy was a human behavior pattern for successive refinement of

model expressions accompanied by parameter estimation for model expressions uncoupled from system equations:

1. Define the purpose of the model
2. Define the system (hence system elements and relations) under constraints imposed by 1. and within constraints imposed by degree of knowledge of elements and relations.
3. Uncouple forcing functions from system processes where possible and write formulations for the forcing functions.
4. Write mechanistic formulations for system relations and where possible, estimate parameters for these formulations from observations on subsystems.
5. "Tune" the model by manipulating values for parameters which proved impossible to estimate with field data or from the literature but which had to be included in the system equations as a consequence of mechanistic elaboration for relations.

A mechanistic model which included effects of time-varying light and wind-mixing was written for Auke Bay phytoplankton dynamics using the modeling strategy. The dimension of the parameter estimation problem was reduced in the process so that although the final set of system equations contained ten parameters, only two parameters were unspecified and available for manipulation in the "tuning" process.

There are two different approaches to modeling expressions for system relations (Charbajin, 1970). The first approach involves

formulation of arbitrary mathematical functions which express observed response of variables to some forcing function. Such a formulation can describe the observed response but because of its empirical nature, does little to elucidate underlying mechanisms. The second approach involves formulation of expressions based on current knowledge of mechanisms which occur in the relations. Such formulations can describe observed system response while providing additional insight into basic mechanisms and interactions. The mechanistic approach has proved successful in modeling plankton dynamics.

Watt (1968, p. 253) divided models for describing populations of organisms in resource management problems into four classes.

1. Models that attempt to explain changes in the size of a population on the basis of the relationship between the size of the reproductive segment of the population and the size of the resultant offspring populations.
2. Models that use regression methods to relate the stock in each age in each year to the stock in one or more age groups the previous year.
3. Models that attempt to explain changes in populations only in terms of factor intrinsic to the population (complicated "steady-state" models). Factors extrinsic to the population such as weather, changing temperature, velocity, or direction of ocean currents, are assumed constant. The model considers such factors as change in growth of individual animals, harvesting intensity, age at which year classes are first harvested, and natural mortality.
4. Models that are complicated but not steady-state models. This category is "open-ended" in that there is no limit to the degree of complexity that can be built into the model. As many environmental factors as required can be built into the model, in addition to a great deal of detail on

competitor species, dispersal and the results of a variety of strategies imposed by man.

While Fleming's (1939) model was of Watt's (1968) class three type, all other models in the literature on plankton dynamics are of Watt's (1968) class four type. McAllister (1970) and Williams (1971) used non-mechanistic approaches in writing expressions for relations in their models while the remainder of the authors used the mechanistic approach, at least in part.

Model Development for Auke Bay Summer Phytoplankton Dynamics

Definition of Model Purpose

Major phytoplankton blooms during summer 1969 in Auke Bay were found to be driven by wind-mixing of nitrate-nitrogen into the euphotic zone from deeper in the water column. The purpose for building a mathematical model for Auke Bay summer phytoplankton dynamics was to demonstrate a possible set of mechanisms, based on physical and biological knowledge, which could cause the observed pattern of blooms in the bay. At the same time, the mathematical model would express the present level of knowledge about the system and provide a basis for further research. In addition, such a model could provide a basis for management of the bay. Impact of growth-inhibiting substances could be studied through computer simulation of

the basic system equations with relations included to express effects of the growth-inhibiting substances.

Definition of the System to be Modeled

Mass is considered to cycle among the biotic and abiotic elements of an ecosystem while energy flows through an ecosystem (Odum, 1963, p. 83). An ecosystem is closed in the thermodynamic sense (Buckingham, 1964, p. 2) under this definition. In actuality there must be some mass transport between ecosystems, since "ecosystem" is a conceptual model (created by Tansley, 1935) and not an entity with clearly evident boundaries. It is more realistic to consider many ecosystems as open systems (in the thermodynamic sense) in steady-state with respect to flux of mass through the systems.

If the biotic element for the Auke Bay water column treated as an ecosystem is defined to be the mass of a population of organisms, and if the abiotic element is defined to be the mass of some organic or inorganic compound, a list of possible elements which could be considered in a model for Auke Bay pelagic ecosystem dynamics can be written (Figure 21). Different organic and inorganic compounds which can be used by biotic elements in growth are designated N_i . P_i are populations of phytoplankton in the bay which are always present in some quantity and which can increase to bloom proportions given some set of physical and biological conditions. D_i are decomposer

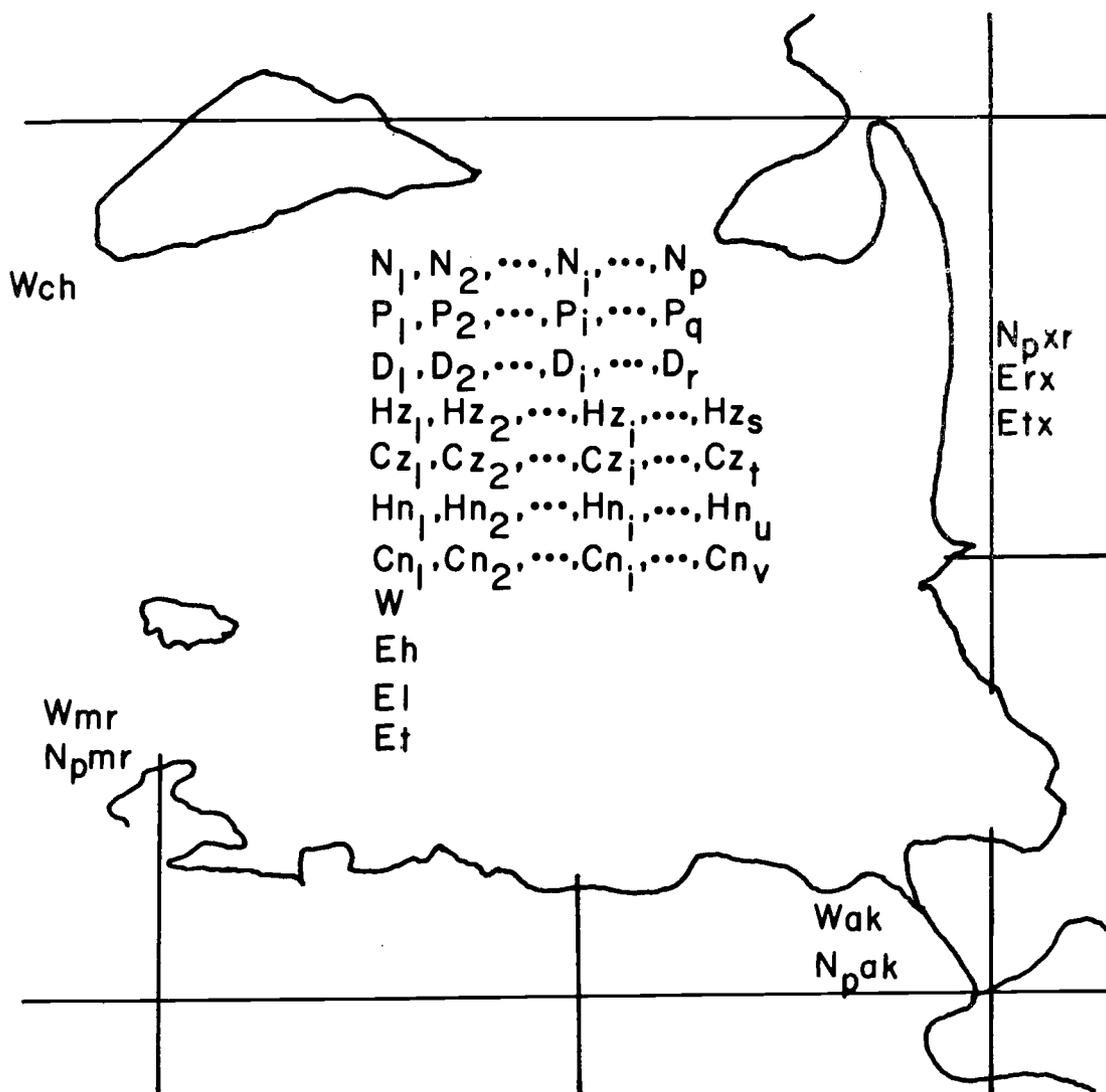


Figure 21. Possible elements for Auke Bay considered as an ecosystem. A full description of the symbolism is given in the text, p. 62.

populations, bacteria and fungi. H_z_i are populations of zooplankton which graze on phytoplankton. C_z_i are populations of carnivorous zooplankton. H_n_i are populations of herbivorous nekton. C_n_i are populations of carnivorous nekton. W is water. Elements which are outside the system but which could enter Auke Bay are nutrients from land runoff (N_{p_xr}), nutrients in Auke Creek water ($N_{p_{ak}}$), nutrients in Mendenhall River water ($N_{p_{mr}}$). In addition to the system elements, exogenous variables, which affect system relations but which are not themselves elements, must be considered. Energy enters Auke Bay as solar insolation (E_{rx}) and as kinetic energy due to wind-induced wave motion (E_{kx}). Part of the solar insolation which enters the bay is available for use in phytoplankton photosynthesis (E_l) and part is present as heat and is unavailable for use in photosynthesis (E_h). Kinetic energy is present as advection and turbulence within the bay (E_t).

It is difficult to determine the total number of populations living in Auke Bay because many rare species are undoubtedly missed in the sampling process. During summer 1969, q was 15, s was 9 and t was 3. Decomposers and nekton were not sampled. Relations among the biotic elements of Auke Bay are of the nature of "who is eaten by whom" and "whose growth is stimulated or inhibited by whose excretory products" although the latter subject is not well known (Wangersky, 1965). The major bloom-forming phytoplankton species in Auke Bay,

Skeletonema costatum, apparently was not eaten by any of the zooplankton living in the bay. Since the purpose of the model was to consider wind-driven phytoplankton blooms and since the major bloom-former was not eaten, major phytoplankton blooms could be uncoupled from water column feeding relations in Auke Bay. It is assumed that direct competition for light and nitrate between S. costatum and grazed phytoplankton species was negligible. Many compounds are known to be required for phytoplankton growth (Fogg, 1965). Bruce (1969) showed that nitrate-nitrogen was the nutrient whose absence limited phytoplankton growth in Auke Bay. Other nutrients were therefore ignored in definition of the system to be modeled.

