AN ABSTRACT OF THE THESIS OF

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Title: AN ECOLOGICAL STUDY OF DIATOMOVORA AMOENA, AN INTERSTITIAL ACOEL FLATWORM, IN AN ESTUARINE MUDFLAT ON THE CENTRAL COAST OF OREGON

Abstract approved: Redacted for privacy
Dr. J. J. Gonor

The distribution and abundance of the interstitial acoel turbellarian, Diatomovora amoena Kozloff, 1965 was studied in an estuarine intertidal sand flat in Yaquina Bay, Oregon, from May 1970 through May 1971.

Monthly measurements of biological (organics, sulfides, chlorophyll, and carotenoids), pore water (salinity, pH, oxygen, and temperature), and sediment (fine sediment percentage, grain size, sorting, skewness, and kurtosis) factors were made along a transect at four intertidal stations with elevations of -2.0, 0.0, 1.6, and 3.0 feet, stratified by selection from a curve for tidal exposure, and at two depths (0.0 cm to 0.5 cm and 0.5 cm to 1.0 cm) of the sediment. Estuarine factors that were monitored continuously included temperature, salinity, tide elevation, and insolation. The interrelationships among these environmental parameters, their roles in the interstitial sediment system, and the hydrology of the groundwater in the beach, were investigated in order to characterize the interstitial environment of the sand flat and to determine the environmental factors limiting the distribution and abundance of *D. amoena*.

Seasonality was indicated in most of the factors measured. The sediment system was strongly reducing during summer and fall as organic production increased. Particle size analyses showed that transport and deposition of fine sediments contributed to the development of reducing conditions.

The properties of the interstitial environment of *D. amoena* were found to be controlled by the level of groundwater, rate of percolation, and degree of mixing within the beach. Density of *D. amoena* was highest during the fall and early winter, and lowest throughout the winter.

Summer production of plant material in the lower intertidal lead to reducing conditions at the sediment surface. Reduction in animal density at the lower two stations was attributed to these reducing conditions, and to the rafting of animals away from the intertidal with the algal mat. Decrease in animal density in the upper two stations was attributed to lethal low temperatures and salinities that occurred during heavy precipitation in the winter and coincided with low tidal exposure. Exclusion of animals from depths greater than 0.5 cm in

the sediment was attributed to lethal levels of sulfide.

Tolerance of D. amoena to temperature, salinity, and sulfide was determined experimentally. The 25 combinations of temperature and salinity, and the 12 combinations of temperature and sulfide that were employed were selected on the basis of actual levels measured in the study area. The temperature and salinity survival results were fitted to a response surface which was used to evaluate these factors in limiting animal distribution.

Survival of acoels was independent of temperature up to 6 hours of exposure, and strongly temperature-dependent after 24 hours of exposure. Initial mortality was attributed to osmotic stress.

Upon exposure to sulfide at 50 μgm S/ml, these animals did not survive beyond 6 hours, demonstrating that sulfide in high concentrations is toxic to D. amoena. At lower concentrations of sulfide (10 μgm S/ml), the acoels were able to live for over 20 hours. Lowering the temperature at both concentrations helped to prolong the lives of the animals.

Levels of sulfide similar to those used in the experiment (10 μgm S/0.5 cm^3 = 50 μgm S/ml) were found at the sediment surface in the lower two stations during September, at which time animal density was found to be decreasing. At the upper two stations in September, where the level of sulfide was 3 μgm S/0.5 cm^3, the acoel population was found to be increasing, thus bearing out the assumption that population density is, indeed, affected by sulfide.

The nature of the interstitial sediment system as a habitat for meiofaunal organisms was explored and the role of the groundwater hydrology, as a buffer against seasonal variation in the estuary, in maintaining this system was examined. A portion of the littoral shore considered in this investigation was conceptualized as a factor model, the principal parts of which were selected for study. The seasonal cycles of the major input factors were found to be relatively stable from year to year, while the timing of these cycles varied. The numerous positive and negative correlations that were found within and between the biological, pore water, and sediment groups of factors indicated the multiplicity of direct and indirect interactions and supported the contention that the tidal flat is a complex interrelated system.

Change in one or more of the major factors, such as precipitation, river runoff, sedimentation, or tidal prism, can be expected to have diverse effects on the littoral sediment environment.

An Ecological Study of Diatomovora amoena, an Interstitial Acoel Flatworm, in an Estuarine Mudflat on the Central Coast of Oregon

by

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INTRODUCTION

One of the most remarkable features of the marine littoral environment is the conspicuous nature of the zonation of shore organisms. The restriction of plants and animals to relatively narrow zones is strongly evident on rocky shores and less apparent on depositing shores. Traces of burrows on tidal flats mark the presence of macroscopic infauna below the surface, while the gentle slope tends to obscure the margins of zones.

The environments of hard and soft substrates differ in several ways. The fauna of unconsolidated shores reside in a three dimensional system, while rocky shore fauna live on a surface in a two dimensional system. This feature of depositing shores suggests that certain phenomena important on rocky shores may be inconsequential on soft substrates and that others are more critical.

The unique features of the marine intertidal environment, regardless of substrate, find their biological expression in terms of discontinuous distributions of populations over short vertical distances, counterparts of which are not usually present in terrestrial ecosystems, and provide a unique opportunity to explore the relative effects of environmental factors on the distribution and abundance of organisms. The dynamic aspects of the estuarine environment may press these factors to extreme conditions (Kinne, 1966) and impose strong gradients over littoral surfaces. Special conditions, peculiar to the estuaries of the Pacific Northwest are abundant rainfall and seasonal upwelling along the coast (Pattullo and Denner, 1965; Keene, 1971; Kinne, 1966). These factors greatly contribute to the strong variability of this estuarine ecosystem.

Wave action is known to elevate the level of particular organisms on rocky shores (Doty, 1957; Lewis, 1964), and this implies that much of the vertical distribution of a species is a result of the physico-chemical environment imposed by the rise and fall of the tide (Newell, 1970), and the capacity of organisms to tolerate the stresses of tidal exposure and immersion. Alternatively, within the extremes of tolerated conditions, a certain degree of variation may be required for existence (Gunter, 1957; Hedgpeth and Gonor, 1969).

Numerous authors have warned against the supposition that a single environmental factor limits distributions of littoral species (Kinne, 1963; Gunter, 1957; Newell, 1970; Stephenson, 1942; Lewis, 1961, 1964). They advise interpretation of distribution on the basis of the interaction of factors acting in concert, relationships which may vary in degree with season, elevation, age, etc. Nevertheless, under extreme conditions mortality has been attributed to single factors (Gunter, 1947; Ziegelmeier, 1970; Hubbs, 1948; Smidt, 1944; Holme, 1967; Glynn, 1965; Colton, 1959). Artificially induced stress may also impose extreme conditions on natural systems.

Although such zones of organisms are, perhaps, best characterized by the organisms themselves (Lewis, 1961, 1964), explanation of their distribution in terms of the physiology, behavior, etc. of individual species in response to environmental variables is an exceedingly complex problem (Newell, 1970).

An important aspect of the estuarine environment is the increasing utilization of the waterways and shores by man. Through "management," designers' plans quickly become irreversibly transformed into concrete, land-fill, dredged harbors and channels, and modified flushing and exchange rates. Greater understanding of natural processes and cycles, based on thorough quantitative ecological research is urgently needed before accurate methods of evaluating environmental impact can be achieved. The scientist must be in a position to predict the probability of events before change is imposed. The environmental pressure placed on the estuarine ecosystem by man is diverse and includes the physical, chemical, and biological spectrum of factors. For example, the significance and the magnitude of the role of the sediment as a nutrient and pollutant sink is just becoming apparent (McKee, Parrish, Hirth, Mackenthum, and Keup, 1970; Bella, 1970; Bella, Ramm, Peterson, 1970; Wood, 1956; Hedgpeth, 1966), while our understanding of the system remains rudimentary.

This investigation considers aspects of the autecology of an interstitital organism living in an intertidal estuarine sediment system. Diatomovora amoena Kozloff, 1965 was selected as a study organism for the following reasons: 1) This Acoel turbellarian is a typical member of the interstitial meiofauna. 2) It is identifiable macroscopically. 3) D. amoena is a herbivore that grazes on benthic diatoms. 4) It is distributed over a limited vertical range within the estuarine littoral zone, and 5) acoels are short-lived turbellaria with an annual turnover of the population.

The principal objectives of this study are to quantitatively define a part of the littoral estuarine sediment system, to explore the roles of various major environmental factors within the system, and to determine how these factors relate to the distribution and abundance of the interstitial organism chosen for this study. These objectives led to the consideration of the following questions:

1. What are the major environmental variables of the littoral organism-sediment system and how is the system maintained?
2. How are these factors operative on a seasonal basis in a three dimensional pore system?
3. What gradients exist which might contribute to the limitation of the spatial and temporal distribution of interstitial organisms?
4. What factors restrict Diatomovora amoena to the upper

0.5 cm in depth of the sediment and to the lower intertidal?

5. How does the tolerance of the organism to major physical and chemical factors in its environment relate to actual levels of these factors experienced by the natural population?

In order to characterize the system and to analyze aspects of the ecology of D. amoena, important parameters of the interstitial system were investigated while seasonal changes in animal density were being followed. These factors were grouped into categories as follows: 1) Biological factors (total organic material, sulfides, chlorophyll a, b, c, and carotenoid content of the sediment), 2) Sediment pore water factors (salinity, pH, oxygen, and temperature), and 3) Sediment physical factors (sediment elevation, percent fine sediments, mean coarse particle size, sorting, skewness, and kurtosis). Interdependence of factors within these categories and interaction of factors between categories was investigated and then examined in terms of animal density.

In addition, seasonal changes in plant biomass, and temperature and salinity of the estuarine water were followed. Attention was also given to other environmental factors affecting the estuarine system as a whole.

Literature Review

The literature dealing with the distribution and abundance, trophic relations, reproduction, and other aspects of the ecology of meiofauna has been summarized by McIntyre (1969) and will not be reviewed here.

The ecological significance of the micro- and meiofauna and flora has been demonstrated recently by Wood (1964, 1965), Marshall (1970), McIntyre, Munro, and Steele (1970), Guille and Soyer (1969), and Gerlach (1971). These studies show that these organisms are responsible for greater production, turnover, densities, and cycling of nutrients than are the macrofauna of sediments.

Works dealing with the micro-meio- and small macrofauna, as defined by Mare (1942), of the estuarine benthos of North America are almost non-existent (Carriker, 1967). Benthic research, however, is beginning to include consideration of the meiofauna (Wieser, 1959, 1960; Sanders, 1956; Coull, 1970; Tiejten, 1969; Pollock, 1970; Brenowitz, 1969). A manual on the study of meiofauna ecology has recently become available (Hulings and Gray, 1971).

With the exception of studies on Foraminifera and some work done by Wieser (1959), there have been no studies on the ecology of the meiofauna of the west coast of North America. The only information available on Pacific Northwest estuarine meiofauna is taxonomic, not ecological.

Earlier studies dealing with various physico-chemical aspects of the interstitial environment include works of Mortimer (1941, 1942), Bruce (1928), Zobell (1946), Pennak (1940), Mare (1942), Perkins (1957, 1958), Reid (1930), and the extensive work by Deboutteville (1960).

Recent articles by Schmidt (1968, 1969), Gray and Rieger (1971), Coull (1970), Tietjen (1969), and Vitiello (1968) indicate a trend towards more quantitative investigations of meiofaunal populations. The papers of Fenchel (1967, 1968a, 1968b, 1969) dealing with the ecology of the microbenthos are especially important, as are the ecological studies by Jansson (1962, 1966a, 1966b, 1967a, 1967b, 1967c, 1968, 1969), and Boaden (1962, 1963), and those concerning distribution by Lasserre (1969), Boaden and Erwin (1969), Rieger and Ott (1969), Schmidt and Westheide (1969), Brenowitz (1969), Guille and Soyer (1969), and Pawlak (1969).

Major publications with sections relevant to the environment and fauna of depositing shores include those by Hedgpeth (1957), Lauff (1967), Morton and Miller (1968), Newell (1970), Remane (1958), Friedrich (1969), and Green (1968).

The physical aspects of coastal tidal phenomena are detailed by Defant (1958), Clancy (1968), Macmillan (1966), and Pritchard (1955, 1956), while consideration from a biological point of view has been given by Lewis (1964), Glynn (1965), Vader (1964), and by numerous authors in The Second Symposium of Marine Biology (1968). Changes in sea level have been extensively examined by Pattullo, Munk, Revelle, and Strong (1955).

The daily ebb and flow of the tides over the littoral region has been quantified in terms of percent exposure by Johnson and York (1915), Huntsman (1918), Klugh (1924), Shelford and Towler (1925), Doty (1946), Gislen (1931), Colman (1933), Beveridge and Chapman (1950), and Dellow (1950). An exposure curve for San Francisco Bay prepared by E. F. Ricketts has been reproduced in Ricketts, Calvin, and Hedgpeth (1968) and in Glynn (1965). The seasonal variation in exposure in the Netherlands Antilles has been reported by DeHaan and Zaneveld (1959).

Numerous physical and chemical factors pertaining to the interstitial environment have been examined by Bruce (1928) and by Steele, Munro, and Giese (1970). Methods for measurement of environmental physical and chemical factors have been reviewed by Forstner and Rützler (1970), Strickland and Parsons (1968), and Black (1965).

The thermal characteristics of the pore water in marine depositing shores have been described by Johnson (1965), Jansson (1967d), and Pollock and Hummon (1971), and temperature as a factor in the aquatic environment was reviewed by Kinne (1963). Interstitial salinity has been investigated by Reid (1930, 1932), Smith (1955a, 1955b, 1956), Johnson (1967), Alexander, Southgate, and Bassindale (1932), and reviewed as a general environmental factor by Kinne (1964).

The physical aspects of pore water discharge or recharge in relation to the ground water elevation of marine beaches are discussed by Boaden (1968), Isaacs and Bascom (1949), Emery and Foster (1948), Glover (1959), Kohout and Kolipinski (1967), Steele, Munro, and Giese (1970), Pollock and Hummon (1971), and Milhouse (unpublished).

Jansson (1967b) and Wieser (1959) have demonstrated the significance of grain size in limiting distribution of interstitial fauna. Methods for the analysis of grain size of marine sediments are given by Krumbein and Pettijohn (1938), Krumbein and Sloss (1963), Inman (1952), Morgans (1956), Shepard (1954), Bouyoucos (1936), Day (1950), and Folk (1966). Emery (1938) and Poole (1957) describe a rapid settling method of analysis.

Measurement of photosynthetic pigments from marine sediments and the interference produced by pheo-pigments has been reviewed by Tietjen (1968) and Riznyk (1969) and the methodology is outlined by Strickland and Parsons (1968).

Methods for the determination of organic carbon in sediments are treated by el Wakeel and Riley (1957), Walkley (1947), Morgans (1956), and by Strickland and Parsons (1968). Wet oxidation procedures are thoroughly reviewed by Maciolek (1962), and integrated with other techniques by Hughes (1969).

The dynamics of the sulfur cycle in estuarine sediments has been reported by Perkins (1957), Baas Becking and Wood (1955), Wood (1965, p. 104), Bruce (1928), and by Fenchel (1969). Methods of analysis are detailed by Patterson (1959), and Strickland and Parsons (1968).

The oxygen content of interstitial water has been examined by Brafield (1964) and Gordon (1960). Oxygen uptake by whole sediment systems has been covered by Carey (1967) and Pamatmat (1968, 1971).

Experiments dealing with the tolerance of interstitial organisms to various physical and chemical factors have been carried out by Jansson (1962, 1967a), Theede, Ponat, Hiroki, and Schlieper (1969), and Schwab (1967).

The hydrogen ion concentration of pore water has received limited attention, but is mentioned by Bruce (1928), Fenchel (1969), Whitfield (1969), Tietjen (1969), Pennak (1965), Ganapati and Chandrasekhara Rao (1962), and Fanning and Pilson (1971).

Description of Yaquina Bay

Topography

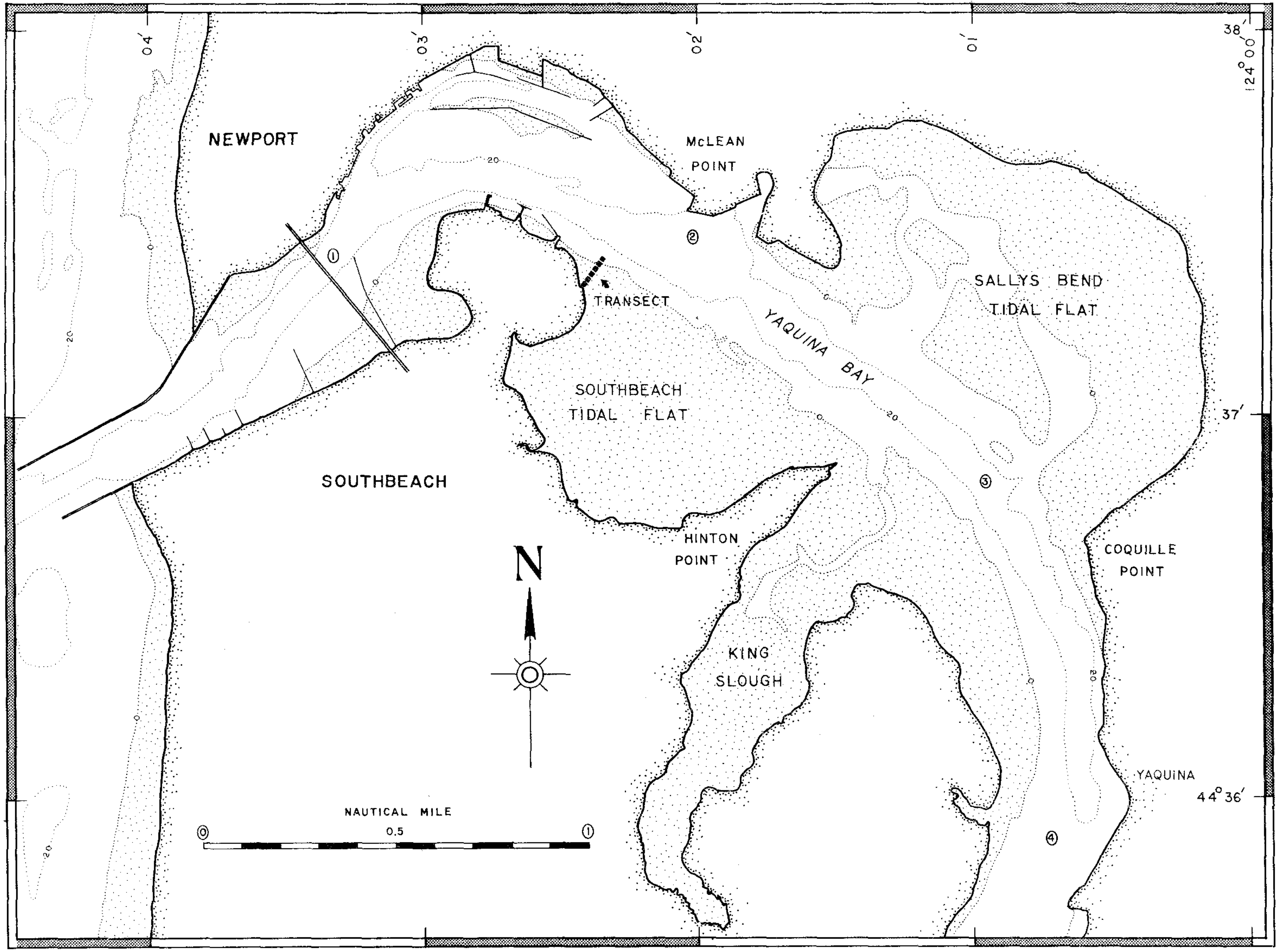
Yaquina Bay forms the submerged river valley portion of the Yaquina River drainage system and opens to the sea at 44°37' N. Lat. and 124°04' W. Long. on the central coast of Oregon. The bay is a true estuary, a semi-enclosed body of water with a permanent salinity gradient from head to mouth, which experiences a seasonal dilution of sea water by freshwater runoff. The drainage system occupies the western slope of the Coast Range, extending inland for some 23 miles (37 km) and draining approximately 244 square miles (632 km^2) (Goodwin, Emmett, Glenne, 1970).