The Auke Bay water column can be treated as an ecosystem only if mass which enters the bay has relatively little effect on the ecological dynamics within the bay. Input of freshwater into Auke Bay from Auke Creek and from the Mendenhall River (W_{ak} and W_{mr} , respectively) did not carry significant quantities of nitrate into Auke Bay (N_{pak} and N_{pmr}). Since blooms of Skeletonema costatum occurred outside the bay when blooms were in progress within the bay and since current speed was very slow at the standard sampling point in the bay, tidal motion and current effects were assumed to have negligible impact on phytoplankton growth in the bay. Therefore, effects of transport of water into Auke Bay from the channel (W_{ch}) were ignored.

The system defined for modeling purposes consisted of elements Skeletonema costatum population and nitrate-nitrogen mass within the Auke Bay water column. Growth of S. costatum was related to nitrate-nitrogen concentration and to light in the euphotic zone. Effects of wind-mixing on phytoplankton standing stock and on nitrate concentration in the euphotic zone were included.

Specification of Functional Form for System Relations

General Structure for Plankton Dynamics Models

An equation for the distribution of a property, S , in the sea with reference to Cartesian coordinates is (Neumann and Pierson, 1966, p. 392):

$$\frac{\partial S}{\partial t} = A_s \nabla^2 S - \nabla \cdot S + Q(x, y, z, t) \quad (6)$$

where the Laplacian represents turbulent mixing effects, the divergence represents advection effects and Q represents sources and sinks for S . Riley et al. (1949) used equation (6) for a theoretical treatment of quantitative plankton ecology in the North Atlantic. These authors outlined the general structure on which all subsequent mechanistic models for plankton dynamics have been based:

$$\dot{\text{Phytoplankton}} = f(\text{growth} - \text{loss})$$

$$\text{growth} = f(\text{light, temperature, nutrients})$$

$$\text{loss} = f(\text{respiration, sinking, grazing, mixing})$$

$$\begin{aligned}
 \dot{\text{Nutrient}} &= f(\text{gain} - \text{loss}) \\
 \text{gain} &= f(\text{mixing processes, organic excretion}) \\
 \text{loss} &= f(\text{uptake during growth processes}) \\
 \dot{\text{Herbivore}} &= f(\text{growth} - \text{loss}) \\
 \text{growth} &= f(\text{grazing on phytoplankton, temperature}) \\
 \text{loss} &= f(\text{death, predation effects})
 \end{aligned}$$

Effects of sinking and mixing were related to vertical components of the divergence and Laplacian, respectively, while all other factors contributing to gain or loss were included in expressions for $Q(x, y, z, t)$.

Wind-Driven Vertical Mixing in Auke Bay

Horizontal advection and mixing had negligible effects on summer phytoplankton blooms in Auke Bay (Table 1) so terms for these effects in the equation for distribution of a property (6) were ignored. Steele (1956) showed that if a water column is considered to be two-layered and if the flux of mass across the boundary occurs in the same fashion as the flux of heat across the boundary, the flux of mass can be computed from temperature profiles:

$$\frac{\partial}{\partial z} \left(\frac{A_z}{\rho} \frac{\partial S}{\partial z} \right) = \frac{1}{z_u} \left(\frac{A_z}{\rho} \frac{\partial S}{\partial z} \right)_{z_u} = U(S - S_o) \quad (7)$$

where S is concentration per m^3 in the upper layer, S_o is concentration per m^3 in the lower layer, U is the mixing coefficient across the boundary, z_u (depth of the upper layer assumed homogeneously mixed),

ρ is water density and A_z is coefficient of vertical eddy diffusivity.

According to Steele (1956), the mixing coefficient, U is:

$$U = \frac{1}{zu\Delta t(T - T_0)} \int_{z_b}^{z_u} (T_2 - T_1) dz$$

where Δt is time between measurement of temperature profiles (days), T and T_0 are mean temperatures in the upper and lower layers, respectively, at the beginning of the time period, T_1 and T_2 are temperature profiles in the lower layer at the beginning and end of the period, respectively, and z_b is the extent of the lower layer.

Auke Bay can be divided at 12 meters (the mean summer depth of the one percent light level above which nearly all of the phytoplankton biomass was located) into an upper layer, the euphotic zone, where phytoplankton growth can occur and a lower layer where phytoplankton growth is light limited. Steady-state models for the ocean thermocline yield a linear relation between wind speed and thermocline depth (Phillips, 1966). If Auke Bay is divided into a two-layered water column with respect to phytoplankton growth, the thermocline depth (and mixed layer depth) would be located in one or the other of the two layers as a function of wind speed. For wind speed less than 4 m/sec (thermocline depth about 13 meters), the mixed layer depth would be within the euphotic zone and turbulence induced by wind-mixing would not extend into the lower, nutrient-rich layer. No appreciable amounts

of nitrate would be carried into the euphotic zone and phytoplankton standing stocks would be low. Increase in wind speed would result in encroachment of the mixed-layer depth into the lower layer of the water column and nitrate would be carried into the euphotic zone, resulting in a phytoplankton bloom in the bay.

Field data from Auke Bay covered only two well-defined periods when wind speeds were high (greater than 4 m/sec for several successive days) while the data covered several periods when wind speeds were low (less than 4 m/sec). On assumption that the apparent curvature in a plot of mixing coefficients, calculated with Steele's technique, against wind speed (Figure 22) was real, the data were logarithmically transformed. A linear regression equation was used to relate transformed data to wind speed ($r = 0.72$).

Phillips (1966) stated that motion in the mixed layer becomes steady when the wind blows for periods longer than one day. Phytoplankton in Auke Bay reached summer maximum standing stock within three days after wind speed increased on 6 July. Estimated standing phytoplankton carbon was 0.12 gm/m³ on 7 July and 0.53 gm/m³ on 9 July. A model for population growth under no restrictions due to interaction with other populations and under no nutrient limitations is:

$$\frac{dN}{dt} = rN \quad (9)$$

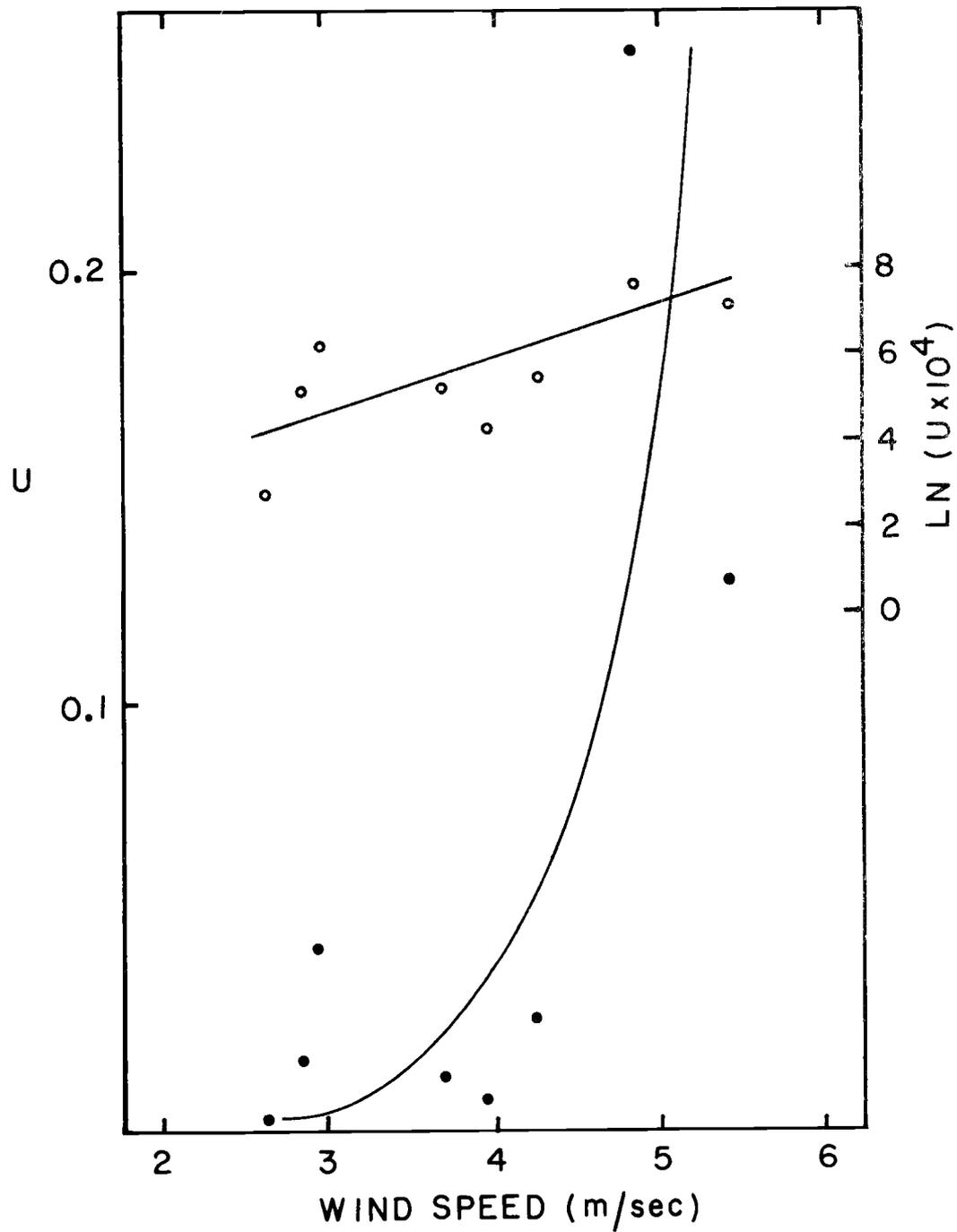


Figure 22. Mixing coefficient, U and logarithmic transform of the mixing coefficient against mean wind speed for the period over which the mixing coefficient was calculated.

where N is population biomass, r is intrinsic population growth rate and t is time. The equation is integrated to:

$$N = N_0 e^{rt} \quad (10)$$

where N_0 is initial population biomass. For the period 7 July to 9 July, assuming the simple model holds for short-term Skeletonema costatum growth under conditions of nutrient sufficiency and in absence of grazing, r was 0.74. In comparison, maximum value for r was 0.94 for laboratory chemostat experiments under optimum conditions (Percy Donaghay, personal communication). Curl and McLeod (1961) obtained a value of 1.24 for r at optimal temperature (15°C) for a batch culture of S. costatum in enriched sea water. A model for Auke Bay phytoplankton dynamics would have to account for daily wind-mixing effects on nitrate concentration in the euphotic zone in order to adequately describe system dynamics. Since mean wind speeds were used in calculating mixing coefficients, and since the mixing coefficient for one of the high wind-speed periods was obtained over a three-day period, three-day running mean wind speeds were used, together with the regression equation, to calculate daily mixing coefficients.

Light, Nitrate and Phytoplankton Photosynthesis

Ryther and Yentsch (1957) developed an empirical formulation for phytoplankton production in the ocean based on light energy and

chlorophyll a data:

$$P = \frac{R}{k} C A \quad (11)$$

where P was integral production under a square meter of sea surface (gm carbon/m²/day), R was daily relative photosynthesis taken from an empirical curve of relative photosynthesis versus daily surface insolation (Figure 23), k was the extinction coefficient of light in the water column, C was mean chlorophyll a concentration in the water column (gm chlorophyll a/m³), and A was the assimilation number for the phytoplankton community, gm carbon/hour/gm chlorophyll a at light saturation. The depth at which light saturation occurs for a phytoplankton community is the depth where photosynthesis is maximum in the water column on a day when surface radiation is high enough so that the photosynthetic maximum is not at the surface (light saturation occurred at 5 meters on 2 July, Figure 15). At depths shallower than the depth of light saturation, light intensity is sufficiently high as to cause destruction of chlorophyll a by photochemical "bleaching". At depths greater than the depth of light saturation, photosynthesis is a linearly increasing function of light intensity.

Smith (1936) wrote an equation which described photosynthesis as a function of some limiting substance:

$$p(p_m^2 - p^2)^{-1/2} = a I \quad (12)$$

where p was photosynthetic rate at light intensity I, p_m was maximum

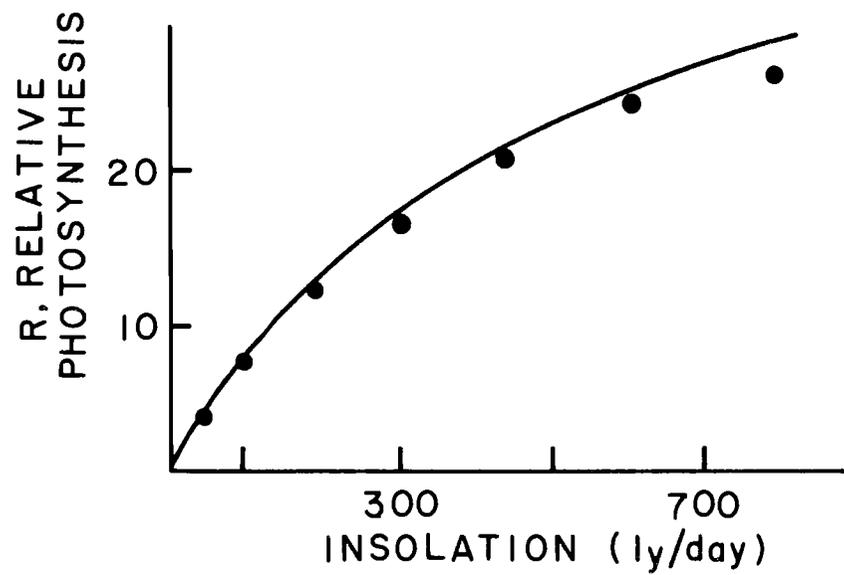


Figure 23. Relative photosynthesis against daily insolation from Ryther and Yentsch (1957).
Data points are computed from equation (14).

photosynthetic rate, \underline{a} has been interpreted by Talling (1957) as the inverse of the light intensity value at which an extension of a straight line from the initial, nearly linear, portion of a the p versus I curve intersects an extension of the asymptote, p_m . Equation (12) can be rearranged to:

$$p = \frac{p_m a I}{(1 + (aI)^2)^{1/2}} \quad (13)$$

If \underline{a} was chosen to be $\frac{1}{450}$ ly/day, equation (13) would approximately fit Ryther and Yentsch's (1957) curve for R versus daily insolation given p_m equal 30 (where p from equation (13) was equivalent to Ryther and Yentsch's (1957) R and p_m was identical to the maximum value for R) (Figure 23). If I is called $L(t)$, an expression for p is:

$$p = \frac{0.0666 L(t)}{(1 + \left(\frac{L(t)}{450}\right)^2)^{1/2}} \quad (14)$$

The extinction coefficient of light, k , in Auke Bay can be related to standing phytoplankton carbon by a linear regression equation (Figure 24):

$$k(P) = 0.174 + 0.815 P \quad (15)$$

where P is standing phytoplankton carbon (gm carbon/m^3) for days when Mendenhall River water was known not to be in Auke Bay ($r = 0.96$). Small and Curl (1968) have shown that such a treatment can describe contribution of particulate chlorophyll to the extinction

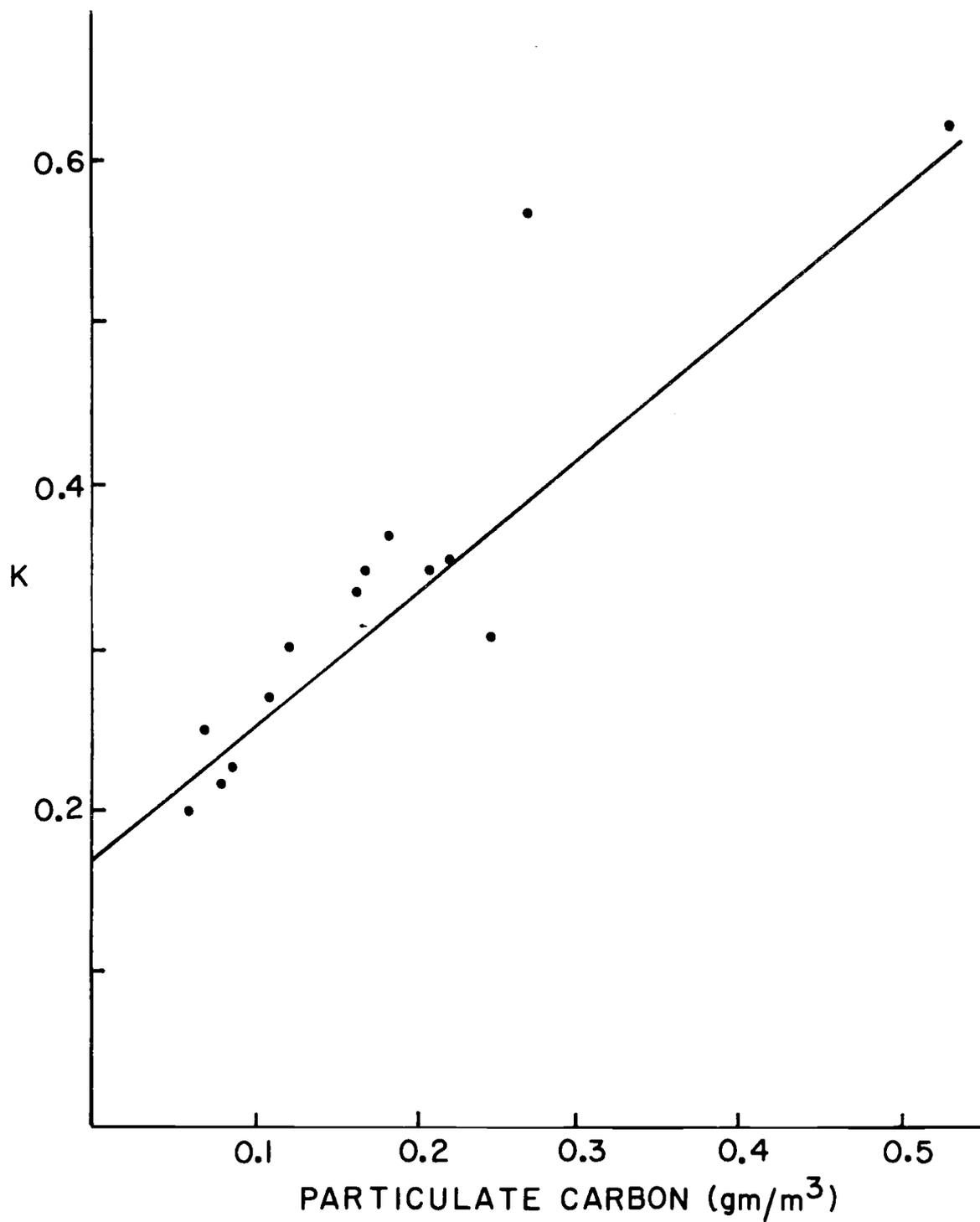


Figure 24. Linear regression of the extinction coefficient of light on standing particulate carbon at ABM. $Y = 0.174 + 0.818$ (Particulate Carbon), $r = 0.96$.

coefficient of light in areas off the Oregon coast where river tripton is so low as to have a negligible effect on the extinction coefficient.