The surface area of Yaquina Bay ranges from 2700 acres (1093 hectares) at MHW to 1110 acres (449 hectares) at MLLW, and exposes 1590 acres (643 hectares) of tidal land (Fish and Wildlife of Yaquina Bay, Oregon, 1968). The bay and estuary have also been defined by Goodwin, Emmett, and Glenne (1970) in terms of the range in cross sectional area from MHHW to MLLW.

The study area is located on one of three large similar mud flats which occupy a total of 1192 acres (482 hectares) or 75% of the tidal land in the lower part of the bay and 80% of the low water bay surface (Figure 1). Southbeach mudflat, the location of the study site, occupies 309 acres (125 hectares) at MLLW on the south shore adjacent to and southeast of the Marine Science Center. These mudflats undoubtedly form a major part of the estuary and play a significant role in the production and recycling of organic matter.

Annual dredging for channel maintenance effectively resuspends fine sediments within the bay, making them available for transport and redeposition, thus adding to the natural sediment flux in the estuary near the study site.

Figure 1. Map of Yaquina Bay at MLLW (0.0 feet) showing location of the study transect sampled and the 20 foot depth contour, redrawn from U.S.C. & G.S. chart no. 6055, 1969. Numbers in circles indicate nautical miles from mouth.


04'
03'
02'
01'
124°00'
38'
37'
44°36'
NEWPORT
McLEAN
POINT
SOUTHBEACH
TRANSECT
YAQUINA BAY
SALLYS BEND
TIDAL FLAT
SOUTHBEACH
TIDAL FLAT
HINTON
POINT
COQUILLE
POINT
KING
SLOUGH
YAQUINA
N
NAUTICAL MILE
0
0.5
1
①
②
③
④
20
0

Sediments

The hydrographic system has a direct effect on the distribution and composition of estuarine sediments. Kulm (1965) designated three realms of deposition within the Yaquina estuary on the basis of sediment texture and mineralogy. The marine realm extends from the coast to McLean Point, and is characterized by well-sorted fine to medium sands and heavy marine minerals. The marine-fluviatile realm is a transitional zone and includes the major tidal flats in the bay from McLean Point to Onetta Point south of Yaquina. The area studied is located in this realm. The sediments consist of well-to poorly sorted fine silt to medium sands, with marked differences between Sally's Bend and Southbeach flats where the study was conducted. The fluviatile realm extends from above Onetta Point to the head of the estuary near Elk City, and is characterized by the absence of "yellow grains" and certain heavy marine minerals.

The tidal flat proper of Southbeach (Kulm and Byrne, 1966) is composed of fine to very fine sand, that is moderately well sorted and positively skewed, and includes subangular to subrounded particles of marine origin. Kulm further designated the Southbeach tidal flat as of marine origin and Sally's Bend tidal flat as of fluviatile origin.

Kulm's results indicate that sedimentation in Yaquina Bay appears to be controlled by the seasonality in type of estuarine system, in river runoff, in direction of littoral drift along the coast outside the bay, and in wind direction. Maximum fluviatile and marine deposition occurs in winter and early spring and is correlated with high river runoff, northerly longshore transport along the coast, strong winds from the southwest, and a partially mixed estuary (Kulm, 1969). During summer and early fall reduced deposition is correlated with little freshwater runoff, southerly directed littoral drift, weak winds from the northwest, and a well-mixed estuarine system.

Climate

The climate of the Yaquina Bay area is characterized by marked wet and dry seasons, mild and rather uniform air temperatures, seasonal wind direction, and insolation submaximal for its latitude. As moist air moves onshore it is cooled by the relatively colder land mass in winter and by topographic uplifting, resulting in seasonal cloudiness and precipitation. As the land mass warms in summer, cool marine air replaces the rising warm air over the land, often resulting in coastal fog. The presence of fog has also been correlated with summer-fall periods of upwelling along the shore; the cooler water cools the local warm, moist air (Holbrook, 1970).

Precipitation

The mean annual rainfall at Newport is 68.18 inches with approximately 70% occurring November through March (Holbrook, 1970). Maximal precipitation occurs during December and January and the minimum occurs during July and August.

Air Temperature

The general temperature regime of Newport has been described by Holbrook (1970), and can be accepted as representative of the Yaquina Bay area. The mean annual true air temperature is 50.8°F and ranges from the January mean of 43.5°F to the August mean of 57.6°F. The annual mean daily maximum and minimum are 57.8°F and 43.8°F respectively and range from 49.5 to 37.5°F during January and from 64.8 to 50.3°F during August. The relatively narrow range of 27.3°F from winter minimum to summer maximum accounts for the rather moderate and uniform temperatures.

Tides and Currents

The tidal currents in Yaquina Bay are mixed and occur semidiurnally, with the paired highs and lows of unequal duration and amplitude. The mean tidal range at Newport is 6.0 feet, the diurnal range is 8.0 feet, and the mean tide level is 4.3 feet (Tide Tables West Coast of North and South America, 1971). According to records provided by G. B. Burdwell of the National Weather Service and taken from the Marine Science Center tide gauge, the mean tidal range is

6.08 feet, the diurnal range is 8.38 feet, and the mean tide level is 4.58 feet.

According to Neal (1966) the tidal range increases upstream and the variation in time of stage of tide was generally less than 30 minutes. The duration of flood tide exceeded the duration of ebb, although the ebb flow was greater than that of flood. Slack water occurred within 30 minutes of the time of high or low water and maximal currents often lagged behind the midtide 60 minutes. The predicted average maximal currents at the bridge are 1.9 knots for flood and 2.1 knots for ebb. Neal (1966) measured maximal surface currents of 1.28 knots ebb and 1.06 knots at flood at 3.5 n.m. near Yaquina, while predicted average values were 1.1 and 1.0 knots. Kulm (1965) found average bottom flood current velocities of 40 cm/sec and a maximum of 75 cm/sec during August and an average flood of 30 cm/sec and a maximum of 45 cm/sec during February at 1.1 and 2.9 n.m. from the ocean.

Hydrography

The mixing of marine and fluvial waters is primarily a function of runoff, tidal flux, and winds. Burt and McAlister (1959) classified Yaquina Bay on the basis of the circulation pattern and the vertical salinity distribution according to the system developed by Pritchard (1955). They concluded that Yaquina Bay was well-mixed during the summer and fall (August to January) between 8 and 16 n. m. from the ocean, and partly mixed during winter and spring (February to May) between 2 and 8 n. m., which includes the study area.

Kulm (1965) verified the conclusions of Burt and McAlister (1959), but pointed out that large differences existed from year to year during the same month. Kulm (1965) and Manske (1968) concluded that the estuary was well-mixed from June to October with a vertical salinity difference of less than 3‰, and that it may vary from well-mixed to partly mixed (4 to 19‰) from November to May.

The role of the volume of freshwater runoff in mixing was stressed by Burt and McAlister (1959), who point out that a stratified condition is probably never achieved in Yaquina Bay owing to the large average tidal range of 6.08 feet. Burt and McAlister concluded that the net flow along the bottom in the channel is downstream during the summer and fall and upstream during the winter and spring.

Water Temperature

Due to the large surface area, shallow depth, and small volume, the seasonal temperature regime of estuarine waters is characterized by broader extremes than that of the nearby ocean, and a gradient from minimal to maximal variation may be expected from the mouth to the head of an estuary (Frolander, 1964). The extent of the variation in surface water temperature along the axis of the Yaquina

Estuary was demonstrated by Frolander (1964) over a 28 hour period. The temperatures at the mouth ranged from 9 to 12°C while temperatures 10 n.m. upstream ranged from 19 to 22°C, indicating the extent of the upstream marine influence and the downstream fluvial effect. Frolander (1964) also observed that the thermal environment between these extremes is a composite of the marine and fluviatile conditions and exhibits the greatest variation in temperature (9-18°C at 5 n.m.) coincident with the tidal regime. The water temperature conditions at the Marine Science Center, 1.5 n.m. from the mouth, could be expected to be under fluvial influence, and would therefore vary little with tide. But temperature measurements made at this site during this study indicate considerable variation with tide. Frolander conducted his study during a neap tide with a predicted tidal range of 7.7 feet. The spring tides five to six days before or after his study had a predicted range of 9.2 feet. The magnitude of the conditions observed by Frolander must, therefore, be considered minimal.

On the basis of average weekly surface water temperature taken at five stations located from 0 to 8 n.m. within the bay over a five year period by the Georgia Pacific Corporation of Toledo, Oregon, and daily maximum and minimum temperatures taken at a single station 5.5 n.m. upstream, Kjeldsen (1966) concluded that the greatest seasonal tidal variation in temperature occurred at 5 n.m., thus providing another means by which to characterize different regions of the bay. The temperature of the surface waters are generally colder from November through March, reaching minimum levels during January and February. Higher temperatures occur during summer and early fall. The warming and cooling periods are separated by a fall (October and November) and a spring (March and April) inversion (Kulm, 1965). The bottom water is generally warmer than winter surface water, and may be cooler during summer periods of coastal upwelling. Summer upwelling effectively confines the highest surface and bottom temperatures to late fall and spring (Kulm, 1965).

Salinity

Yaquina Bay is a positive type of estuary with a salinity gradient extending from the mouth to the head. Frolander (1964) assessed the extent of the variation in salinity of the surface water and found that the salinity at the mouth only varied by 1‰, while the range 10 n. m. upstream was 7‰. The greatest range (9.5‰), however, was found approximately 7 n. m. upstream. During August, a period of reduced runoff, the apparent upstream salinity flux was evidently still greater than the temperature flux. Frolander (1964) concluded that the greatest change in salinity and temperature with tidal phase occurred at mid-bay. These conclusions may be in need of adjustment considering further information presented in this study.

Kjeldsen (1966) summarized the average weekly surface salinities over a four year period at the five Georgia Pacific Corporation stations and concluded that the largest seasonal change occurred at 5 nautical miles. Kulm (1965) and Kjeldsen (1966) found a definite correlation between precipitation and salinity. Kulm (1966) correlated precipitation with the average monthly difference in salinity between surface and bottom waters in Yaquina Bay, while Kjeldsen (1966) correlated precipitation with runoff velocity. Both authors emphasized the strong climatic control of the estuary as evidenced by the salinity regime. A change in salinity often lags behind the first rains by as much as a month, while subsequent changes are effected within 24 hours with heavy precipitation (Kulm, 1965).

The saline summer surface water within the estuary (33-34‰), which has its source in locally upwelled bottom water along the coast, is diluted during the winter by high river runoff, establishing a partially mixed system. The salinity of winter bottom water is evidently controlled by the intrusion of marine water (Kulm, 1965).

Manske (1968) reported on the bottom salinity and temperature conditions in the bay during 1965 and concluded that freshwater runoff limited the upstream penetration of the winter salt wedge, and may lower downstream salinity. Conversely, summer coastal upwelling may produce distinct thermal gradients upstream.

The bottom temperature and salinity observed at 1.5-2.0 and

3.0 n.m. from the mouth during 1965 were rather uniform throughout the year (Manske, 1968). The temperature ranged from 6 to 13°C and the salinity from 25 to 34‰. Bottom temperatures and salinities further upstream were greater during summer and smaller during winter. Manske's estimates of conditions at this point in the bay are inadequate in light of information presented in this study, which found greater ranges of both temperature and salinity.

Oxygen

Oxygen has not been examined thoroughly in Yaquina Bay. Available evidence (Kulm, 1965) indicates that the lowest concentrations (4.5 ml/L or 70% saturation) occur during the summer, with the intrusion of poorly oxygenated upwelled water into the estuary. Winter concentrations (6.5 ml/L) exceed summer concentrations and approach or may exceed saturation. Apparently at 3.5 n.m. little oxygen stratification exists at any time of the year.

Description of Study Site

The study site is located on the south side of Yaquina Bay 1.8 n.m. from the entrance, 300 yards due east of the Marine Science Center on the northernmost portion of the Southbeach tidal flat (Figure 1). The sand flat in the immediate area varies in width from 250 to 600 ft from MHHW to MLLW. The transect studied is on

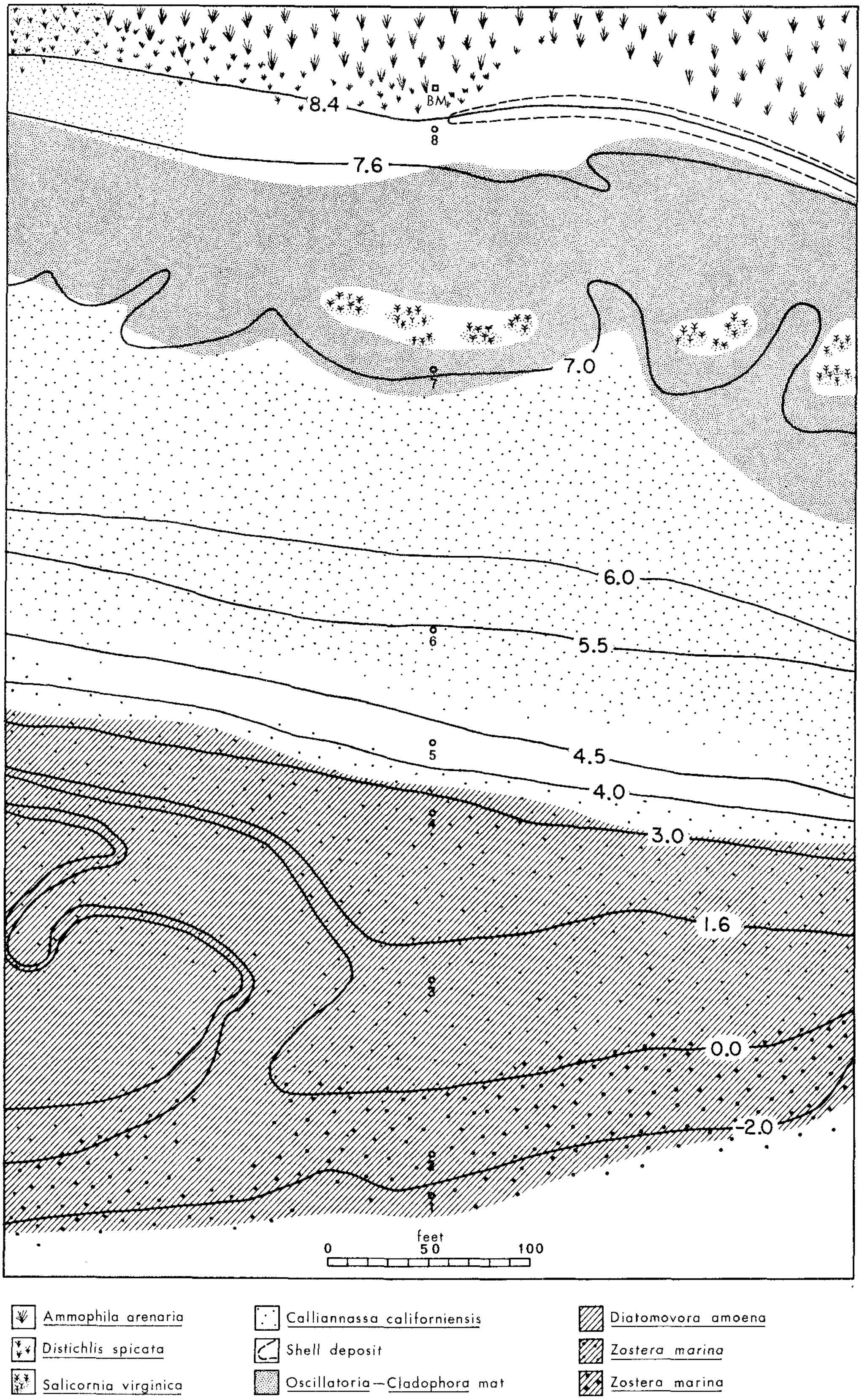
<u>nasuta</u>, <u>Tresus</u> <u>nuttalli</u> and others) add carbonates to the flats, with noticeable deposition of shell material at the surface in the high

a line 19° from magnetic north, is 500 ft in length, and ranges in elevation from -2.5 ft to 9.0 ft, with slope of approximately 1.5° (Figure 2). Inman and Shepard (Shepard, 1963) indicate that beaches of very fine sand (2 to 4 phi) have an average slope of 1°. The slope of the study site is therefore typical for beaches composed of sand with similar particle size. The transect is nearly perpendicular to the main channel of the estuary and grades into a low dune area at the top.

A mature bed of eel grass, Zostera marina, is present throughout the year in the lower intertidal from -3.0 to 0.0 feet. The lower intertidal is a site of deposition as the eel grass traps fine sediments and counters erosion by retarding wave action and tidal currents. A mat composed of Cladophora sp. and a blue-green alga (Oscillatoria sp.) occurs between 6.5 and 7.6 feet and patches of Salicornia virginica range from 7.0 to 7.6 feet. A transitory eel grass bed forms seasonally between 0.0 and 3.5 feet owing to the drainage pattern of water from the nearby channel flowing across the study site and ground water percolation. A seasonal algal mat of Enteromorpha tubulosa, E. intestinalis, and Ulva angusta (?) may cover the lower intertidal from -3.0 to 3.0 feet.

Bivalves residing in the flat (Clinocardium nuttalli, Macoma nasuta, Tresus nuttalli and others) add carbonates to the flats, with noticeable deposition of shell material at the surface in the high

Figure 2. Contour map showing the study area in the Southbeach tidal flat with stations numbered 1 through 8 and the contour elevations given in feet above MLLW. BM = Bench Mark.


8.4
BM
8
7.6
7.0
7
6.0
6
5.5
5
4.5
4.0
4
3.0
1.6
3
0.0
-2.0
2
1
feet
0
50
100
Ammophila arenaria
Distichlis spicata
Salicornia virginica
Callianassa californiensis
Shell deposit
Oscillatoria—Cladophora mat
Diatomovora amoena
Zostera marina
Zostera marina

intertidal (7.6-8.4 feet) and *in situ* in the lower intertidal. Processes leading to the deposition of shell material include seasonal *in situ* anaerobic conditions in the low intertidal and sea gull predation with subsequent transport of shell to the high intertidal.

The polychaete *Arenicola arenicola* occurs in the lower intertidal and the anomuran decapod *Callianassa californiensis* is a dominant member of the infauna at mid-tide level. Both organisms are responsible for extensive reworking of the sediment. Their activities result in coarser and more homogeneous sediment and the production of a prodigious volume of processed and compacted organic material in the form of fecal pellets. Kulm (1965) examined portions of the Southbeach tidal flat and found little change in sediment composition with depth, the apparent homogeneity being explained by the biological activity. McCrow (1972) found *Callianassa* living at a depth of 60 cm and MacGinnitie (1934) found them at a depth of one meter. MacGinnitie calculated that *Callianassa* was responsible for redeposition of 20 to 50 ml of sediment per day per shrimp and turnover of the entire sediment column to 30 cm in eight months.