The assimilation number for a phytoplankton community has been shown by Curl and Small (1965) to depend qualitatively on the nutrient richness of the water where the phytoplankton were growing at the time of measurement of phytoplankton productivity and chlorophyll a. Curl and Small (1965) found values from 5 to 10 in nutrient-rich, recently upwelled water. Values of A from 3 to 5 indicated borderline nutrient deficiency while values of A from 0 to 3 indicated nutrient depletion. Values of A from 2.5 to 4.0 at light saturation were obtained during the midsummer Skeletonema costatum bloom in Auke Bay. Nitrate concentrations were around 0.5 μ mole during the period.

Eppley, Rogers and McCarthy (1969) suggested that growth rate of phytoplankton could be related to nitrate concentration in the water in which they grow by a Michalis-Menton expression. I chose to relate the assimilation number, an expression for growth rate, to nitrate concentration:

$$A(N) = \frac{A_{mx} N}{N + K} \quad (16)$$

where A(N) is the assimilation number, now a function of nitrate concentration in the euphotic zone, A_{mx} is the maximum value for A(N), N is nitrate concentration (μ mole) and K is the Michalis-Menton constant (nitrate concentration at $1/2 A_{mx}$). The field data are very

sparse and many different curves could be fit through values for A plotted against nitrate (Figure 25). However, if A_{mx} is chosen to be 10 in accord with the results of Curl and Small (1965), and if the data pair A equal 4.0 at nitrate concentration 0.5μ mole is selected as representative of the field data, the parameter K is 0.75.

The rate of phytoplankton photosynthesis can now be described by combining equations (14), (15) and (16):

$$PS = \frac{0.0666 L(t)}{\left(1 + \left(\frac{L(t)}{450}\right)^2\right)^{1/2}} \frac{A(N)}{k(P)} \quad (17)$$

Multiplication of (17) by C (gm chlorophyll \underline{a} /m³) would yield Ryther and Yentsch's (1956) equation (11) with dimension of gm carbon/m²/day. Since the model for Auke Bay phytoplankton dynamics was intended to relate mean phytoplankton carbon in the euphotic zone to mean nitrate concentration in the euphotic zone, equation (17) had to be averaged over the euphotic zone. The Auke Bay euphotic zone was assumed to be 12 meters deep so the right side of equation (17) was divided by 12. Ryther and Yentsch's (1956) equation (11) related phytoplankton production to chlorophyll \underline{a} . Since the Auke Bay phytoplankton dynamics model was to be written in terms of phytoplankton carbon, the right side of equation (17) was divided by 44, the mean ratio of phytoplankton carbon to chlorophyll \underline{a} in Auke Bay (see Estimation of Phytoplankton Carbon, p. 81). The completed expression

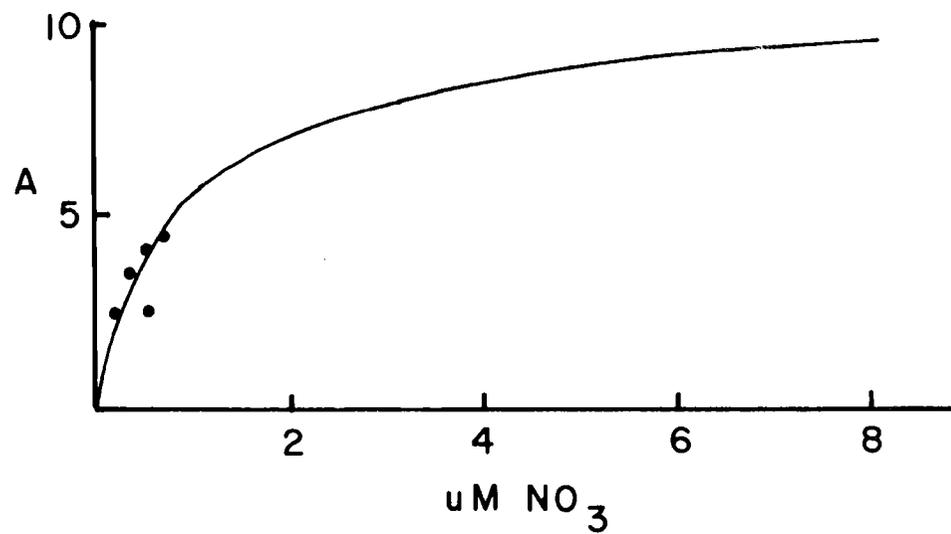


Figure 25. Michalis-Menton relation between assimilation number, A and standing nitrate-nitrogen. The curve is generated from equation (16) using the data pair $A = 4.0$ at nitrate = $0.5\mu\text{mole}$.

for phytoplankton photosynthesis as a function of light (time-varying), assimilation number (function of nitrate concentration) and extinction coefficient of light (function of phytoplankton carbon) was:

$$PS = \frac{0.000126 L(t)}{\left(1 + \left(\frac{L(t)}{450}\right)^2\right)^{1/2}} \frac{A(N)}{k(P)} \quad (18)$$

where PS was gm carbon/gm phytoplankton carbon/m²/day.

Phytoplankton Loss Expression

Possible sources for loss of phytoplankton carbon from a population are: sinking of cells from the population in the euphotic zone into deeper layers of the water column; excretion of organic carbon from cells; death of phytoplankton cells; grazing of phytoplankton by zooplankton. The major bloom-forming species in the Auke Bay summer phytoplankton, Skeletonema costatum, was not grazed by zooplankton living in the bay so grazing has been ignored for modeling purposes. All other losses have been lumped into one expression since mechanistic relations for the other sources of loss have not been qualitatively or quantitatively formulated.

Two different expressions were used for D, loss of carbon from the phytoplankton population:

$$D = C(1) \quad (19)$$

where C(1) was a constant, and

$$D = \frac{A_{mx}}{A(N)} (C(2) - C(3)) + C(3) \quad (20)$$

where A_{mx} was the maximum value for the assimilation number, A , $A(N)$ was assimilation number as a function of nitrate concentration in the euphotic zone, equation (16), $C(2)$ was maximum loss rate for the phytoplankton and $C(3)$ was minimum loss rate. The parameters $C(1)$ or $C(2)$ and $C(3)$ were incrementally changed so as to "tune" the model.

Nitrogen

Nitrate-nitrogen was the nutrient primarily responsible for driving summer phytoplankton blooms in Auke Bay. The only major source for nitrate in the Auke Bay euphotic zone was the deeper layers of Auke Bay. From equation (7), change in nitrate in the Auke Bay euphotic zone due to wind mixing can be expressed as:

$$\dot{N} = (20.0 - N) U \quad (21)$$

where N was nitrate concentration in the euphotic zone, 20.0 was nitrate concentration in the lower layer (assumed constant over the summer) and U was the mixing coefficient.

Redfield (1934) showed that the mean atomic ratio of carbon to nitrogen in tissues of marine plankton was 106:16. Uptake of nitrogen by phytoplankton growth is assumed to be proportional to photosynthetic incorporation of carbon dioxide into phytoplankton carbon so that an

expression for change in nitrate concentration in the euphotic zone due to phytoplankton photosynthesis is:

$$\dot{N} = -12.6 \text{ PS P} \quad (22)$$

where 12.6 is the atomic ratio of nitrogen to carbon translated to mg-at $\text{NO}_3\text{-N/m}^3$ (or μ mole NO_3) divided by gm phytoplankton carbon/ m^3 , PS is the photosynthetic rate (equation 18) and P is standing phytoplankton carbon.

Estimation of Standing Phytoplankton Carbon

Lorenzen (1968) showed that linear regression of particulate carbon on chlorophyll a could be used to estimate phytoplankton carbon for phytoplankton blooms composed primarily of one species. Carbon to chlorophyll a ratios varied at least monthly in the North Sea (Steele and Baird, 1965). Steele and Baird (1965) interpreted the intercept of linear regression of carbon on chlorophyll a as a measure of detrital carbon.

Linear regressions of total euphotic zone particulate carbon on total euphotic zone chlorophyll a were performed for three different periods of the summer. The first regression included data gathered during the initial Thalassiosira aestivalis bloom. The second regression included data gathered during a period when flagellates and dinoflagellates made up the phytoplankton community. The third regression consisted of particulate carbon and chlorophyll a values for the

period when Skeletonema costatum dominated the phytoplankton. Slopes were nearly identical for the three periods although intercept values were different (Figure 26). Differences in intercepts are interpreted as differences in particulate carbon not related to living phytoplankton. Possible identity of this "background" carbon could be bacterial carbon, non-living phytoplankton carbon or detrital carbon carried into the bay through freshwater runoff. Total euphotic zone chlorophyll a values were multiplied by the mean of the slopes to provide an estimate of total euphotic zone standing phytoplankton carbon.

Estimation of Standing Nitrate-Nitrogen

Standing nitrate-nitrogen was estimated with the mean of summed values of nitrate over the upper 10 meters of Auke Bay. Values of nitrate per meter were obtained from linear interpolation of measurements taken at 0, 5 and 10 meters.

Numerical Solution and System Equation "Tuning"

Equations (18) and (20) were combined with the mixing coefficient, U, to form an ordinary differential equation for change in phytoplankton standing carbon in the Auke Bay euphotic zone with time:

$$\frac{dP}{dt} = P(PS - D - U) \quad (23)$$

where P was gm carbon/m³.

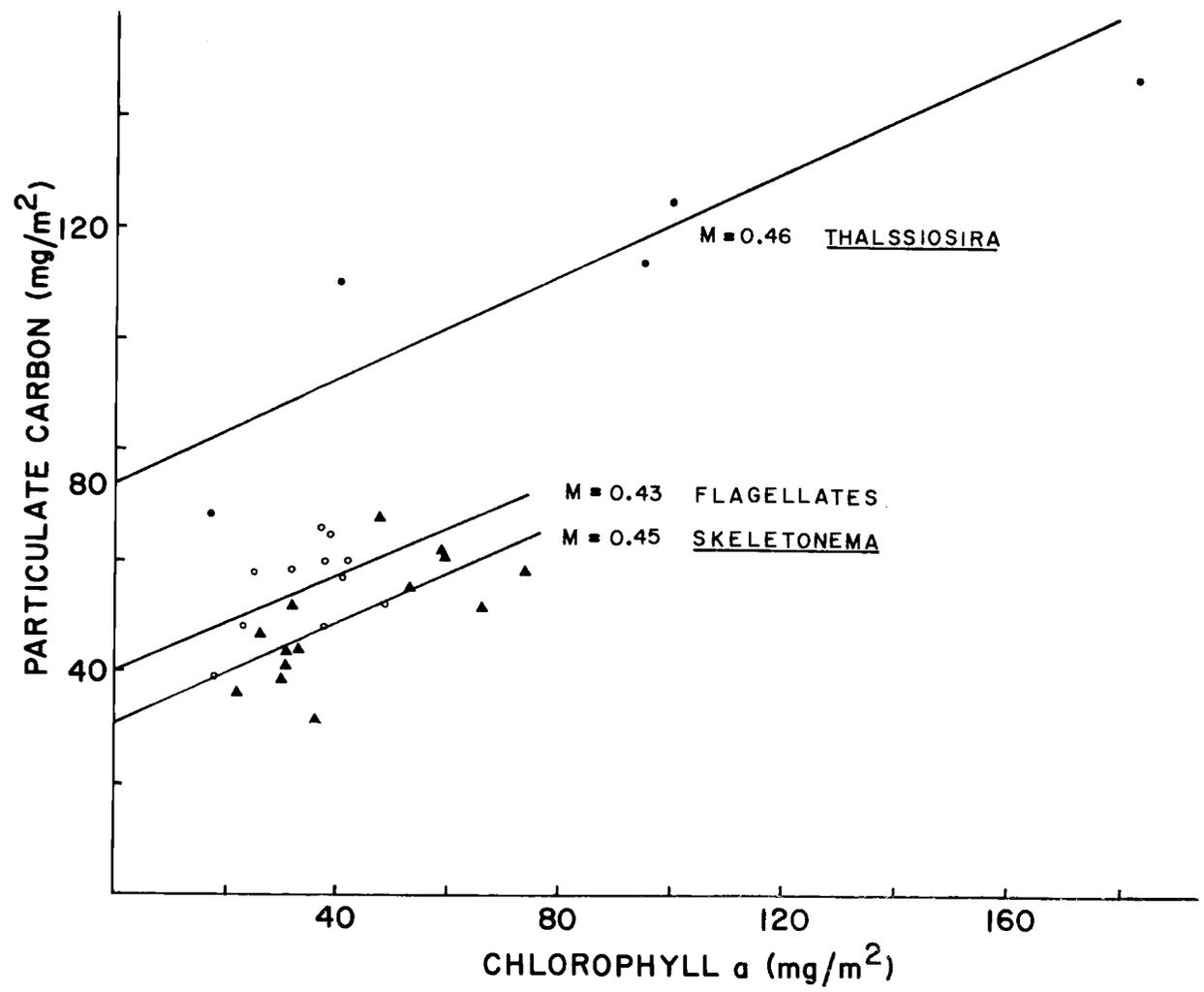


Figure 26. Linear regressions of particulate carbon on chlorophyll a during periods when different species dominated the phytoplankton community.

Equations (21) and (22) were combined into an ordinary differential equation for change in nitrate in the euphotic zone with time:

$$\frac{dN}{dt} = (20.0 - N) U - 12.6 (PS)P \quad (24)$$

where N was mg-at $\text{NO}_3\text{-N/m}^3$, (μ mole NO_3).

A flow diagram (Overton, 1972) for the system equations is given in Figure 27.

Numerical solutions for the equations were obtained with a Runge-Kutta fourth order technique using a 0.1 day step size. Values for daily insolation (Figure 12) and for U (Figure 28) were stored in tables. Fortran subroutines used linear interpolation to compute insolation and U for any time.

Since the field data did not include pre-bloom conditions, initial values for phytoplankton standing carbon and for nitrate in the euphotic zone were not known. Initial nitrate concentration in the euphotic zone was assumed to be 20.0 μ mole, while initial phytoplankton standing carbon was assumed to be 0.001 gm/m³. Phytoplankton growth was assumed to begin on 9 May in Auke Bay for purposes of computer simulation of summer phytoplankton blooms.

The model for Auke Bay summer phytoplankton dynamics contained ten parameters, eight of which were estimated for expressions uncoupled from the final system equations. The two unspecified parameters of equation (20) could not be estimated from field data since loss of carbon from the standing phytoplankton population was not

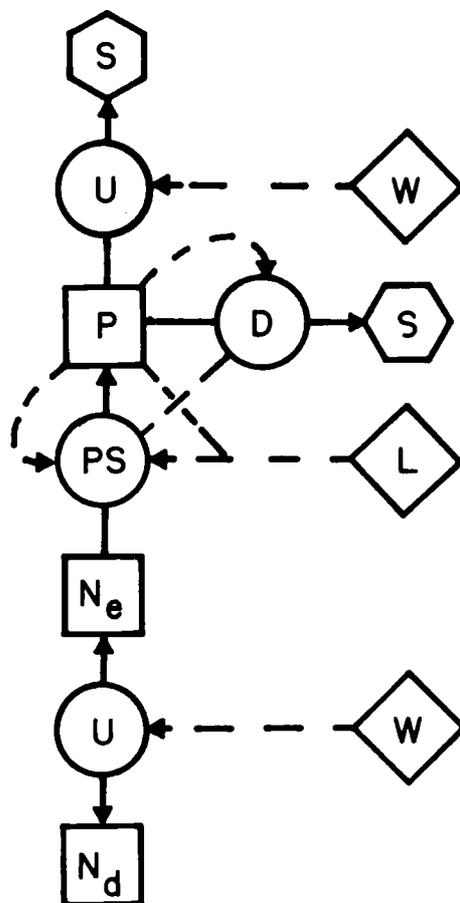


Figure 27. Flow diagram for Auke Bay summer phytoplankton dynamics model. \square are system elements, \circ are system processes (formulations for system relations), \hexagon are sinks or losses from the system, $- - \rightarrow$ are influence paths, \diamond are forcing variables. Symbols are those of equations 23 and 24. In addition, W is wind, N_e is nitrate in the euphotic zone (N in equation 24), N_d is nitrate in the lower layer (20.0 in equation 24), and L is light.

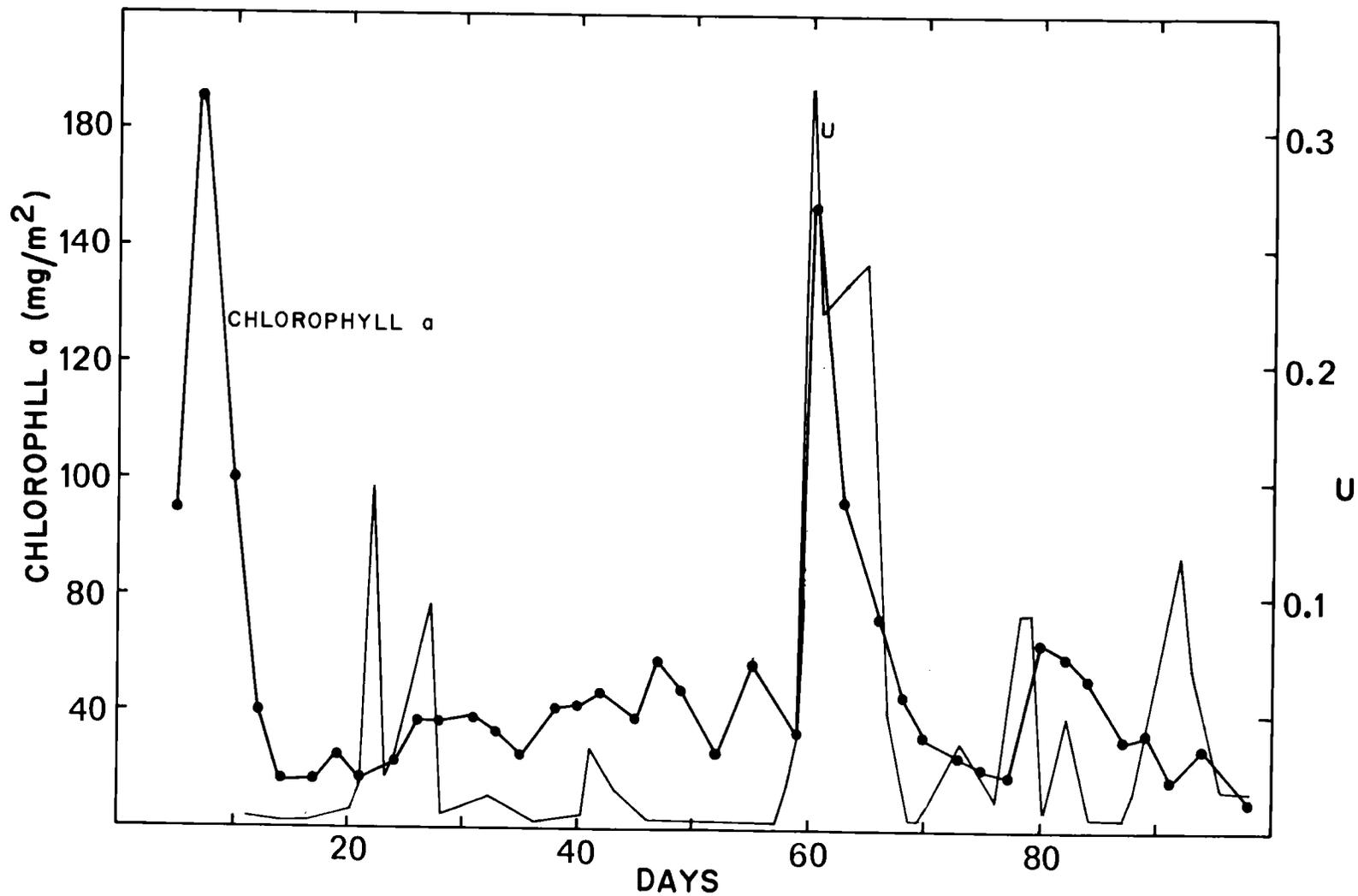


Figure 28. Mixing coefficient, U, calculated from wind-speed data on a daily basis and integral values for chlorophyll a over the summer, 1969.

measured. Effects of different values of the two unspecified parameters on total model response (fit of overall model response to field data) were studied in a series of computer simulation "runs". Curves A, C, and D (Figure 29) illustrate effects of changes in the two unspecified parameters (Table 5). Parameter values were incrementally changed until a set of parameters was found which gave a subjective "best fit" of model response to field data. This process is called "tuning the model" (R. C. Dugdale, Oceanography Departmental Seminar, Oregon State University, 1971).