Several permanent channels as well as many shallow transitory and meandering channels exist on the upper and lower flat. Kulm (1965) hypothesized that increasing the main channel depth through dredging has probably increased the velocity of ebb currents and induced the downcutting and lateral erosion of tidal channels. The more permanent channels tend to form deltas at their intersection with the estuary. One such channel lies just east of the transect and produced a small delta in the study area near the lower intertidal.

The lateral slope of the beach, perpendicular to the transect, increases in elevation from east to west. On an ebbing tide the beach drains along the lateral slope trending from the southeast to the northwest. The flooding tide also follows the contour of the beach in the reverse direction and contributes to the homogeneous distribution of sediments.

The presence of a semi-permanent channel and the natural cross-transect drainage field results in the maintenance of a permanent wet sediment surface from the lowest intertidal level to an elevation of 3.5 feet. The stronger tidal currents near the main channel of the estuary are damped at the lower tidal levels by the eel grass bed. Windrows have been observed along the water surface at high tide marking the lower limit of the eel grass beds.

Beach ripples are a dominant feature of the intertidal from 5.5 ft to 7.0 ft, and have been attributed to winds, waves, tidal currents, and eddy currents (Bird, 1969). Their absence from the lower intertidal may imply that lower current velocities could be found at lower elevations. The burrowing activity of the ghost shrimp Callianassa dramatically obscures the ripple character, but also contributes materially to ripple formation, as flow over the irregular surface of this portion of the beach becomes more turbulent and less laminar.

The strongly seasonal trend in berm-ridge formation was not as evident along the transect as it was in the adjacent beach 50 yards to the west. Berm ridges as high as 15 cm were observed during the summar and fall, running obliquely to the shore.

Ordinarily the sources of sediment for the Southbeach tidal flat would include fluvial and marine sediments. Kulm (1965), however, recognized the "marine" character of the flat on the basis of particle size parameters, shape, mineralogy, and the presence of "yellow grains." The sediments decrease in sorting away from the channel and increase in size. The sediment is moderately sorted ($\bar{x}$ = 1.00) and is skewed to the fine fraction.

METHODS AND MATERIALS

Establishment of Study Site

The elevations of eight fixed stations along the transect were chosen from a mean annual tidal exposure curve and represent elevations of abrupt or constant change in slope throughout the tidal range. The stations were marked in the field along the transect by iron pipe driven to a depth of 9.5 feet, leaving 0.5 feet of pipe exposed with the top of the posts marking the station elevation. The sediment elevation corresponding to the pipe elevation lay at a distance landward from each pipe. This avoided the effects of scour from turbulence around the pipes at high tide.

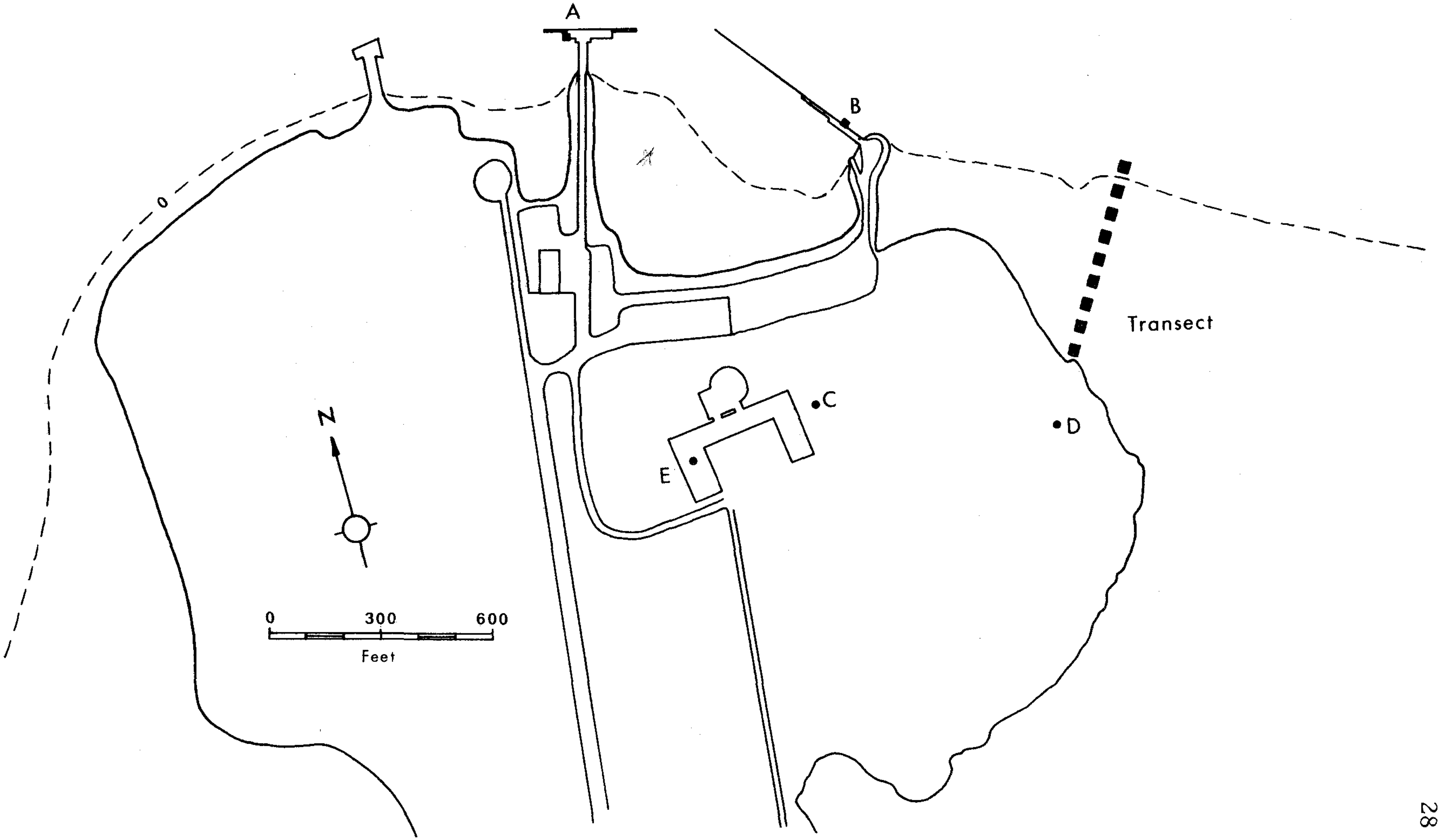
Establishment of Monitoring Stations and Use of Contributed Data

Various other field stations were established near the study site in order to monitor certain environmental factors continuously (Figure 3). The sediment water table was monitored at a permanent well point at the Marine Science Center and at a temporary well point near the study site. Estuarine surface water temperature and near surface air temperature were recorded from a floating dock at the Marine Science Center.

Measurements of other environmental factors were provided by various research programs being conducted in the Department of

Figure 3. Map showing location of transect and environmental monitoring stations at the Marine Science Center.

A Tide gauge at dock
B Temperature recorder on floating dock
C Well point near laboratory
D Well point near transect
E Salinity recorder at laboratory


A
B
Transect
C
D
E
0
N
0
300
600
Feet

Oceanography, Oregon State University. These factors included tidal level, total short wave insolation, estuarine salinity, and sea surface temperature. Tidal level and insolation were recorded in permanent facilities at the Marine Science Center dock (Figure 3). Tidal level was recorded at 6 minute intervals on a Fisher-Porter punch tape tide gauge. Computations of daily tidal levels and monthly mean statistics of tidal levels were provided by the Department of Oceanography.

Total short wave insolation was recorded in langleys per minute on a Leeds and Northrup strip chart recorder fitted with a disc integrator (Disc Instruments). The sensing element was an unshielded horizontal surface Eppley pyrheliometer with a derived constant of 7.21 $mv/cal/cm^2/min$. The instrument accuracy was ±0.3% of scale and the manual error in reading was 1.85 ly or one-half cycle. These data were provided by Mr. D. Elvin through Dr. J. Gonor. Salinity of estuarine bottom water was recorded continuously with a recording hydrometer (Thayer and Redmond, 1969) from the sea water system in the Pacific Fisheries Laboratory at the Marine Science Center (Figure 3) and expressed in parts per thousand. The accuracy was reported as 1% by Thayer and Redmond, and was recalibrated against a Hytech salinometer.

Precipitation data was provided by the U. S. Weather Bureau station at Newport, Oregon.

Sampling Technique and Measurement of Interstitial Factors

Preliminary sampling revealed that the acoel population was confined to the lower intertidal. Four stations along the transect were chosen to represent important tidal elevations, in terms of exposure. The scheme was, therefore, stratified according to tidal exposure. Field sampling, except as noted, was confined to the four stations in the lower intertidal, numbered from lower to higher, one through four at elevations of -2.9, 0.0, 1.6, and 3.0 feet above MLLW, respectively. These stations included the range in elevational distribution of the organisms. The actual permanent sampling stations were located 2 meters to the left or right of the transect line and at a sediment elevation corresponding to the elevations of the tops of the reference pipes. The stations were in turn marked by wooden doweling pressed into the sediment leaving 1 cm exposed.

The basic plan consisted of sampling at approximately monthly intervals. Additional sampling for animals was conducted at biweekly intervals during the reproductive season. For each monthly sampling two independent points were randomly selected within a 2 meter diameter circle around each station marker. Pairs of numbers taken from a random number table were used to determine polar coordinates (0 to 360°) and distances (10 to 100 cm), and these were used to locate the sampling points within the 3.1 m^2 area around the station marker. The same two pairs of coordinates and distances were used at each station during a sampling period, but different pairs were used each month. A set of core samples and measurements taken at each of the two randomly selected points constituted the replicated monthly sample for a station.

Factors that required samples of sediment for determination were measured in samples taken with small hand-operated corers. These factors included animal density, sediment particle size parameters, total organic content, total free sulfide content, and the concentration of the photosynthetic pigments chlorophyll a, b, c, and of total carotenoids.

Three cores were taken at each tidal station replication point and were designated as follows: 1) Biological, 2) Geological, and 3) Chemical. A triangular plastic frame was used to orient the corers in a consistent and uniform manner, with the centers of the three corers 9 cm apart. The area enclosed by these corers was fixed at

125 cm^2 by the plastic frame, and was assumed to be homogeneous. The acrylic plastic coring tubes had an internal diameter of 3.2 cm and sampled an area of 8 cm^2. Each coring tube was 10 cm long, had a wall thickness of 3.5 mm and was beveled externally. The coring tubes were pressed to a depth of about 5 cm and extracted by occluding an air vent in a rubber stopper in the top of the tube with a pinch cock. After the coring tube was withdrawn the bottom was stoppered and the corer placed vertically within a styrofoam ice chest for transport to the laboratory. Normal sampling utilized six coring tubes per tidal station. The total sampling required two days of collecting, pairing the two lower and two upper of the four tidal stations each day.

Samples of interstitial water were taken adjacent to the core frame with a syringe fitted with a valve and a needle embedded in a porous stone which was pressed into the sediment with the needle tip 1 cm below the surface. Two 1 ml samples for chlorinity were taken 20 cm apart and combined. Similarly, 1.5 ml samples for pH were pooled and fixed with 8 ppm $HgCL_2$. Samples of 2.5 ml for oxygen determination were drawn into syringes which were then plugged until used. All samples were stored in capped vials or syringes in an ice chest before use.

The sediment temperature was measured at 0.5 and 5.0 cm depth at each of three coring points with a needle thermistor probe read on a YSI telethermometer. The probe was calibrated to a standard thermometer. True air temperature was measured 3 cm above the ground surface with a calibrated fast response thermistor probe housed in a double walled white plastic shield and read on the telethermometer.

Paired random samples of macrophyte biomass, covering an area of 30 cm^2, were taken periodically at each station. The samples were washed to remove sediment and other materials, dried at 70°C and weighed.

The sediment elevation was monitored at all eight tide stations along the transect by measuring the change in elevation of the sediment surface in reference to the fixed elevation of the tops of the station pipes. This procedure assumed that change in sediment elevation observed at the station pipe also represented change in elevation at the true sample station surface.

Measurement of Estuarine Factors

Paired water samples for oxygen, chlorinity, and pH determinations were taken in the nearby estuarine water during routine sediment sampling at LLW. The surface water temperature was also measured.

During the high tide preceding the low tide when the sediment samples were taken, surface and bottom estuarine water samples were taken at the Marine Science Center floating dock. It was presumed that there was no difference in the water over the study site and that at the floating dock approximately 100 yards away.

Temperature and salinity were measured with a portable induction salinometer, and samples for oxygen determinations were taken with a Frautschy sampling bottle.

The ground water level was measured periodically with a tape measure fitted with a small float in two standing well points.

Estuarine surface water temperature and near surface air temperature were recorded continuously on a dual channel Rustrak strip recorder located on the floating dock at the Marine Science Center. The thermistor probes used were Yellow Springs Instrument Company general purpose probes and were considered linear over the temperature ranged observed. The sea water probe was contained within a white pipe fitted with a styrofoam float, which held the probe at a fixed depth of 10 cm. The air probe was housed within a white pipe shield (Gonor and Thum, 1970), situated 50 cm above the water surface. The recorder has a temperature range of 0.25°C with an accuracy of 2% of span (0.5°C) and a readability of 0.25°C.

Laboratory Procedures

All field samples were stored in a styrofoam ice chest maintained below ambient collecting temperature in the field and while in transit to the laboratory, and thereafter stored in a 10°C coldroom.

As the biological cores were extruded from the coring tubes, the first and second 0.5 cm length of sediment core were each sliced off, bisected across the diameter, and stored in plastic partitioned petri dishes with several milliliters of sea water at 10°C. Animals could be maintained in the sediment samples and stored in this manner for several days without mortality. Later, each half of the 0.5 cm section was transferred to a plastic sieve having a 100 micrometer mesh nylon screen. The sieves were placed in glass petri dishes containing enough sea water to immerse the bottom of the sieve. Several drops of neutral red stain were mixed in with the sediment which was then covered with filter paper and two sea water ice cubes, and left to stand in a coldroom for a day (Uhlig, 1968). The sediment remaining on the sieve and in the underlying petri dish was examined for animals, which were fixed in Bouins fluid and stored in 70% alcohol. This method ensured nearly 100% removal of animals from the sediment sample. Animal density was recorded as the number of animals found per 2 cm^3.

The geolical cores were sectioned in an identical manner and particle size was analyzed by settling velocity. Each half of the 0.5 cm thickness of sediment was treated with 5 ml of 1.51 N HCl to remove carbonates. The sediment was resuspended and dispersed within a 0.025 N solution of the commercial water softener Calgon (sodium hexametaphosphate) in a mixer for five minutes. The entire suspended sample was poured to a 1000 ml graduate filled with the same Calgon solution. The entire volume was mixed vigorously for one minute, and then allowed to settle for 60 seconds. A 20 ml sample was withdrawn from the graduate at a depth of 20 cm and dried to constant weight at 70°C to determine the fine particle content.

The sample was then resuspended and the coarse fraction retained by pouring the contents of the graduate through a 0.062 mm mesh size sience. The particle size distribution of the coarse fraction was determined with a settling tube as described by Emery (1938) and modified by Poole (1957). The coarse and the fine fractions of the sediment were each expressed as a percent of the total dry weight of sediment in the 2 cm^3 sample. The size distribution within the coarse fraction was examined statistically for the following moment parameters: mean particle size, sorting, skewness, and kurtosis.

The first and second 0.5 cm sections of the chemical cores were isolated in a manner similar to the other cores, but were segmented into eighths. Opposite eighths (0.5 ml in volume) were removed as duplicate samples for analysis of pigment, sulfide, and organic content.

Chlorophyll a, b, c, and total carotenoid concentrations were determined by the method described by Strickland and Parsons (1968). The samples were placed in 5 ml of 90% acetone and extracted in the dark for 18-20 hours at 10°C. The absorbtion spectra of the samples was then recorded at 480, 510, 630, 645, 665, and 750 millimicrons on either a recording Bausch and Lomb Spectronic 505 or a Beckman DB-G Grating Spectrophotometer. The samples were read in 1 cm light path quartz cuvettes and were corrected for turbidity at 750 millimicrons. The amount of chlorophyll and total carotenoids was calculated from the empirical formulas of Strickland and Parsons (1968) as modified from Richards and Thompson (1952). The pigment content was expressed as micrograms of pigment per 0.5 cm^3 of sediment.

The sulfide content was determined by the method described by Strickland and Parsons (1968). The optical density was read at 600 millimicrons in a Bausch and Lomb Spectronic 20. The readings were standardized by reference to an Orion sulfide ion electrode in an antioxidant buffer (Orion Research Inc., 1969). The sulfide concentrations were then expressed as micrograms of sulfide per 0.5 cm^3 of sediment where 1 μgm S/0.5 cm^3 equals 5 μgm S/ml.

The total organic content was determined by wet oxidation with a sulphuric acid-dichromate oxidant as described by Strickland and Parsons (1968). The optical density was read on a Bausch and Lomb Spectronic 20 at 600 millimicrons. The procedure, as described by Strickland and Parsons (1968), measures the decrease in extinction of the yellow dichromate solution at 440 millimicrons; however, the wavelength of 600 millimicrons used in this study measures the absorption of the reduced acid-dichromate state (Entenmen, 1957) or the production of the green coloring. Total organic concentration was expressed as milligrams glucose per gram of sediment or of approximately 0.6 ml of sediment.

The chlorinity of interstitial water samples and low tide estuary samples was measured by automatic coulometric-amperometric titration with a Buchler-Cotlove Chloridometer (Cotlove, Trantham, and Bowman, 1958). Duplicate titrations were run at a medium rate of titration (240 ohms), standardized to 1 mEq Cl/L and converted to chlorinity or salinity in parts per thousand according to the definition of Wooster, Lee, and Dietrich (1969) and Lyman (1969).

The pH of interstitial water samples and low tide estuary samples was measured on a Beckman Expandomatic pH meter.

The dissolved oxygen concentration was determined by modification of the Winkler procedure as described by Strickland and Parsons (1968). All titrations were carried out with a micro-metric microburet syringe (Micro-Metric Instrument Co.). The dissolved oxygen concentrations were expressed as milliliters of oxygen per liter, or converted to percent saturation at *in situ* temperature and salinity.

Temperature - Salinity Tolerance Experiment

Tolerance of *D. amoena* to temperature and salinity stress was determined experimentally under controlled conditions. Water salinities of 5, 10, 15, 25, and 30‰ were used in combination with constant temperatures of 5, 10, 15, 20 and 25°C. These combinations were selected on the basis of observed conditions obtaining in Yaquina Bay. Animals were isolated from sediment samples and maintained at ambient conditions (10°C and 33‰) occurring at the time of collection, in small Stendor dishes for a period of 24 hours before use. Ten animals were placed in each dish. For the experiments the ambient sea water was replaced with 5 ml of filtered sea water adjusted to the experimental temperatures and salinities. The dish was then transferred to a water bath which controlled the temperature to ±0.5°C. Two-hundred fifty animals in all were utilized in 25 combinations of temperature and salinity. The complete experiment was run twice.