Table 5. Parameter values used in computer simulation runs (Figure 29).

| Curve | A_{mx} | K | C(2) | C(3) |
|-------|----------|-------|------|------|
| A | 10.0 | 0.75 | 0.3 | 0.05 |
| B | 20.0 | 4.00 | 0.6 | 0.10 |
| C | 10.0 | 0.75 | 0.6 | 0.10 |
| D | 10.0 | 0.75 | 0.9 | 0.15 |
| E | 5.0 | 0.312 | 0.6 | 0.10 |

Model Validation and Investigation of Model Properties

If exact values for magnitudes of system elements could be obtained, the solution of a perfect model for the system (as defined by a particular set of variables) would be an exact fit to the field data under all possible ranges of forcing functions. Such a model would

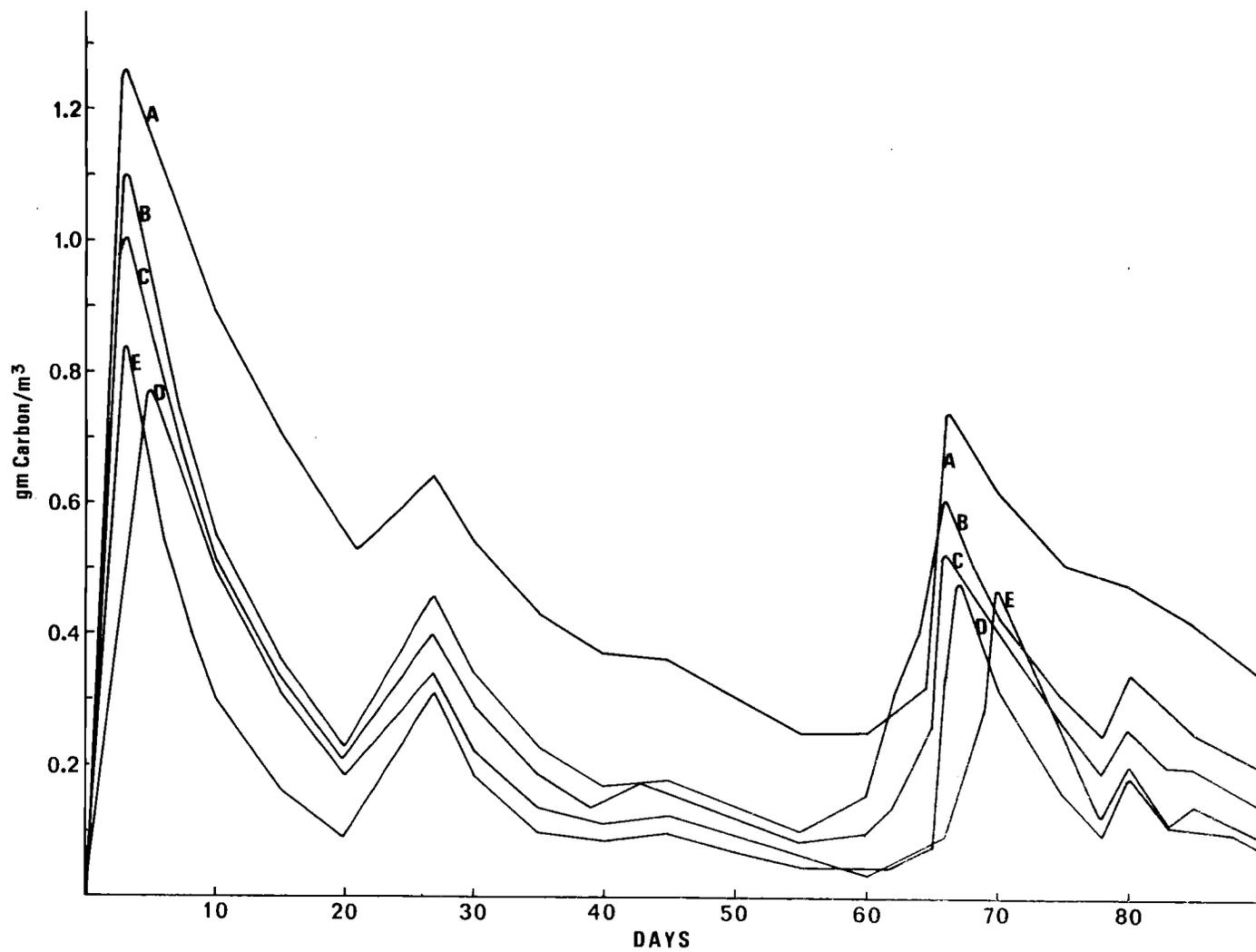


Figure 29. Computer simulation responses of the Auke Bay summer phytoplankton dynamics model under different sets of parameters (Table 5).

unquestionably be a valid model for the system. There are several sources of error which arise in modeling ecological dynamics: (1) assumptions made in system definition may be of varying degrees of "strength", (2) model expressions may be poor representations for system relations, (3) there are errors in parameter estimation. Criteria for judging validity of imperfect models for ecological systems whose elements can only be measured with relatively large error have not yet been defined. Part of the problem of defining model validity criteria lies in choice of those features of the realized system the model is intended to mimic. Dale (1970) commented that if the variance of model response compared to field data or if the transient response of the model to forcing functions is required as an expression of model validity, the statistical problems involved in specification of criteria become complicated. An additional aspect of the problem is that criteria should allow comparison of the same model structure for different sets of data. For example, we might like to know if the model for Auke Bay summer phytoplankton dynamics was valid for different but hydrographically equivalent bays. Validity criteria are required which are independent of the measure of system elements for such comparisons to be meaningful. Measure-free criteria have not yet been defined.

The purpose of the model for Auke Bay summer phytoplankton dynamics was to demonstrate a set of mechanisms which could cause

the observed pattern of blooms in the bay. For the model to be valid, model response should be in phase with the field data; the model response should exhibit minima and maxima at the same time minima and maxima occurred in the data. In addition, magnitude of model response should be equivalent to magnitude of the field data over all time. The problem of validation of the Auke Bay summer phytoplankton dynamics model lies in setting limits beyond which deviations in phase and magnitude comparisons of model response with data results in an invalid model.

Part of the answer to the problem lies in specification of how well the model response can be expected to fit the field data based on error in measurement of system elements and on assumptions used in model development. As a result of the sampling schedule used in Auke Bay (samples were taken Monday, Wednesday and Friday each week through the summer), the first major phytoplankton maximum ($t = 7$, Figure 30) was known to (-) one day or (+) two days, the second major peak ($t = 61$, Figure 30) was known to ± 1 day and the third major peak ($t = 80$, Figure 30) was known to (-) one day or (+) two days. Knowledge of time of occurrence of other minor maxima as well as time of occurrence of phytoplankton minima is indicated by horizontal bars (Figure 30). As a consequence of using three-day running mean wind speeds to calculate mixing coefficients, a one-day lag could occur between high wind speeds in the wind record and high

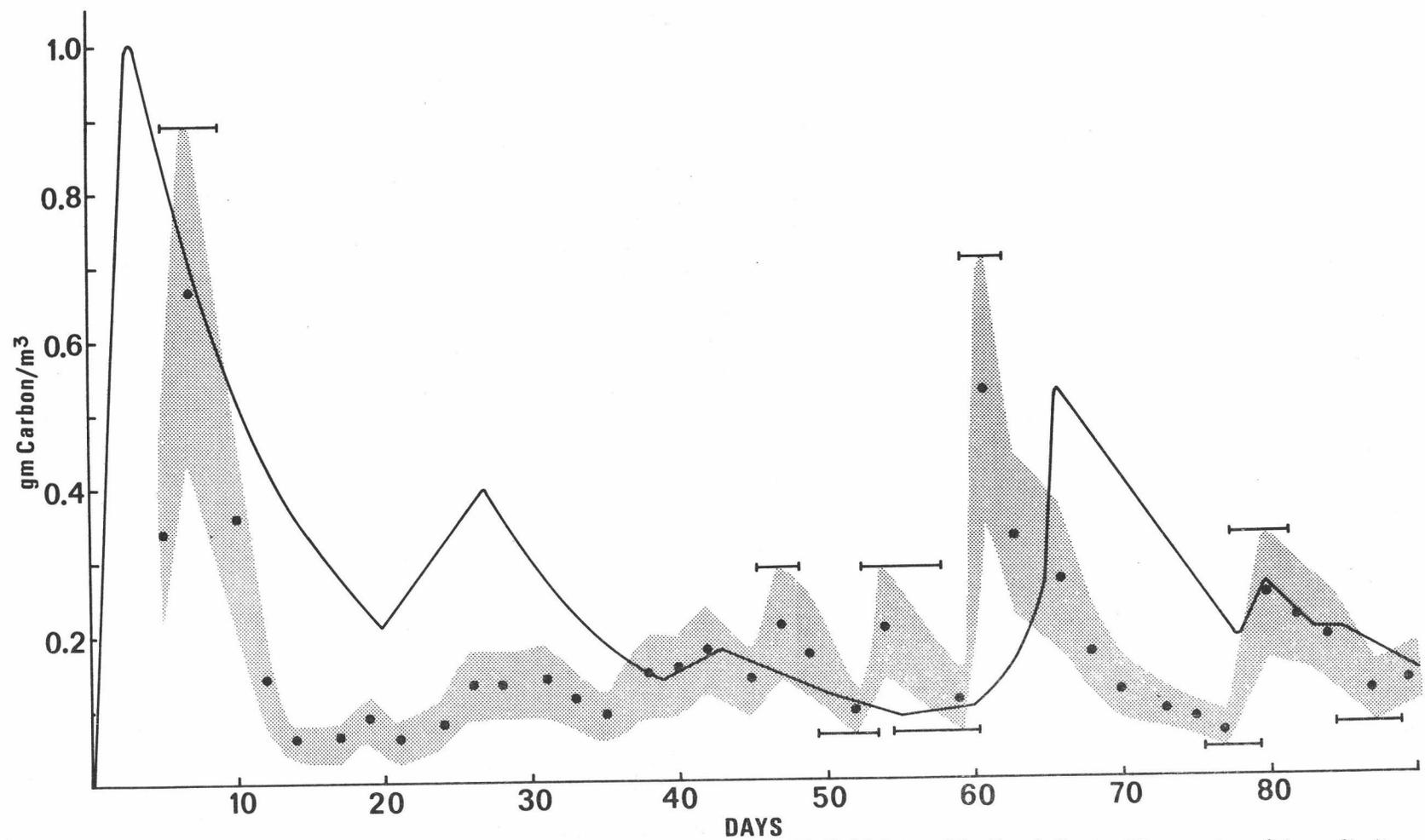


Figure 30. Aukey Bay summer phytoplankton dynamics model response compared with field data. Stippling indicates 95 percent confidence limits (± 35 percent of mean on 5 July) which were assumed to hold for every data point. Horizontal bars indicated temporal confidence in data point location. Model response parameters are those of curve C, Table 5.