The ultimate criterion used for evaluating mortality was the cessation of ciliary activity; however, retarded locomotion, secretion of mucus, and contortions of the body often preceded loss of ciliary movement.

The maximal estimated error due to sample size and replication effects was ±10%.

Sulfide Tolerance Experiment

Tolerance of *D. amoena* to low oxygen and the presence of sulfides was examined under optimal temperature (15°C) and salinity (25‰) conditions, as determined from the temperature-salinity tolerance experiments. The worms were treated as described in the temperature-salinity experiment, but were maintained in 25 ml volumetric flasks. The ambient sea water was replaced with temperature-adjusted nitrogen-sparged sea water (25‰) containing 0, 50, 150, 250, 350, and 450 µgm S/ml. Initial and final oxygen concentrations were determined in all flasks with a Beckman Physiological Gas Analyzer macro-membrane electrode. The sulfide concentrations were determined colorimetrically as described in the treatment of sediment samples.

A second experiment was conducted at 10° and 15°C utilizing lower concentrations of sulfide (0, 10, 25, 50, 75, and 100 µgm S/ml).

Statistical Analyses

For most environmental factors each set of replicated monthly samples from each station produced four measurements of each factor. The mean of the four measurements and standard deviation of the distribution of the mean were calculated. All calculations were carried out on an Olivetti-Underwood Programma 101. The factors so treated included the particle size parameters (mean grain size, sorting, skewness, kurtosis), photosynthetic pigments (chlorophyll a, b, c, and total carotenoids), free sulfides, total organics, and animal density. Analysis of these factors has been illustrated graphically in a series of modified Dice-Leraas figures, wherein the mean is shown as a bar surrounded by plus or minus twice the standard estimate of error of the mean (rectangle). White rectangles designate the first 0.5 cm of sediment, while black rectangles designate the second 0.5 cm. The length of the rectangle represents approximately 95% of the distribution of the error estimate of the mean. This interval was used as a confidence interval in order to visually determine the significance of difference between samples, following the guidelines of

Simpson, Roe, and Lewontin (1960, p. 352).

With the assistance of Dr. L. Kulm of the Department of Oceanography, and his students, the sediment parameters of the coarse fraction were computed at the Oregon State University Computer Center. An OS_3 Fortran Sandtex Program version 2.1 written by R.L. Stewart for the CDC 3300 computer was used to calculate the graphic parameters of Trask (1932), Inman (1952), and Folk and Ward (1957), as well as the moment measures. Only the parameters of Folk and Ward were considered further.

The degree of linear interaction of the environmental variables was analyzed by calculation of the partial correlation coefficient (r) between all factors. These calculations were computed through the Oregon State University Computer Center by Dr. N. Hartmann, Department of Statistics, Oregon State University. Correlation matrices were constructed for each station for each month as a measure of error within stations. These data were pooled spatially as a transect matrix for each month or pooled temporally as an annual matrix for each station elevation. Finally, these data were pooled in time and space as a single year matrix. The null hypothesis that the population correlation coefficient ρ was not different from zero was applied at the 0.05 percent level of significance (Snedecor and Cochran, 1967, p. 184; Sokal and Rohlf, 1969, p. 516). Where the sample size was large, as in the case of pooled matrices, a second arbitrary filter was applied. Correlation coefficients below 0.50 were not accepted unless the 95% confidence limits of such smaller values included the 0.50 level.

The factorial temperature-salinity tolerance data were fitted by multiple regression analysis to the quadratic model of Box and Youle (1955), in order to evaluate the linear and quadratic effects of temperature (T, T^2) and salinity (S, S^2) and the effects of temperature and salinity interaction $(T \times S)$ with time. The model was of the general quadratic form:

$$Y = b_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2$$

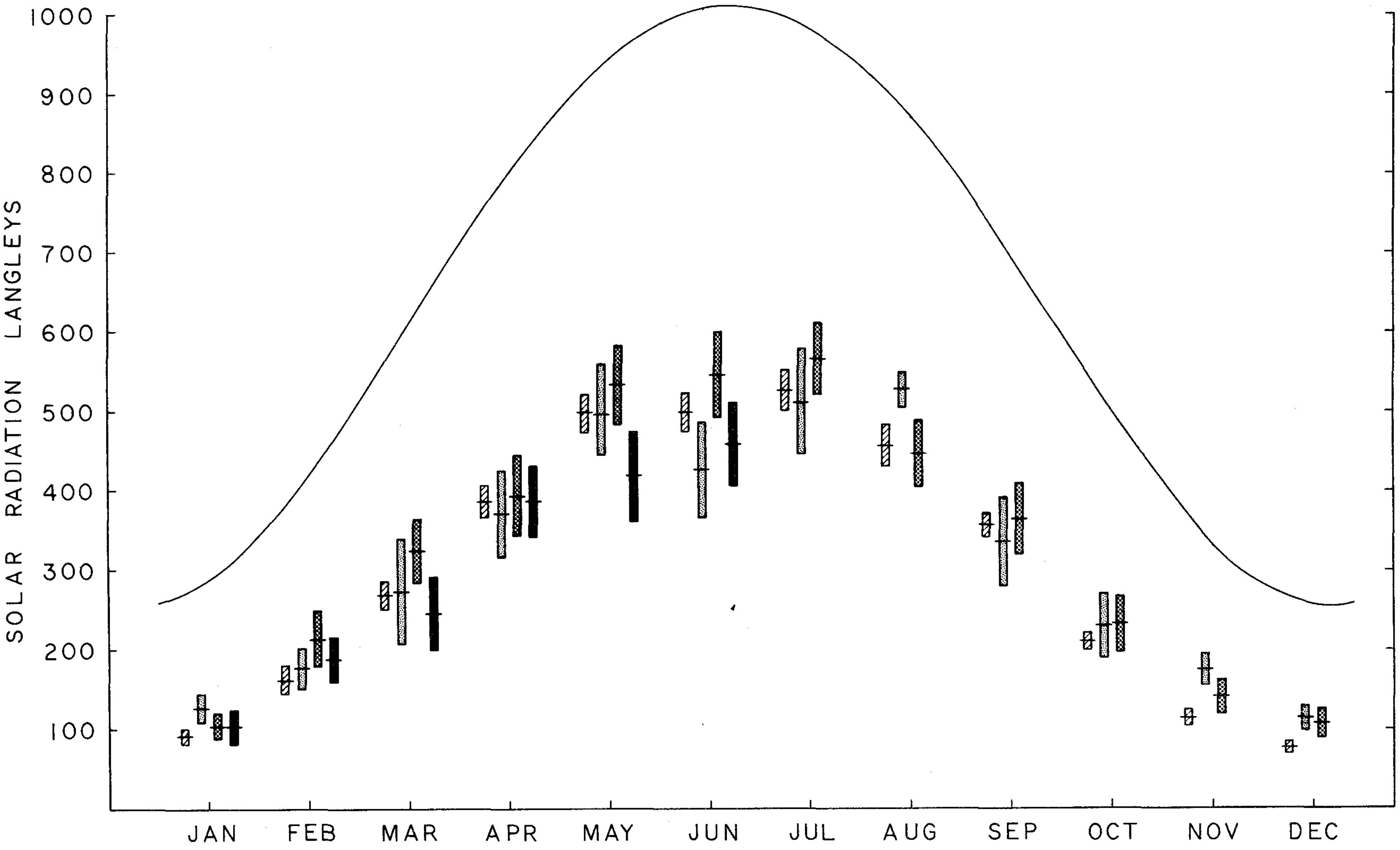
where Y = percent survival, x_1 = temperature in °C, x_2 = salinity in ‰, b_0 = constant, b_1 = linear effects of temperature, b_2 = linear effects of salinity, b_{11} = quadratic effects of temperature, b_{22} = quadratic effects of salinity, and b_{12} = effects of temperature - salinity interaction. The least squares method of analysis used in the calculation of the regression coefficients was carried out through the Oregon State University Computer Center by Dr. N. Hartmann. A 10% contour interval for survival was obtained for the x_1 and both x_2 roots. Tests of level of significance of the regression coefficients (b terms) were carried out at the 0.05 and 0.01 level of significance.

RESULTS

Insolation

Total short wave radiation reached maximal values during May, June and July, but generally did not exceed 60% of the total at the top of the atmosphere for this latitude (Figure 4). Summer values of 550 langleys per day were common, while winter values during December and January were usually less than 125 langleys per day. Insolation was significantly interrupted by coastal fog and cloudiness during June when it would otherwise have been maximal (Kubota, 1967). Inspection of the total short wave insolation recordings indicated that coastal fog and cloudiness were often confined to the mornings and usually cleared by mid-day with rising land temperatures and increased relative humidity. The variance of total short wave daily insolation per month at Newport was graphically compared with the long term average of monthly means at Astoria (1953-1969) and found not to differ significantly (Figure 4). The variability of daily insolation at Newport expressed as 95% confidence limits was generally greater than that based on monthly means at Astoria. The small differences were not considered significant since the Astoria data did not include daily variability. The radiation records therefore indicate that the observation period was typical for annual insolation in this coastal region. Insolation dependent light and temperature effects,

Figure 4. Total short wave insolation recorded at the Marine Science Center dock at Southbeach, Oregon during 1969 (fine stipple), 1970 (coarse stipple), and 1971 (solid) shown by the mean (bar) and ±2 x standard error (rectangle) compared to the 10 year average monthly values for Astoria, Oregon (cross hatched). Continuous curve represents total short wave radiation at top of atmosphere for this latitude (adapted from Kubota, 1967).


SOLAR RADIATION LANGLEYS
1000
900
800
700
600
500
400
300
200
100
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

such as warming of tidally exposed flats in summer, observed during this study, are within the normal year to year range of these effects.

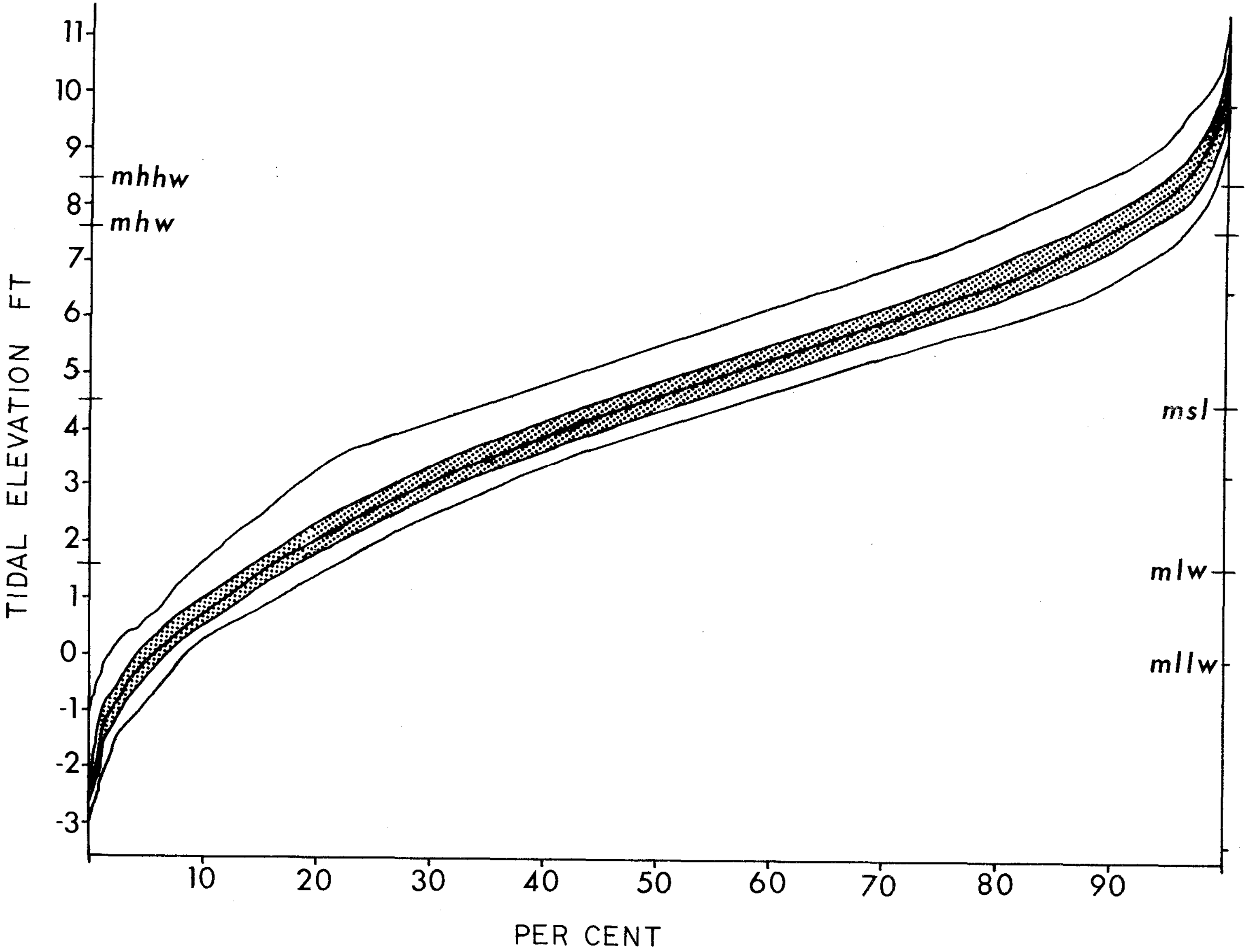
Tides

A detailed tidal exposure curve for the year was synthesized from monthly exposure curves provided by Dr. J. Gonor, Department of Oceanography, Oregon State University. The original monthly exposure curves were calculated with the aid of a computer from hourly tidal elevations data taken from the tide gauge located at the Marine Science Center dock. In the annual exposure curve the range and 95% confidence limits, expressed as plus and minus twice the standard error, are shown about the mean, along each of the station elevations chosen (Figure 5). The curve changes significantly in slope at approximately the levels of MLW (1.6 feet) and MHW (7.6 feet). The difference in average exposure between the year 1968 and the period from 1967 through 1969 was less than 1%. The average percent exposure for any intertidal level was considered constant. Because the tide gauge is near the study site and wave action is small, correction for effective tidal height was not necessary.

The seasonal aspect of tidal exposure was considered at the following long term (February, 1967-January, 1971) average elevations: MLLW (0.0 feet), MLW (1.6 feet), MSL (4.6 feet), MHW (7.6 feet), and MHHW (8.4 feet) (Burdwell, personal communication).

Figure 5. Curve of percent tidal exposure with elevation for 1968 tide gauge data taken at the Marine science Center. Center line, mean percent exposure for year, outer curves annual range, stippled area, ±2 x standard error for year, based on monthly percent exposure values.

MHHW, mean higher high water; MHW, mean high water;
MSL, mean sea level; MLW, mean low water;
MLLW, mean lower low water.


TIDAL ELEVATION FT
11
10
9
mhhw
8
mhw
7
6
5
4
3
2
1
0
-1
-2
-3
msl
mlw
mllw
10
20
30
40
50
60
70
80
90
PER CENT

These levels also served as the principal levels in establishing the elevations of the field stations. The average percent exposure per month is indicated at these fixed levels (Figure 6) for a period of 33 months from data provided by Dr. Gonor. Two additional levels (-2.0 and 3.0 feet) that represented abrupt or constant change in slope in the annual exposure curve (Figure 5) are also shown in Figure 6. Several patterns were apparent. Exposure increased during the summer and decreased during the winter each year, and at all elevations. Variation in exposure was greater in the mid- and upper tidal elevations than at the extreme elevations. The actual elevations, however, did not remain static, but varied with the seasonal rise and fall of the monthly sea level (Figure 7). Sea level was consistently lower in summer and higher in winter each year and this annual fluctuation was expressed at all levels. The seasonal rate of fall in sea level was greater than the rate in rise of sea level.

The daily observations for the heights of HHW, LLW, HLW, and LHW from May 1970 to May 1971 are plotted separately in Figure 8. In this figure, for example, all levels for low low water for the period are joined by a continuous line. The fortnightly spring and neap tide change in range of all four tidal levels is evident. The same seasonal trends in change in sea level, as noted above, were apparent in each curve. The curves were relatively smooth and regular during the spring and summer, but became irregular during fall and winter.

Figure 6. The monthly average percentage of tidal exposure at selected intertidal elevations at the Marine Science Center tide gauge during 1967-1969. Elevations given in feet above MLLW (0.0).

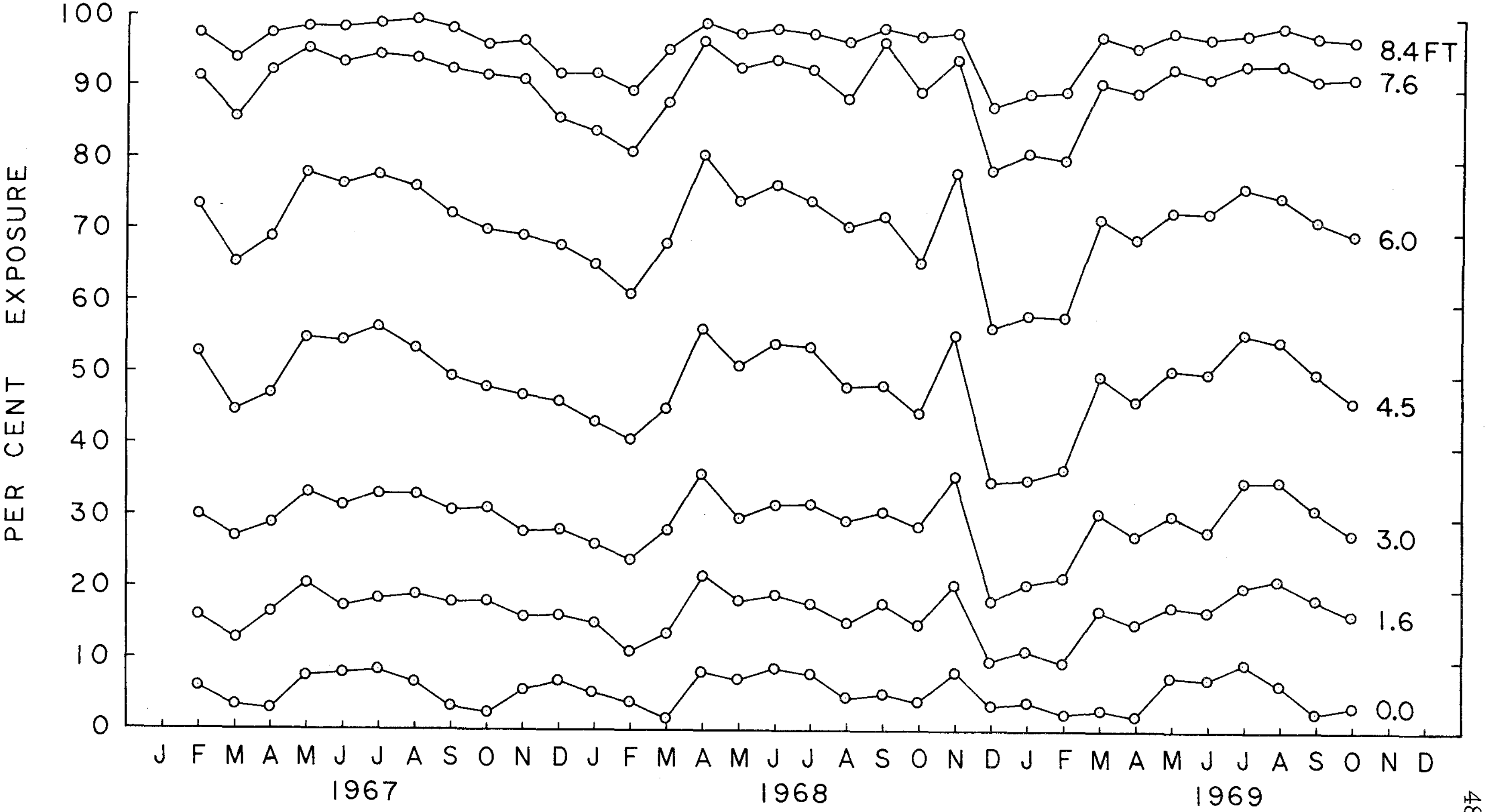

PER CENT EXPOSURE
100
90
80
70
60
50
40
30
20
10
0
8.4 FT
7.6
6.0
4.5
3.0
1.6
0.0
J F M A M J J A S O N D
1967
J F M A M J J A S O N D
1968
J F M A M J J A S O N D
1969

Figure 7. Variation in monthly mean higher high water (MHHW), mean high water (MHW), mean sea level (MSL), mean low water (MLW), and mean lower low water (MLLW) during 1967-1969 at the Marine Science Center dock tide gauge. Elevations in feet based on MLLW = 0.0.

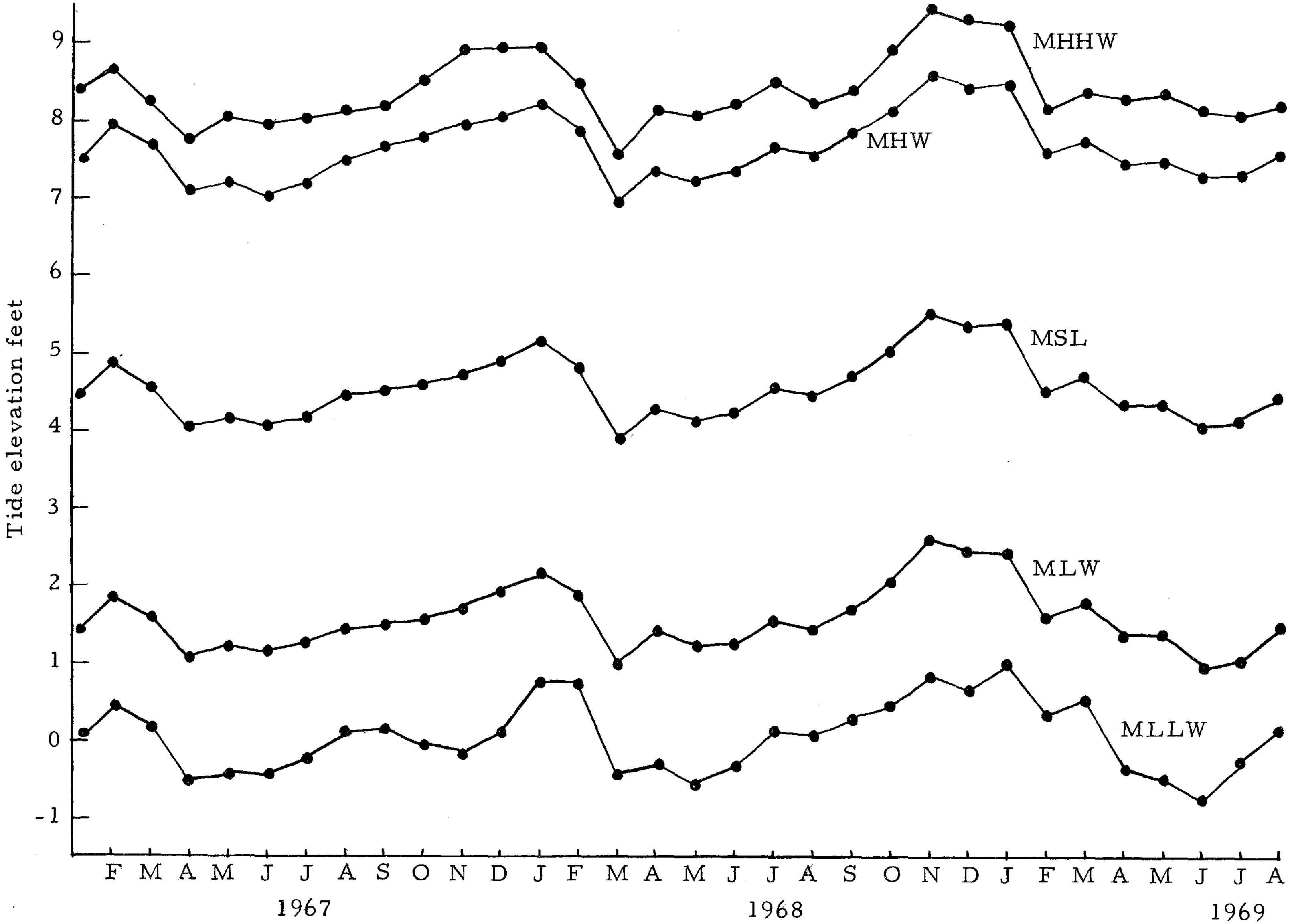
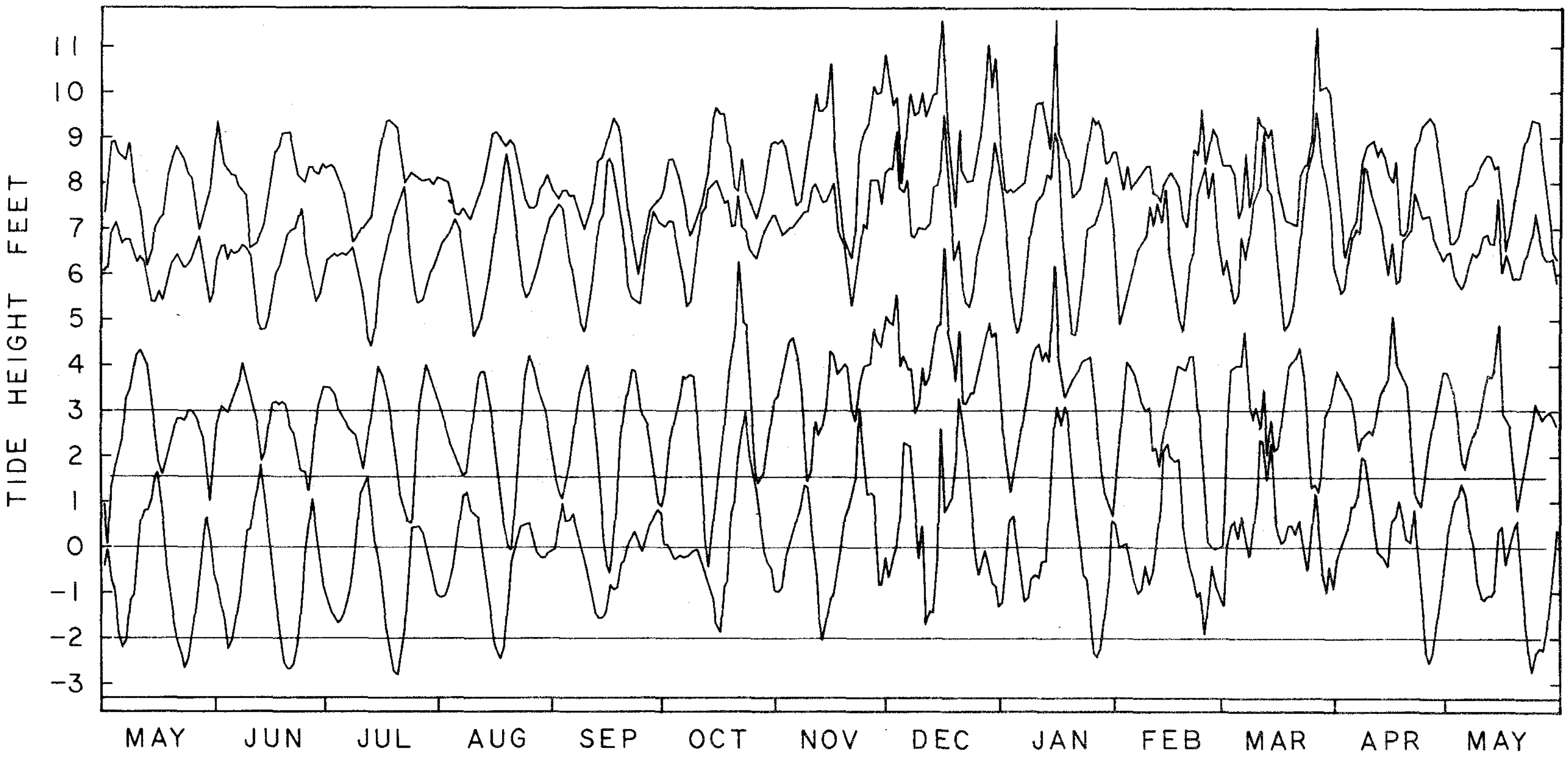

Tide elevation feet
9
8
7
6
5
4
3
2
1
0
-1
MHHW
MHW
MSL
MLW
MLLW
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1967
1968
1969

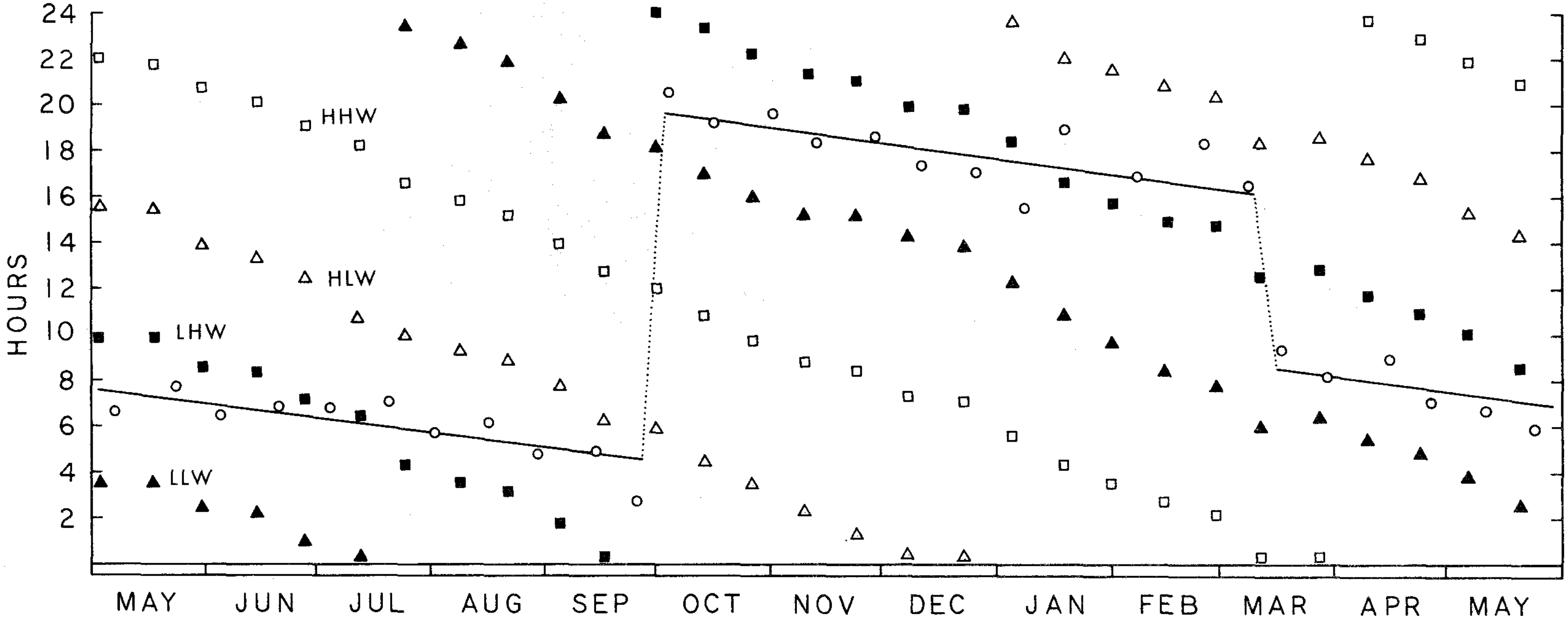
Figure 8. Variation in daily observed elevations of higher high water (HHW), lower high water (LHW), higher low water (HLW), and lower low water (LLW) recorded at the Marine Science Center tide gauge from May 1970 through May 1971. Elevation in feet with MLLW = 0.0. Lines drawn for sampling station elevation.


TIDE HEIGHT FEET
11
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

In Figure 8 four lines are drawn through the four daily tide curves at the elevations of the principal field stations. At the -2 foot level exposure was restricted to low low water periods and mainly occurred during the spring and summer months. The 0.0 foot level (MLLW) was routinely exposed by low low water, and by high low water on only several occasions during September and October. The third station at 1.6 feet was exposed by low low water daily, except for a few days each month, October through April. Exposure at this level by the high low tide was largely restricted to several successive days each month, November and December excluded. At 3.0 feet, exposure generally occurred twice a day. The low low water uncovered this elevation almost every day of the year while it was uncovered at high low water on successive days about half of the time, on fewer days during winter, and on none during December. Mean sea level (4.5 feet) and 4.0 feet were exposed nearly twice a day every day by the two low water tides. The four tidal stations not only differ significantly in degree of exposure, but the two upper stations may encounter exposure twice daily because of the additional high low water exposure.

The time of day at which four tidal levels, HH, LL, LH, HL, were exposed at the extreme portion of each of the neap tides during a month (the nodal point in the tidal envelope) has been summarized in Figure 9. This extreme neap tide period represented a maximal upper boundary for elevation of low low water, because all lower low

Figure 9. Time of neap tide extremes and the time of occurrence of lowest spring lower low water tides (circles and fitted line) recorded at the Marine Science Center tide gauge from May 1970 through May 1971.


HOURS
24
22
20
18
16
14
12
10
8
6
4
2
HHW
HLW
LHW
LLW
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

low tides occurred between the extreme neap tides. The two low tides and the two high tides were necessarily 12 hours apart, and occurred progressively earlier each day throughout the year. It could be expected from these data that the time of low low water would occur progressively earlier each day throughout the year. However, the time of day at which the lowest low tides occurred during the extreme spring tides each month did not conform to the expected trend. Rather, the extreme low low tides were maintained between 0400 and 0800 hours in the morning during the spring and summer and between 0400 and 0800 hours in the evening during the fall and winter as indicated by the fitted lines. This phenomenon has been observed by other workers (e.g., Emery, 1960, p. 129; Ricketts, unpublished). The points of transition between morning and evening occurred within two weeks of the autumnal (September 21) and vernal (March 21) equinoxes. Since the level of high low water occurs 12 hours after low low water, the high low tides were presumed to follow an inverse pattern and occurred in the evening during the summer and in the morning during the winter. Finally, since the times of high high and low high waters precede the times of low low and high low waters by a relatively constant amount, a similar pattern was expected for the two high tide levels.

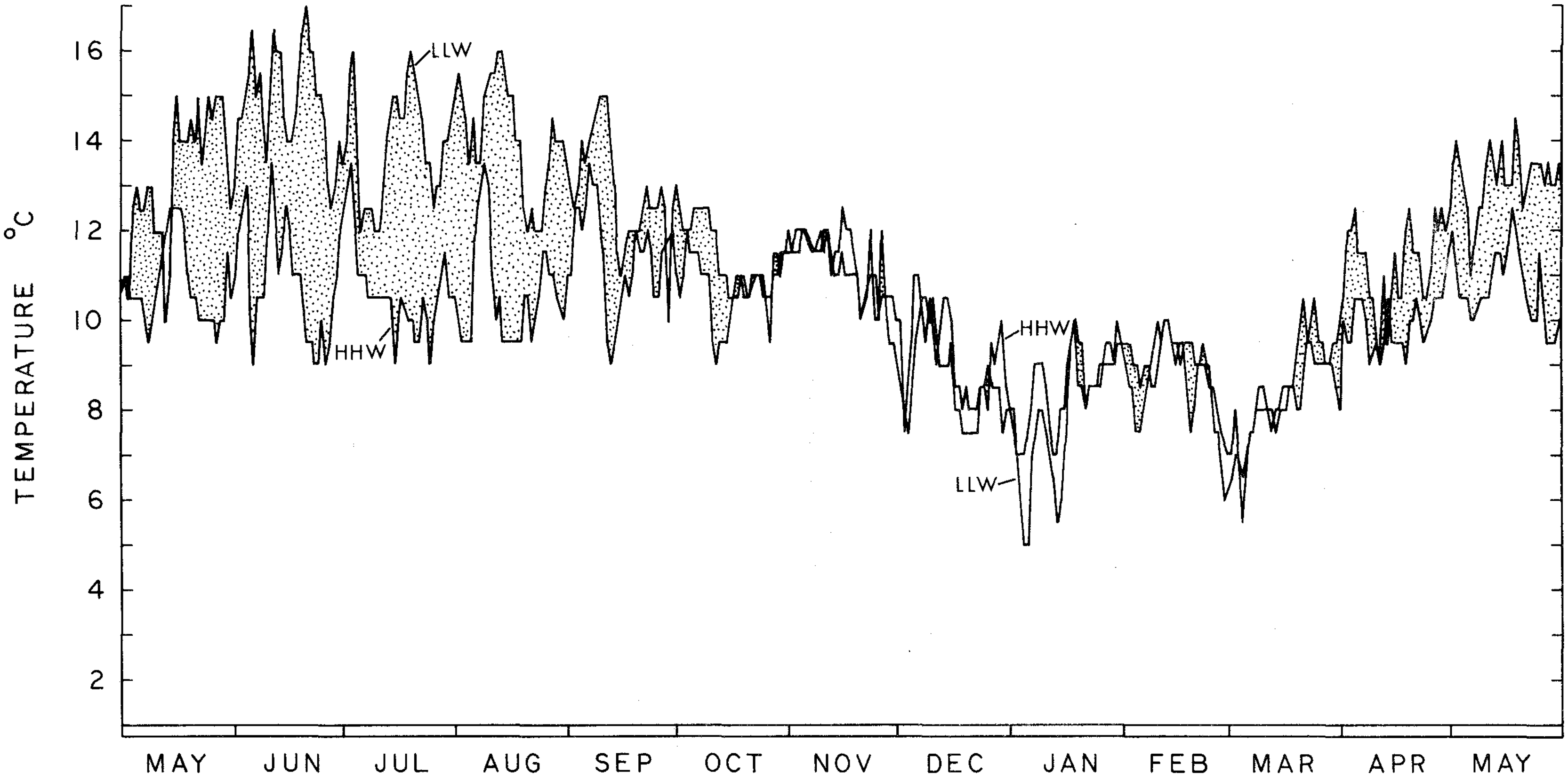
Several conclusions may be made regarding the timing of the patterns of exposure of the sampling stations described in Figure 8.

First, exposure of the -2.0 foot level was confined to the early morning during the summer. Second, the 0.0 foot level was also exposed in the morning during the spring and summer but was exposed in the evening during the fall and winter. Third, exposure at 1.6 feet occurred for longer periods of time during mid-morning in the spring and summer and during mid-evening in the fall and winter than exposure at the 0.0 foot station. This station was also exposed briefly by high low water in the morning during fall, and evening during spring. Fourth, the 3.0 foot level was uncovered by low low water for even longer periods in the morning during summer and spring, and in the evening during fall and winter by low low water. It was also exposed by high low water in the evening during the summer and spring and in the morning during the fall and winter.