mixing coefficient values. Under the constraints imposed by sampling and by estimation of mixing coefficients, the best model for Auke Bay summer phytoplankton dynamics would be expected to exhibit maxima in model response within ± two days of data maxima.

The narrowest 95 percent confidence limits for chlorophyll a in Auke Bay were ± 35 percent of the mean. If such confidence limits are assumed to hold for every day of the sampling schedule, the best model for Auke Bay summer phytoplankton dynamics would be expected to exhibit a response within ± 35 percent of each data point.

The question of validity of the Auke Bay summer phytoplankton dynamics model involves consideration not only of the fit of model response to field data. The manner in which the model response was forced to fit the data through manipulation of unspecified parameters is important. If manipulation of the free parameters has little effect on the pattern of blooms exhibited in the model response, a stronger case can be made for model validity. If parameter manipulation is important in creating the bloom pattern in the model response, the validity of the model is weakened.

Curve C (Figure 27) was chosen to be a "best" fit model response upon subjective consideration of the fit of several model responses to the field data. Curve C and field data are plotted in Figure 30. Confidence limits on magnitude of field data are indicated by stippling. There are several discrepancies between model response and field

data. Phytoplankton response leads the first data maximum at seven days by five days, a consequence of arbitrary choice of model start time.

A maximum occurred at 27 days in phytoplankton response when none occurred in the field data. Different phytoplankton species growing in Auke Bay were assumed to respond identically to light and to nitrate. Differences in growth response between phytoplankton species are known to exist (Fogg, 1965). Interspecific interactions were assumed to be negligible in model development, although inhibition of growth of one species of phytoplankton by organic compounds excreted by a previous bloom of a different species is known to occur (Wangersky, 1965). Since nitrate increased at the surface and at 5 meters in Auke Bay during the period of time the 27-day spurious peak occurred in phytoplankton model response (early June, Figure 18), and since light was high during that period (Figure 12), one or both of these assumptions must be weak. It is possible that a multi-species model could remove the spurious peak in phytoplankton response but initial attempts to construct such a model were not successful.

Phytoplankton response lags data maximum at 61 days by 6 days. The major discrepancy in the fit of nitrate response to field data (curve A, Figure 31) occurred at 64 days when a maximum in model response was not evident in the field data. The two discrepancies are related. The lag in phytoplankton response resulted in a surplus

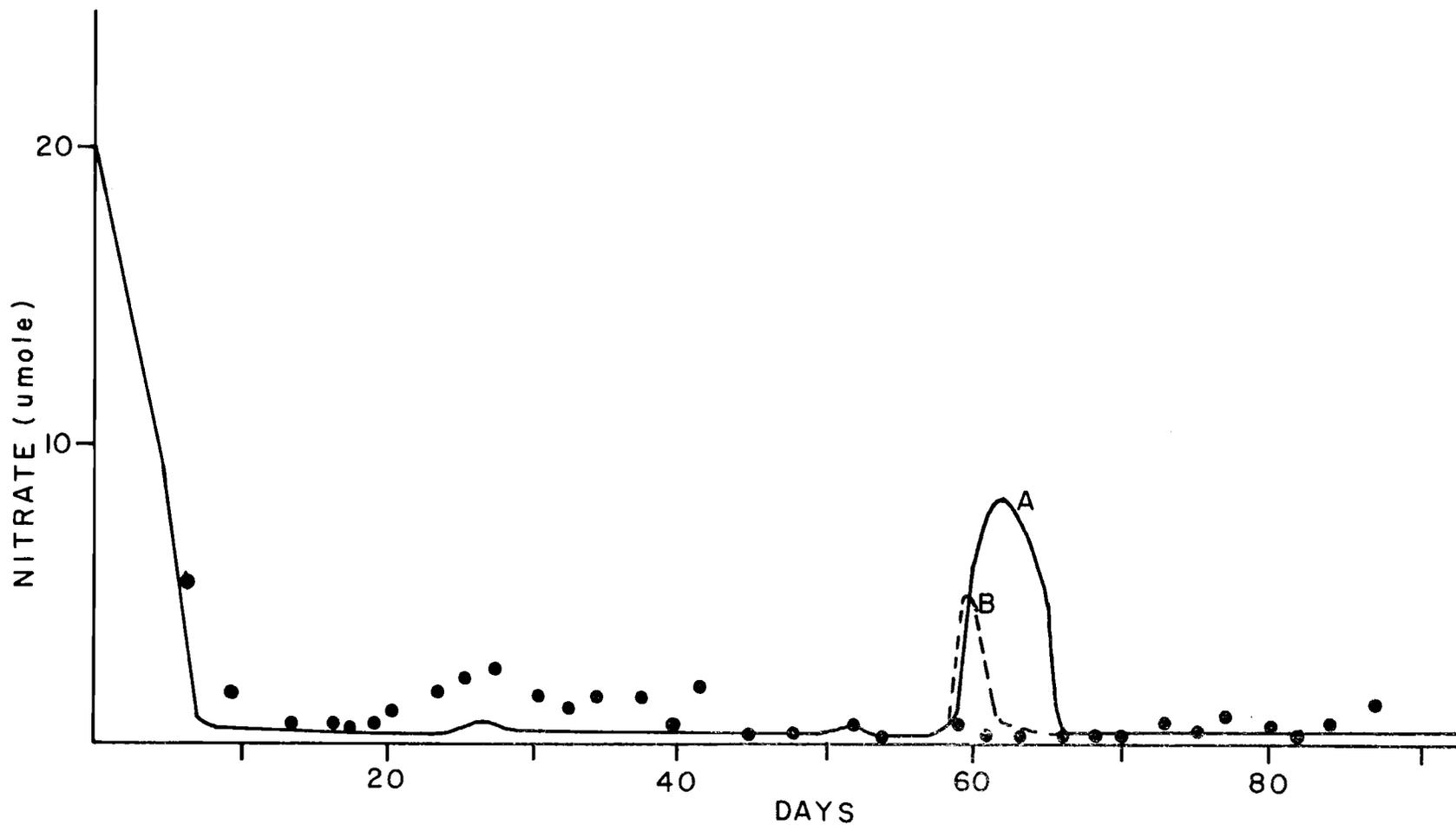


Figure 31. Auke Bay summer phytoplankton dynamics model response for nitrate-nitrogen compared with mean values for nitrate-nitrogen in the upper 12 meters at ABM over summer, 1969. Ninety-five percent confidence limits on field data were ± 13 percent of mean value on 5 July. A, insolation data. B, constant 700 ly/day.

of nitrate following the peak of mixing. The surplus disappeared as phytoplankton increased. When constant, high light values (700 ly/day) were used in a simulation "run" instead of insolation data, the phytoplankton response to midsummer mixing (curve A, Figure 32) was slightly faster than the response of the natural phytoplankton community (curve D, Figure 32). The discrepancy in nitrate response was greatly reduced (curve B, Figure 31). Evidently the formulation for effects of light on phytoplankton photosynthesis used in the model gave "sluggish" model response at low light intensities (about 150 ly/day during midsummer, Figure 12).

Curl and Small (1965) reported infrequent observations of A_{mx} values about 20 in nutrient-rich water off the Oregon coast, although the typical value was about 10. Effect of use of A_{mx} equal 20 (with corresponding $K = 4$, Table 5) was to increase magnitude of model response (curve B, Figure 29) compared to curve C, a "best" fit, past ten days. The midsummer maximum (66 days) for curve B led the maximum for curve C by one day. In contrast, use of A_{mx} equal 5 (with corresponding $K = 0.312$, Table 5) resulted in a four-day lag in the midsummer maximum (curve E, Figure 29) with respect to curve C (Figure 29). Effect of the low value of K was more pronounced on phase than on magnitude.