Water Temperature

The daily temperature of the surface water at the time of high high tide, 1.8 n.m. inside the estuary, recorded at the Marine Science Center dock (Figure 10) was considered indicative of inshore coastal conditions. The temperature averaged about 10.5°C during the summer and rose to about 11.0°C from September to November. Winter cooling started in November and continued to a low in March (8.0°C), and was followed by an increase in temperature during spring to 10.5°C. Variations as large as 4.0°C were observed during the

Figure 10. Temperature of the surface water in the estuary at the time of daily higher high water (HHW) and lower low water (LLW) recorded at the Marine Science Center floating dock from May 1970 through May 1971. Temperature range stippled when LLW temperature exceeds HHW temperature.



TEMPERATURE °C
2
4
6
8
10
12
14
16
LLW
HHW
HHW
LLW
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

summer, and 1 to 3°C during the winter. Periodic variations in temperature corresponded to the fortnightly tidal amplitude.

The daily estuarine surface water temperature at the time of low low water was taken to be representative of the upstream temperature regime (Figure 10). The seasonal range in temperature was 12°C (5-18°C). The low low tide temperatures began to increase in late March and the fortnightly cycle became apparent. The tidal effect on temperature remained evident throughout the year with varying degrees of amplitude; 4.0°C in summer, to 2.4°C in winter.

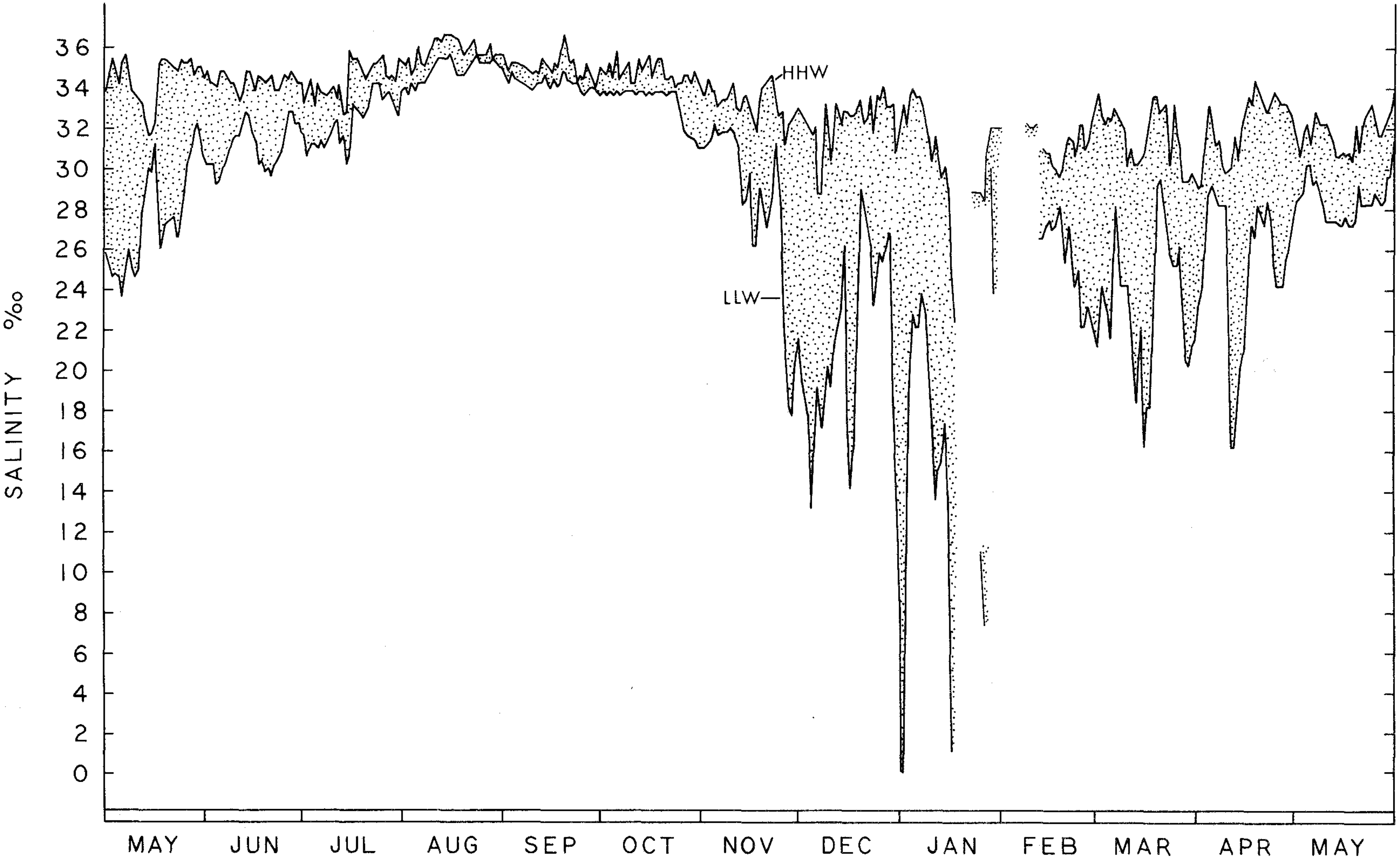
The daily range in surface temperature was determined by comparing the estuarine surface temperatures at the time of high high and low low tides (Figure 10). The estuary was generally isothermal within 1°C in winter, and strongly heterothermal in summer. Two winter lows of about 7.0 to 7.5°C were observed, one during January and one in March, at which time the upstream low low tide water was slightly cooler than the oceanic high high tide water (8.5°C). Summer low low water temperatures (15°C) usually exceeded high high water temperatures (10.5°C) by 4.5°C, and under extreme conditions, by 7°C.

The surface water thermal conditions at the times of the two intermediate tidal levels (high low, low high) were generally contained within the range recorded by the high high - low low interval. Several differences were found. At the time of high low water maximal temperatures, present during the summer, and minimal temperatures, present during the winter, occasionally exceeded those at the time of low low tide. High low tide temperatures were always greater than low low tide temperatures during the summer, but were often colder during the winter. Daily low high tide temperatures were commonly greater than high high tide temperatures and less than low low temperatures in the spring and summer. They were similar to low low temperatures during the fall and winter. Upstream high low water was warmer than low high water in summer, colder in winter, and transitional during spring and fall.

Salinity

The daily range in the salinity of bay bottom water as recorded in the sea water system at the Marine Science Center, was determined by reading the salinity at the time of the four extreme tidal levels each day. The salinity at the time of low low tide and at high high tide generally marked the daily maximum and minimum salinity (Figure 11). These data were considered representative of the continuous values, presuming linearity between readings. Continuous records were unavailable during a portion of January and February. The salinity was maximal during August (33.5‰) and was about 32‰ from July through August, ranging about 1.5‰. The daily range in salinity gradually increased and the total salinity decreased from

Figure 11. Salinity of the bottom water in the estuary recorded in the Marine Science Center sea water system at the time of daily higher high water (HHW) and lower low water (LLW) from May 1970 through May 1971. Salinity range stippled.


SALINITY ‰
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
HHW
LLW
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

November through January. Strong daily variability continued until April when the salinity began to rise.

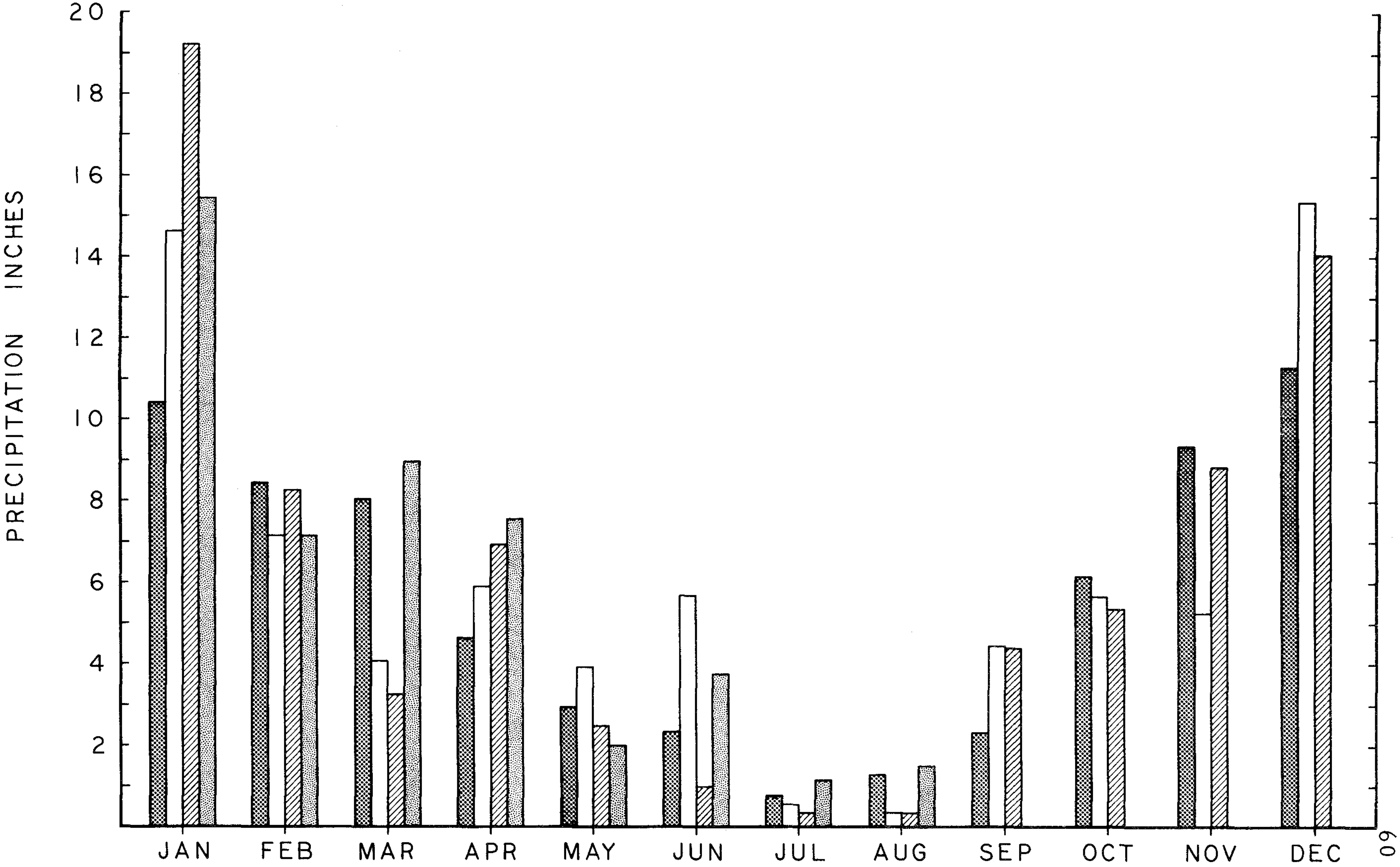
The salinity at the time of high low water was never greater or less than the range between high high and low low water. The low high water salinity, however, was occasionally slightly greater (1‰) than high high water salinity.

Precipitation

The total monthly rainfall during 1969, 1970, and part of 1971 was compared to the long term monthly average (Figure 12). The monthly precipitation for all years was similar to the average during the first part of the rainy season (September through November). Departure from average was more evident from December through June, with only minor precipitation during July and August. Rainfall during December and January was much greater than normal, while an apparent abnormal drop occurred in March in both 1969 and 1970. A higher than normal amount was recorded in June during 1969 and 1971. The pattern of precipitation during 1969 was similar to that during the study period with the exception of the drop in March and the peak in June.

The total rainfall during 1970 was 74.47 inches, while that in 1969 was 73.05 inches (U.S. Weather Bureau, 1969-1971). Since most of the precipitation occurred during the winter months, the

Figure 12. Total monthly precipitation during 1969 (blank bars), 1970 (cross-hatched), and 1971 (fine stipple), and the long term monthly averages (coarse stipple) for Newport, Oregon.

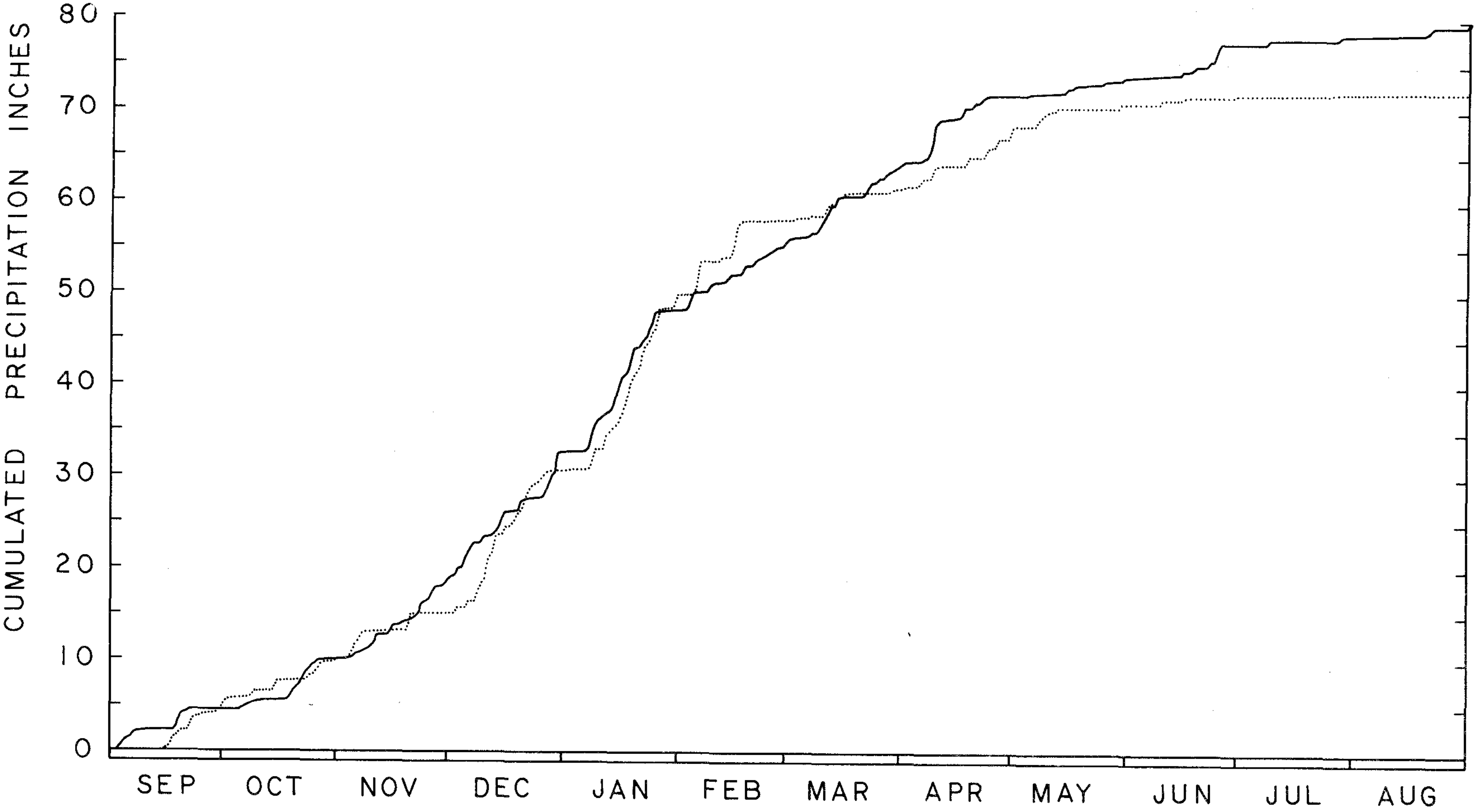

PRECIPITATION INCHES
20
18
16
14
12
10
8
6
4
2
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

reporting of precipitation on a calendar basis of January through December effectively combines separate rainy seasons. When the year was considered from September to August, years were separated by a dry season with a year including only a single wet season. By this method the total rainfall measured was 80.14 inches during the 1970-1971 season, and was 72.52 inches during the 1969-1970 season (Figure 13). The strong seasonality was apparent from the change in slope in the curves. Precipitation during July and August was generally only several hundredths of an inch per day in the form of fog condensation, and was noticeably less than the actual direct precipitation in September, which measured in tenths of inches.

Precipitation calculated on a daily basis gave a clearer means by which to compare months and years (Figure 14). Although the total precipitation increased from September through November, the daily value did not increase significantly until December. Due to the large variation during January, daily amounts during succeeding months are not significantly less than those in January until April or May.

Precipitation averaged 0.5 and 0.6 inches per day during December and January and averaged 0.01 to 0.02 inches during July and August. The daily precipitation during the investigation did not differ significantly from that during the preceding year. The periodicity in the rate of precipitation is indicated in Figure 14.

Figure 13. Cumulative precipitation during 1969-1970 (dotted line), and 1970-1971 (solid line) at Newport, Oregon.


CUMULATED PRECIPITATION INCHES
80
70
60
50
40
30
20
10
0
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG

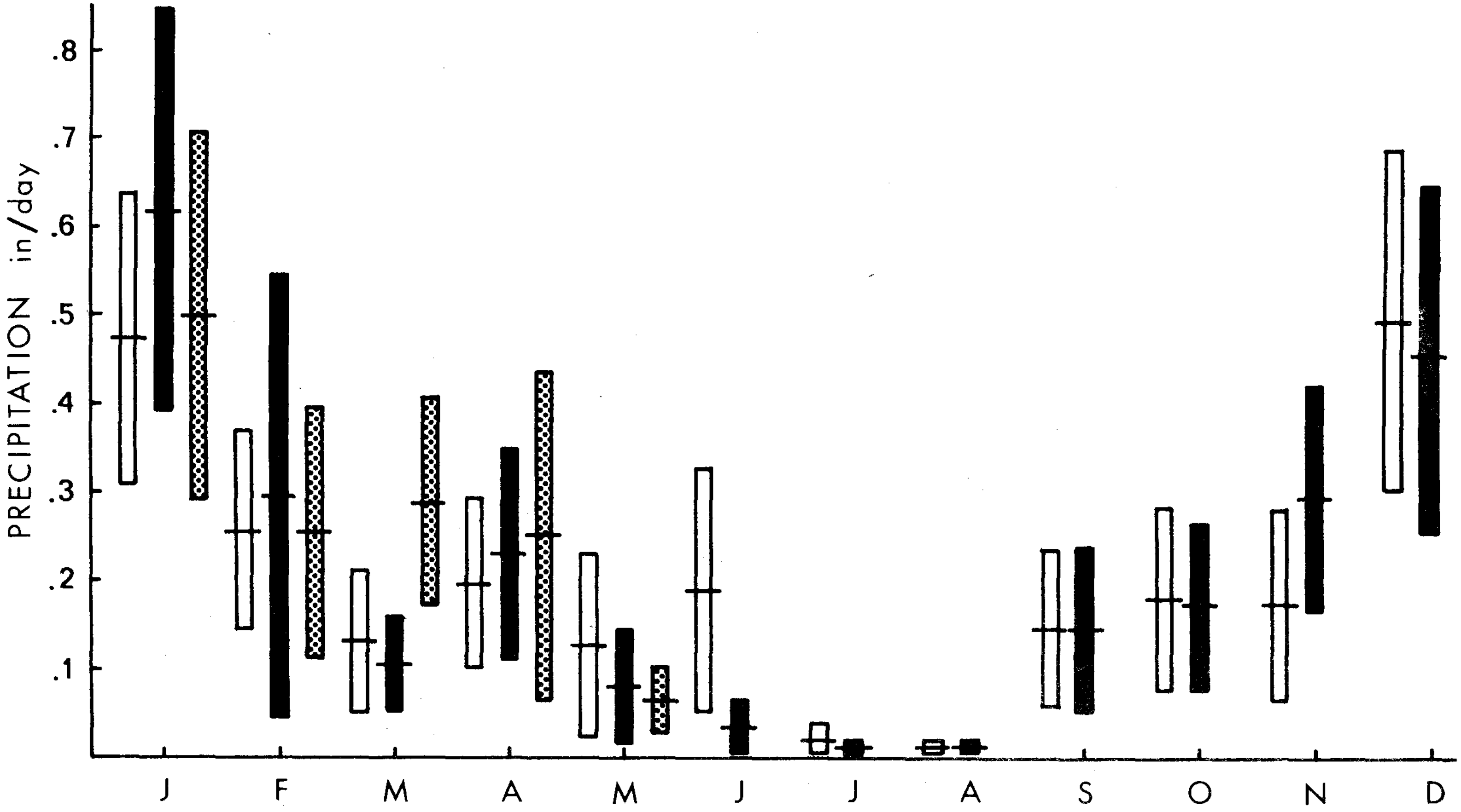


Figure 14. Rate of daily precipitation for each month during 1969 (blank), 1970 (solid), and 1971 (stipple) shown by the mean (bar) and ±2 x standard error (rectangle) at Newport, Oregon.

No freshwater runoff data were collected during the period of investigation and those taken by the Georgia Pacific Corporation, Toledo, Oregon proved inadequate. Kjeldsen (1967) obtained weekly data during 1962-1966 from Georgia Pacific Corporation and showed that average monthly runoff during the summer was 150 cubic feet per second, increasing to 1000 cubic feet per second during the winter. Kjeldsen found a close correlation between precipitation and velocity of runoff, and confirmed the importance of separation of rainy seasons.

Water Table

The elevation of the water table, above MLLW, was monitored throughout the year at the Marine Science Center and near the study site (Figure 3). The well points were apparently located back far enough from the beach to escape normal tidal influence, as no measurable diurnal change in groundwater elevation was found over an extreme spring tidal cycle in either winter or summer.

The water table rose from the summer minimum level of about 7 feet during August to a maximum level of 11.5 to 13.5 feet in January. The drop in water table was more gradual than the rise, and both well points responded in a similar pattern (Figure 15). The well point closer to the Marine Science Center was set farther back from the beach and at a higher elevation. Greater maximum water levels were expected at this site owing to the anticipated lens shaped water

Figure 15. Change in observed water table elevation near the study transect (solid line) at the Marine Science Center (dotted line) and in a theoretical water table from a non-draining column of sediment with a porosity of 40% (dashed line) for the period of October 1970 to August 1971. Elevation in feet above MLLW.

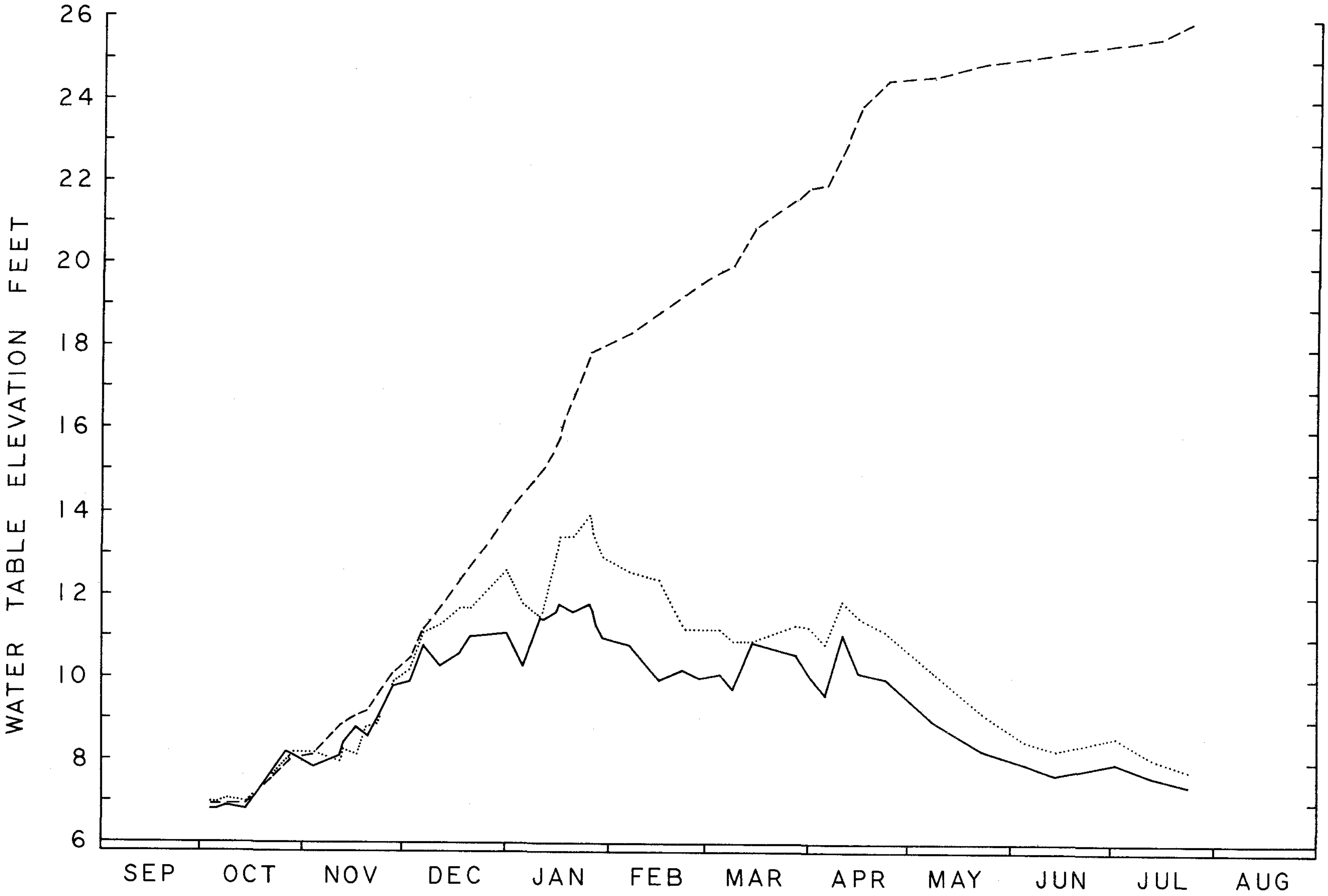

26
24
22
20
18
16
14
12
10
8
6
WATER TABLE ELEVATION FEET
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG

table throughout the sand spit (Milhouse, personal communication).

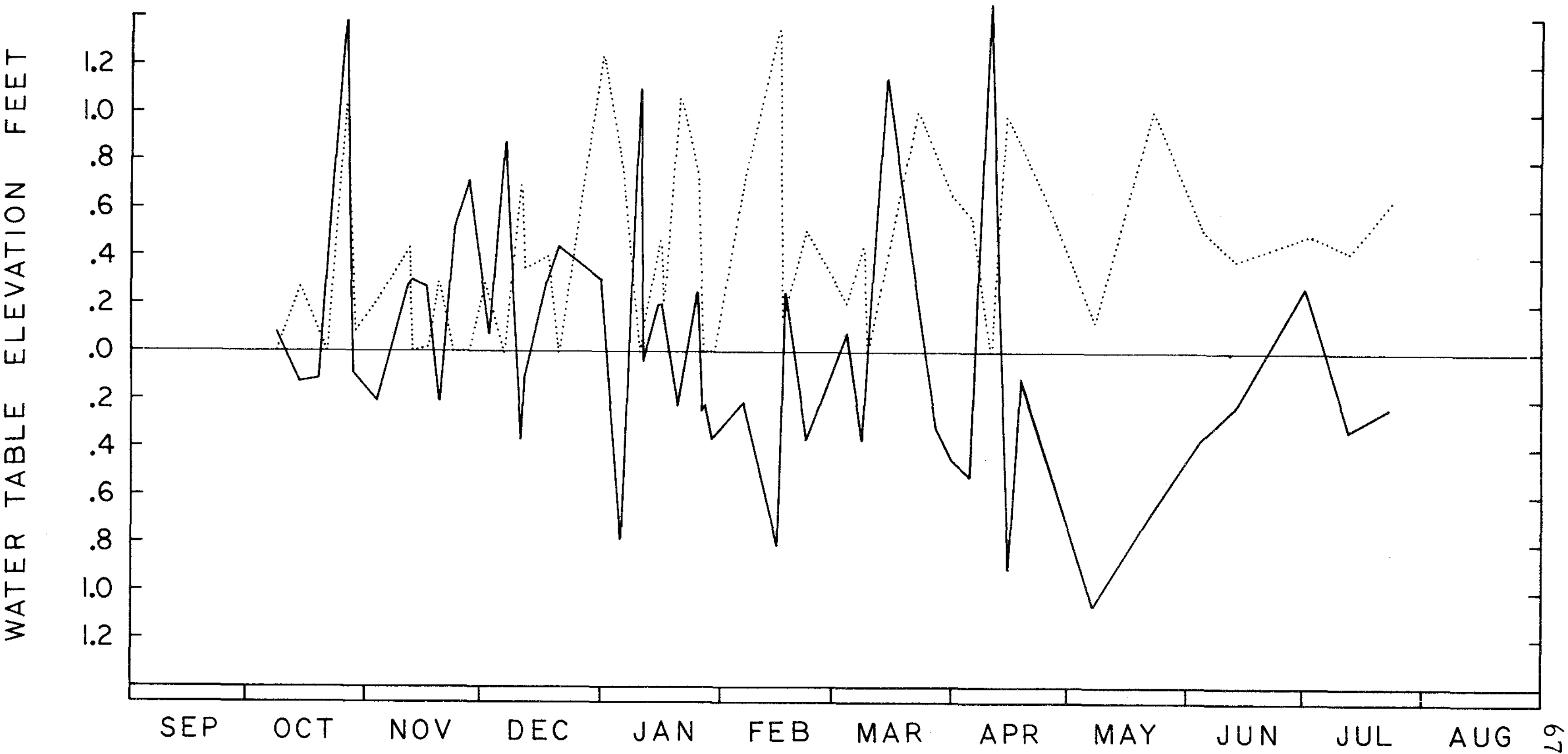
The theoretical elevation of the water table at the transect site was recalculated from the precipitation data on the basis of a sediment porosity of 40% and is shown cumulatively in Figure 15. This theoretical curve represents the expected water table elevation in a non-draining column of sediment. The difference between the instantaneous change in the theoretical water table and the instantaneous change in the observed water table (Figure 16) represented the actual volume that drained through the littoral surface into Yaquina Bay. The theoretical water table followed the observed water table rather closely until December, when the sediment pores became filled. Drainage from the stored high water table continued long after the rainy season.

Groundwater Hydrology

Groundwater Hydraulic Surface

The tidal effect on discharge and recharge of interstitial pore water was studied over the entire beach surface during September of 1970 by R. Milhouse and the author. The depth of the hydraulic surface was measured at four elevations (3.5, 4.2, 6.0, and 8.4 feet) as they were exposed by the tide (Figure 17). The hourly tidal elevations were recorded by the permanent tide gauge at the Marine Science Center dock.

Figure 16. Comparison of the instantaneous change from October 1970 to August 1971 in the theoretical (dotted line) and observed (solid line) water tables at the transect well point. Theoretical curve based on a sediment porosity of 40%.


WATER TABLE ELEVATION FEET
1.2
1.0
.8
.6
.4
.2
.0
.2
.4
.6
.8
1.0
1.2
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG

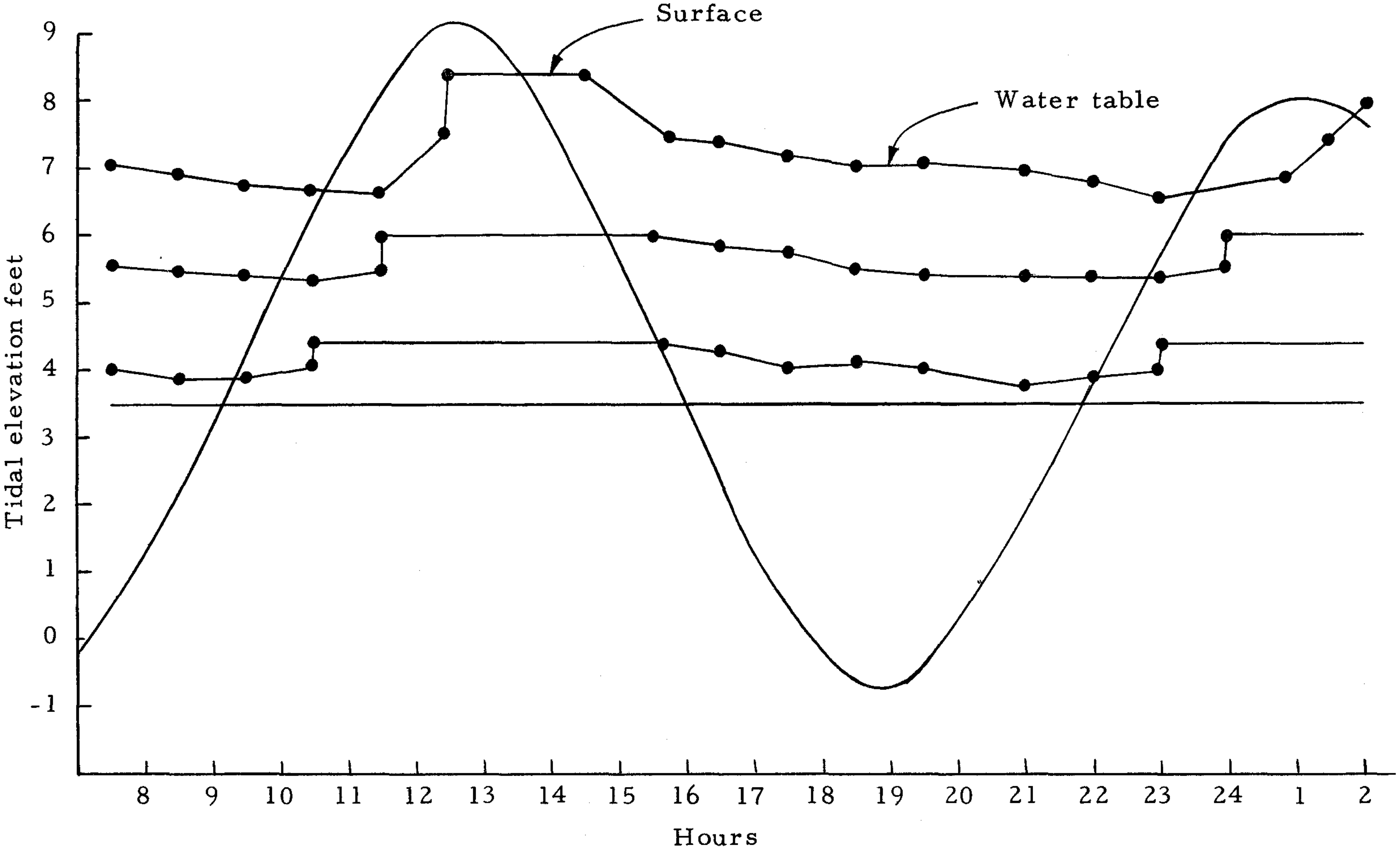


Figure 17. Change in water table elevation at four tidal levels along the transect line in September 1970 and tide curve observed for the same period. Elevations in feet based on MLLW = 0.0. Figure adapted from Milhouse (1971).

On a spring tide during September the change in depth of the hydraulic surface of the water table increased with station elevation and ranged from 1.70 feet at the 8.4 foot station to 0.0 feet at the 3.5 foot station. The amount of time at which the hydraulic depth was zero, i.e., at the surface, decreased with lower station elevation. The intersection of the hydraulic surface of the water table with the sediment surface was premanently fixed at the 3.5 foot elevation and varied less than ±0.25 feet throughout the year. As the tide flooded the stations above the 3.5 foot intersection point, the pores were filled and the ground water level was brought to the surface. The magnitude of this filling of the pore spaces increased with elevation and was 0.71 feet at the 8.4 ft station, 0.52 at 6.0 feet, 1.13 at 4.5 feet and 0.0 at the 3.5 foot station (R. Milhouse, unpublished).

Salinity

The chlorinity of the interstitial groundwater was determined from samples taken at depths into the sediment of 0.5, 15, 30, and 75 cm as the five elevations (0.0, 1.6, 4.5, 6.0, and 8.4 feet) were exposed by the tide (Table 1). The chlorinity was converted to salinity according to the method of Lyman (1969). Sampling of elevations submerged by the tide was limited to the upper intertidal. The upper stations were consequently the most completely sampled and the lower stations the least. Samples could not always be taken in the

Table 1. Salinity (‰) of the pore water along the transect in Yaquina Bay, at five station elevations (ft) and four depths (cm) during a tidal cycle on September 16-17, 1970 compared to the surface and bottom water of the estuary at the Marine Science Center dock.

Station Elevation (ft)	Depth (cm)	Time (hrs)						
		0600	0800	1000	1100	1200	1400	1600
8.4	0.5	--	--	34.4	33.8	33.2	--	--
	15	--	--	34.6	33.2	32.9	30.9	--
	30	--	--	33.4	33.0	31.4	3.8	33.8
	75	22.6	18.0	33.0	31.4	21.9	14.4	29.9
6.0	0.5	--	--	--	--	--	--	33.7
	15	--	--	--	--	--	--	32.7
	30	33.4	32.6	34.8	--	--	--	34.1
	75	33.6	32.3	32.5	22.2	--	--	33.7
4.5	0.5	--	--	--	--	--	--	31.5
	15	--	33.3	--	--	--	--	33.7
	30	33.3	33.5	34.8	--	--	--	32.9
	75	33.7	34.0	32.5	--	--	--	33.8
1.6	0.5	32.4	--	--	--	--	--	--
	15	--	26.7	--	--	--	--	--
	30	28.7	25.9	--	--	--	--	--
	75	18.7	13.7	--	--	--	--	--
0.0	0.5	32.9	--	--	--	--	--	--
	15	--	--	--	--	--	--	--
	30	--	--	--	--	--	--	--
	75	--	--	--	--	--	--	--
Estuary water								
Surface		--	30.3	30.5	30.4	31.5	--	31.3
Bottom		--	31.1	31.0	31.7	31.7	--	31.7

(continued)

Table 1. Continued.