A(+) or (-) 50 percent change in value of the two unspecified parameters (change with respect to curve C, Table 5) modified the

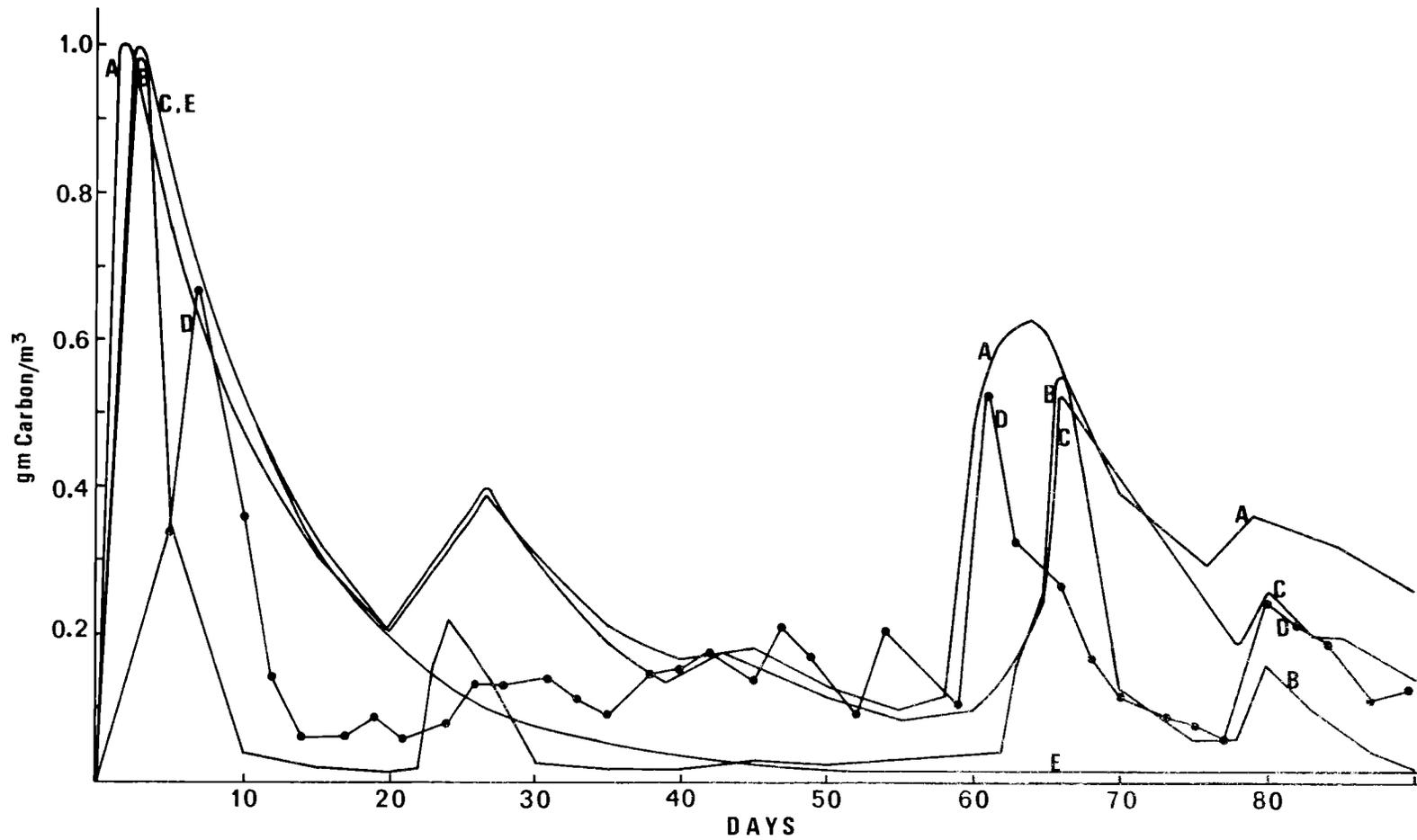


Figure 32. Computer simulation responses of the Auke Bay summer phytoplankton dynamics model under different forcing functions (Table 6).

magnitude of the model response without greatly affecting the phase relationship of model response to data. A (+) 50 percent parameter change resulted in a one-day phase lag between curves C and D (Figure 29) at 67 days while detail was lost at 80 days for a (-) 50 percent change in parameter values (curve A, Figure 29).

A simple constant (equation 19) was proposed as an alternative to the more complicated loss expression (equation 20) used in the Auke Bay summer phytoplankton dynamics model. Curve B (Figure 32) illustrates the effect of the constant loss rate (Table 6) on model response. Model response peaks were sharper with mid-peak magnitudes considerably lower than data values (curve D, Figure 32). Model response phase relationships were not significantly affected.

Table 6. Parameter values and forcing functions used in computer simulation runs (Figure 32).

| Curve | A_{mx} | K | C(1) | C(2) | C(3) | U(t) | L(t) |
|-------|------------|------|------|------|------|---------|---------|
| A | 10 | 0.75 | --- | 0.9 | 0.1 | Fig. 27 | 700 |
| B | 10 | 0.75 | 0.3 | --- | --- | Fig. 27 | Fig. 12 |
| C | 10 | 0.75 | --- | 0.6 | 0.1 | Fig. 27 | Fig. 12 |
| D | Field Data | | | | | | |
| E | 10 | 0.75 | --- | 0.6 | 0.1 | 0.001 | Fig. 12 |

The Auke Bay summer phytoplankton dynamics model was strongly controlled by the mixing coefficient, U. Use of a low,

constant value for U in a simulation "run" resulted in a decline in phytoplankton after the initial peak to a low steady-state value (curve E, Figure 32). A shift in maximum summer values for U from 59 days to 30 days resulted in a shift in model response maximum from 67 days to 35 days (Figure 33). The 80-day phytoplankton maximum was not affected in phase or magnitude by the shift, indicating the independence of effects of high wind-mixing at 60 days and at 78 days (Figure 28).

Summary

The Auke Bay summer phytoplankton dynamics model generates phytoplankton blooms in response to increases in the wind-mixing coefficient, U . Changes in free parameters have negligible effect on phase relations, hence a strong case can be made that the mechanism which causes summer phytoplankton blooms in Auke Bay is, as required by the data, wind-mixing of nitrate into the euphotic zone from deeper in the water column. The Auke Bay summer phytoplankton dynamics model therefore fulfills its purpose, which was to demonstrate such a mechanism.

The model is not perfect since lags occur in model response compared with field data. While the presence of nitrate, mixed into the euphotic zone by wind-induced turbulence effects in the water column, is a necessary condition for development of phytoplankton

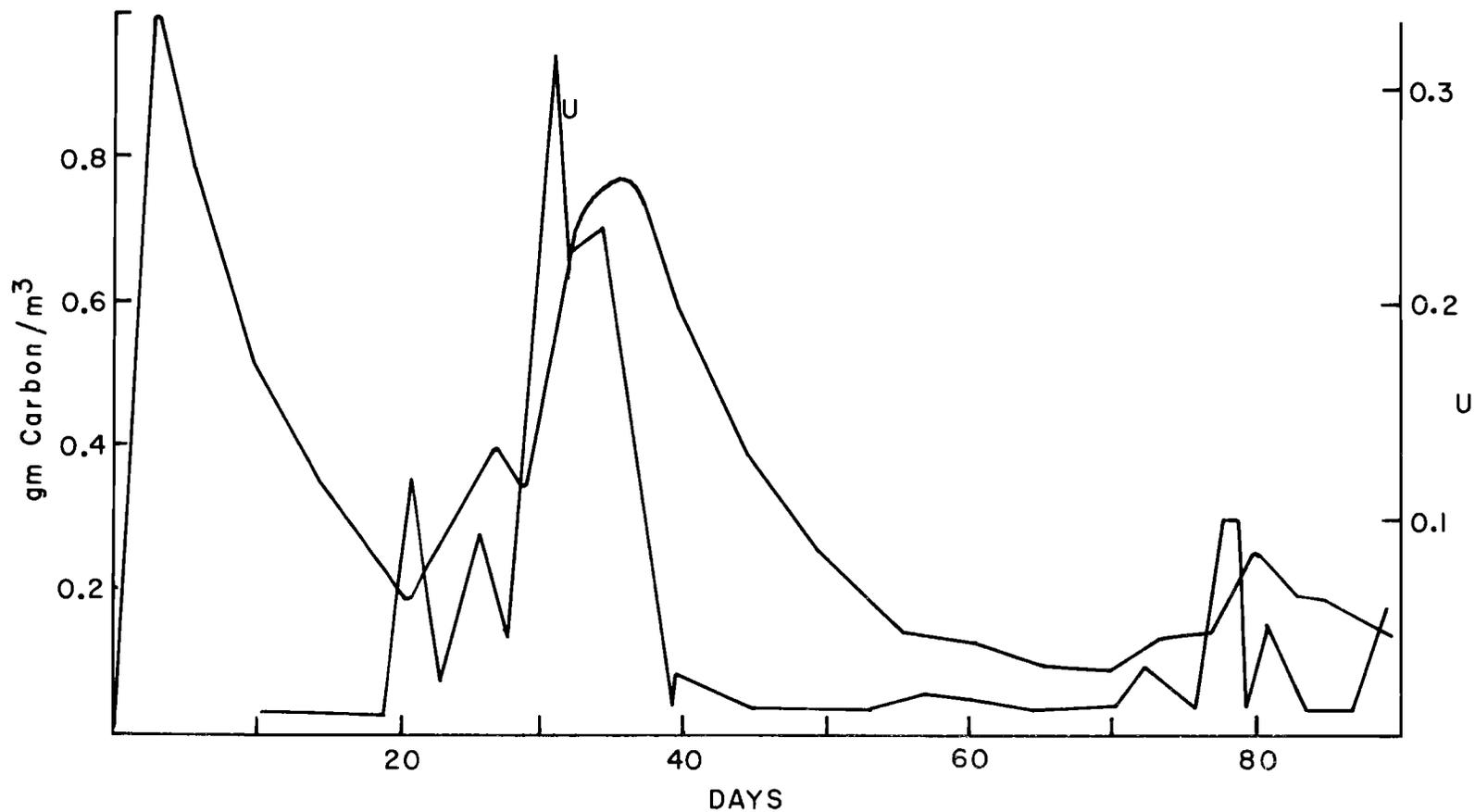


Figure 33. Computer simulation response of the Auke Bay summer phytoplankton dynamics model with peak mixing coefficient, U, moved from 59 days to 30 days.

blooms in Auke Bay during the summer, it is not a sufficient condition as shown by the spurious peak which occurred in phytoplankton response at 27 days (Figure 30).

The model must be extended to account for absence of blooms during periods when nitrate and light in the euphotic zone could support blooms. The model must be tested with additional data records before it can be considered adequately validated.

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