Station Elevation (ft)	Depth (cm)	Time (hrs)						
		1800	2100	2300	0100	0300	0500	0700
8.4	0.5	--	--	--	33.9	33.2	--	--
	15	--	--	--	32.0	--	--	--
	30	--	--	--	34.9	34.2	--	--
	75	19.8	22.0	18.9	32.3	11.2	28.0	29.9
6.0	0.5	34.0	--	34.2	--	--	33.9	--
	15	32.7	--	33.6	--	--	32.5	--
	30	33.6	33.6	33.5	--	--	33.3	33.3
	75	33.2	33.6	33.6	--	--	32.4	33.6
4.5	0.5	33.9	33.7	--	--	--	33.7	32.6
	15	33.2	32.2	--	--	--	33.2	--
	30	33.9	33.9	--	--	--	33.9	33.7
	75	33.8	33.9	--	--	--	33.4	33.0
1.6	0.5	30.8	28.3	--	--	--	--	32.6
	15	31.8	22.0	--	--	--	--	31.3
	30	16.9	17.5	--	--	--	--	30.2
	75	18.1	13.3	--	--	--	--	28.5
0.0	0.5	33.7	--	--	--	--	--	32.7
	15	--	--	--	--	--	--	--
	30	--	--	--	--	--	--	--
	75	--	--	--	--	--	--	--
Estuary water								
Surface		31.5	31.2	31.0	31.5	31.5	31.7	31.5
Bottom		31.6	31.7	31.7	31.8	31.8	32.1	31.5

upper intertidal during low tide because the pore water volume decreased with drainage.

The salinity of the pore water at 0.5 cm in depth was similar between 4.5 and 8.4 feet throughout the day and ranged between 33 and 34‰. Salinities at lower station elevations were less. At the 8.4 and 1.6 foot stations marked changes in salinity were observed with depth from 0.5 to 75 cm, while salinity was rather homogeneous to the depth of 75 cm at the 6.0 and 4.5 foot stations.

At 8.4 feet, high tide estuarine water with a salinity of 33.8 to 33.5‰ found at 0.5 cm in depth from 1100 to 1300 hours was the source of saline water at 15 cm at 1400 hours, 30 cm at 1600 hours, and 75 cm at 1800 hours. The salinity of 19.8‰ at 75 cm at 1800 hours apparently was the result of mixing of fresh groundwater (0.5‰ at 75 cm at 1300 hours) and salt water originating at the surface. Similarly, at 0800 hours, the salinity of 18.0‰ at 75 cm in depth was the result of mixing from the high tide of the previous day.

At the 8.4 foot section, the change from 18.9‰ to 33.0‰ at 75 cm in depth suggested that the high tide exerted a pressure over the intertidal surface greater than that of the discharging groundwater, causing the groundwater to back up at the upper elevations. Note the salinities of 4.8‰ and 3.8‰ at 30 cm between 1300-1400 hours, Table 1. As the tide ebbed, the pressure was released and the level of the fresh groundwater dropped through horizontal percolation, thus allowing the sea water that had filled the pores near the surface at high tide to percolate down further into the sediment. A similar cycle occurred at the 1.6 foot station where the minimum mixed salinity at 75 cm was 13.3‰ on the ebbing tide. Data were insufficient to estimate the rate of direction of flux at this elevation. However, the general decreasing salinity with depth, the value 16.9‰ at an intermediate level at 1800 hours, and the saturated pore space suggested a vertically discharging system at the 1.6 ft level. The depth of the fresh ground water at high tide and its pressure response could not be determined at the lower stations. The persistent low salinity of 19 to 22‰ from 1800 to 2300 hours at 8.4 feet at a depth of 75 cm indicated the absence of tidal pressure during the ebbing tide.

As the stations became submerged, the salinity at the sediment surface was presumed to be that of the estuary measured off the Marine Science Center dock. The salinity of the estuary water ranged from 30.3‰ to 32.1‰ during the 24 hour period. The salinity of the near surface interstitial water at 8.4 feet (>33.0‰) always exceeded that of the estuarine water. The high salinity of the surface interstitial water was evidently derived from evaporative concentration of salts.

The interstitial salinity at 8.4 feet was apparently the result of concentration from the surface with forced mixing from the bottom, and at 1.6 feet the salinity was the result of dilution from the bottom by vertical pore water percolation.

Temperature

The temperature of the sediment at 0.5, 5, 15, 30, and 75 cm depth was taken with a hypodermic thermistor probe as the same five elevations (8.4, 6.0, 4.5, 1.6, and 0 feet) were exposed by the tide (Table 2). The time of the measurements corresponded to the time of the interstitial chlorinity samples.

The temperature of the sediment at 0.5 cm below the surface was strongly influenced by tide and insolation, and showed greater variation with elevation. Temperatures at 8.4 feet ranges as much as 14.9°C (8.8 to 23.7°C) while the temperature range at 0.0 feet (2.7°C) was mostly confined to the range in water temperatures (9.4 to 12.1°C). The temperatures at the upper stations were high enough to cause evaporative concentration of salts at the sediment surface.

The sediment temperature at 75 cm in depth was more uniform, and ranged only from 14.5 to 15.8°C at 8.4 feet. The temperature and range decreased at this depth with lower elevation. It was more difficult to trace the temperature effect of the heated surface water at 8.4 feet, as it penetrated the sediment at high tide, than to follow the salinity effect.

Table 2. Temperature (°C) of the sediment along the transect in Yaquina Bay, at five station elevations (ft) and five depths (cm) during a tidal cycle on September 16-17, 1970, compared to the surface and bottom water of the estuary at the Marine Science Center dock.

Station Elevation (ft)	Depth (cm)	Time (hrs)						
		0600	0800	1000	1100	1200	1400	1600
8.4	0.5	8.8	12.0	20.2	23.7	23.6	17.1	17.5
	5	10.2	11.6	15.4	18.5	19.3	14.8	18.0
	15	12.4	12.5	12.8	13.3	14.4	15.1	15.0
	30	12.8	14.0	13.9	13.5	14.0	14.5	14.5
	75	14.8	15.0	15.0	15.0	15.4	14.7	14.7
6.0	0.5	8.2	10.8	17.4	19.1	--	--	14.4
	5	8.7	9.6	13.3	15.3	--	--	13.9
	15	9.9	9.9	10.0	10.8	--	--	12.0
	30	9.9	10.2	10.2	10.7	--	--	11.6
	75	11.2	11.3	11.2	12.4	--	--	11.2
4.5	0.5	8.8	12.3	16.3	--	--	--	14.1
	5	9.3	10.4	13.1	--	--	--	12.5
	15	10.1	10.6	10.6	--	--	--	11.2
	30	10.7	11.1	11.1	--	--	--	11.3
	75	11.2	11.7	11.8	--	--	--	12.0
1.6	0.5	9.0	11.7	--	--	--	--	--
	5	9.3	10.1	--	--	--	--	--
	15	10.1	10.1	--	--	--	--	--
	30	10.4	10.7	--	--	--	--	--
	75	10.7	11.3	--	--	--	--	--
0.0	0.5	9.5	--	--	--	--	--	--
	5	9.6	--	--	--	--	--	--
	15	--	--	--	--	--	--	--
	30	--	--	--	--	--	--	--
	75	--	--	--	--	--	--	--
Estuary water								
Surface		--	11.9	11.6	11.9	10.0	--	10.9
Bottom		--	11.1	11.0	9.6	9.4	--	10.0

(continued)

Table 2. Continued.

Station Elevation (ft)	Depth (cm)	Time (hrs)						
		1800	2100	2300	0100	0300	0500	0700
8.4	0.5	13.0	10.6	10.7	11.6	11.0	11.7	13.5
	5	15.0	12.3	11.8	11.8	11.4	12.1	12.8
	15	14.7	14.6	14.0	13.5	13.0	13.9	13.3
	30	14.0	14.6	14.4	14.1	14.0	14.1	13.9
	75	14.5	14.8	14.7	14.5	14.7	14.7	14.6
6.0	0.5	11.2	9.5	9.9	--	--	11.0	12.2
	5	12.8	10.4	10.2	--	--	10.7	11.4
	15	12.2	11.7	11.6	--	--	10.6	10.7
	30	11.8	11.8	11.3	--	--	10.7	10.7
	75	11.1	11.2	11.2	--	--	11.1	11.1
4.5	0.5	11.1	9.0	--	--	--	11.0	12.1
	5	11.8	9.8	--	--	--	10.6	11.6
	15	11.2	11.2	--	--	--	10.7	10.8
	30	11.1	11.3	--	--	--	11.0	11.0
	75	11.4	11.4	--	--	--	11.2	11.6
1.6	0.5	9.8	9.1	--	--	--	--	11.7
	5	11.0	9.5	--	--	--	--	10.8
	15	10.5	10.6	--	--	--	--	10.5
	30	10.5	10.6	--	--	--	--	10.5
	75	11.2	11.0	--	--	--	--	11.0
0.0	0.5	10.2	--	--	--	--	--	11.4
	5	11.0	--	--	--	--	--	10.6
	15	--	--	--	--	--	--	--
	30	--	--	--	--	--	--	--
	75	--	--	--	--	--	--	--
Estuary water								
Surface		11.0	12.1	11.9	10.5	10.7	10.5	10.7
Bottom		10.8	11.4	10.7	10.1	9.8	9.8	10.2

At the 8.4 foot station at 15 cm in depth, high temperatures of 16.8, 15.1, and 15.0°C were recorded between 1300 and 1600 hours, with cooler temperatures recorded at shallower and deeper depths, suggesting that the warm temperature resulted from the earlier sinking of surface water which was at 23.6°C at 1100 and 1200 hours. These data corresponded in a general way to the cycle of mixing found in the pore water salinity. The abrupt change in temperature at 75 cm at the 8.4 foot station from 15.8 to 14.7°C between 1300 and 1400 hours indicated the mixing effect of cold freshwater from the bottom with water warmed earlier by conduction at the surface. Temperatures at the other stations were more homogeneous with depth than those at the highest station.

Porosity

The porosity of the surface sediment in summer was determined at seven elevations from 8.4 to -1.0 feet by R. Milhouse. The porosity was observed to increase slightly down the slope of the beach. Porosity was also determined with depth to 15-20 cm at 8.4, 7.0, 6.0, and 4.2 feet and was found not to vary from surface values. The presence of a permanent interstitial algal mat at 7.0 feet, however, reduced the permeability and disturbed the porosity measurement. A porosity of 40 percent was representative of the beach.

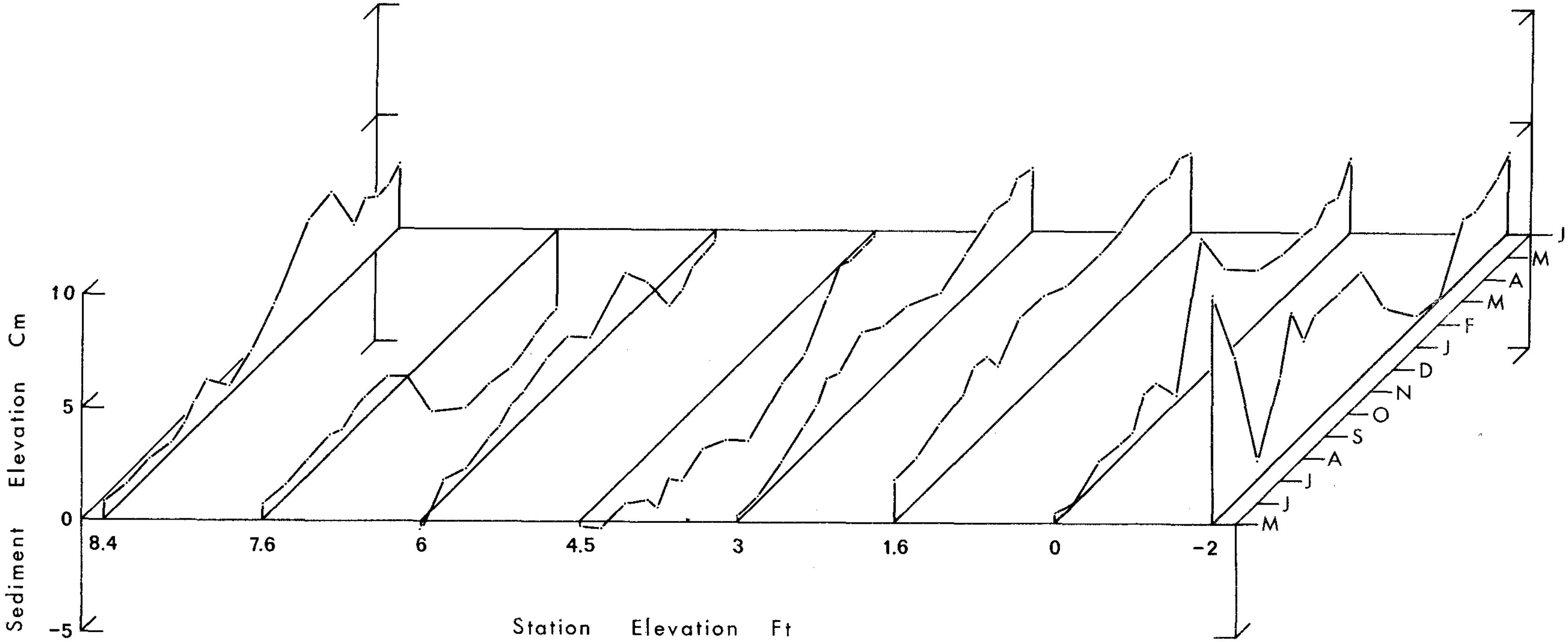
On the basis of these determinations, the depth of the hydraulic surface, and several measurements of percent saturation at low water, Milhouse calculated the volume of water that entered the sediment surface on a flooding tide as: 0.028 ft^3/ft^2 at 8.4 feet, 0.021 ft^3/ft^2 at 6.0 feet, 0.006 ft^3/ft^2 at 4.5 feet, and 0.0 ft^3/ft^2 at 3.5 feet. If the water table were to be maintained at a constant low level during the summer the volume entering the beach during a high tide must be lost during a low tide by pore water percolation below the intersection zone at the 3.5 foot elevation. Absence of ground water pressure from the fore-dune during the summer would make discharge of this volume of sea water through percolation unlikely above the 3.5 foot elevation.

Sediment Elevation

The change in sediment elevation at the eight stations was considered representative of the entire beach. The actual elevations of the sediment surface measured at the pipes were about 6 inches below the elevations above the sampling points. The change in elevation observed was presumed to mirror change at these elevations (Figure 18).

Deposition or erosion of sediment throughout the beach was generally less than 5 cm throughout the year of observation. The largest changes in elevation were observed at the lowest and highest stations, located at -2.0, 0.0, 7.6, and 8.4 feet. The smallest changes of

Figure 18. Elevation of the sediment surface at the eight fixed intertidal stations along the transect from May 1970 to June 1971.


Sediment Elevation Cm
10
5
0
-5
8.4
7.6
6
4.5
3
1.6
0
-2
Station Elevation Ft
M
J
J
A
S
O
N
D
J
F
M
A
M
J

3.0 cm or less and the smallest rate of change were observed at 1.6, 3.0, and 6.0 feet where the change was positive, or depositional. Cyclic erosion and deposition resulted in the same elevation at 4.5 feet at the beginning and end of the study period, although the elevation ranged 4 cm throughout the year. The two low stations were erosional through the winter (December to March) and depositional the rest of the year. Conditions at the lowest station were complicated by runoff and delta formation from a nearby channel. The highest station was depositional from winter through spring. The abrupt erosion of the otherwise stable beach at 7.6 feet was due to sudden disruption of the hard-packed surface layer.

The most stable part of the beach was the lower mid-tide portion at 3.0 and 1.6 feet.

Sediment Particle Size

Fine Sediments

Large differences in the percentage of the sediment were found within stations at different depths and seasons and between stations (Figures 19 and 20). The percentage of fine particles was generally less than 10% during the winter in the upper two stations but often exceeded 20% at the lower two stations. The fine fraction ranged between 10 and 20% during the summer throughout the beach.

Figure 19. Percentage of fine sediment fraction of samples taken at two intertidal elevations on the transect as shown by the mean (bar) and ±2 x standard error (rectangle) in samples from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.

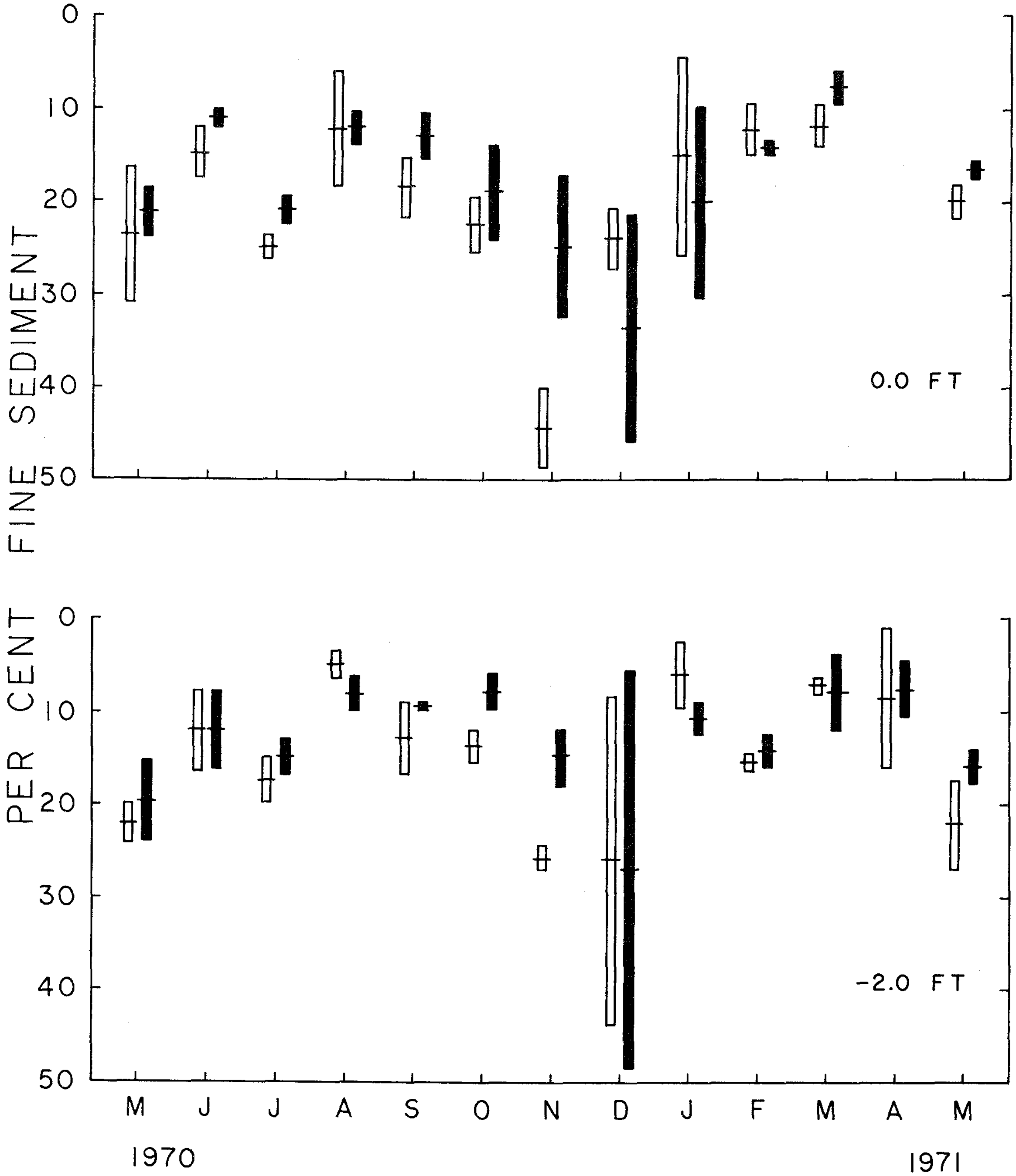
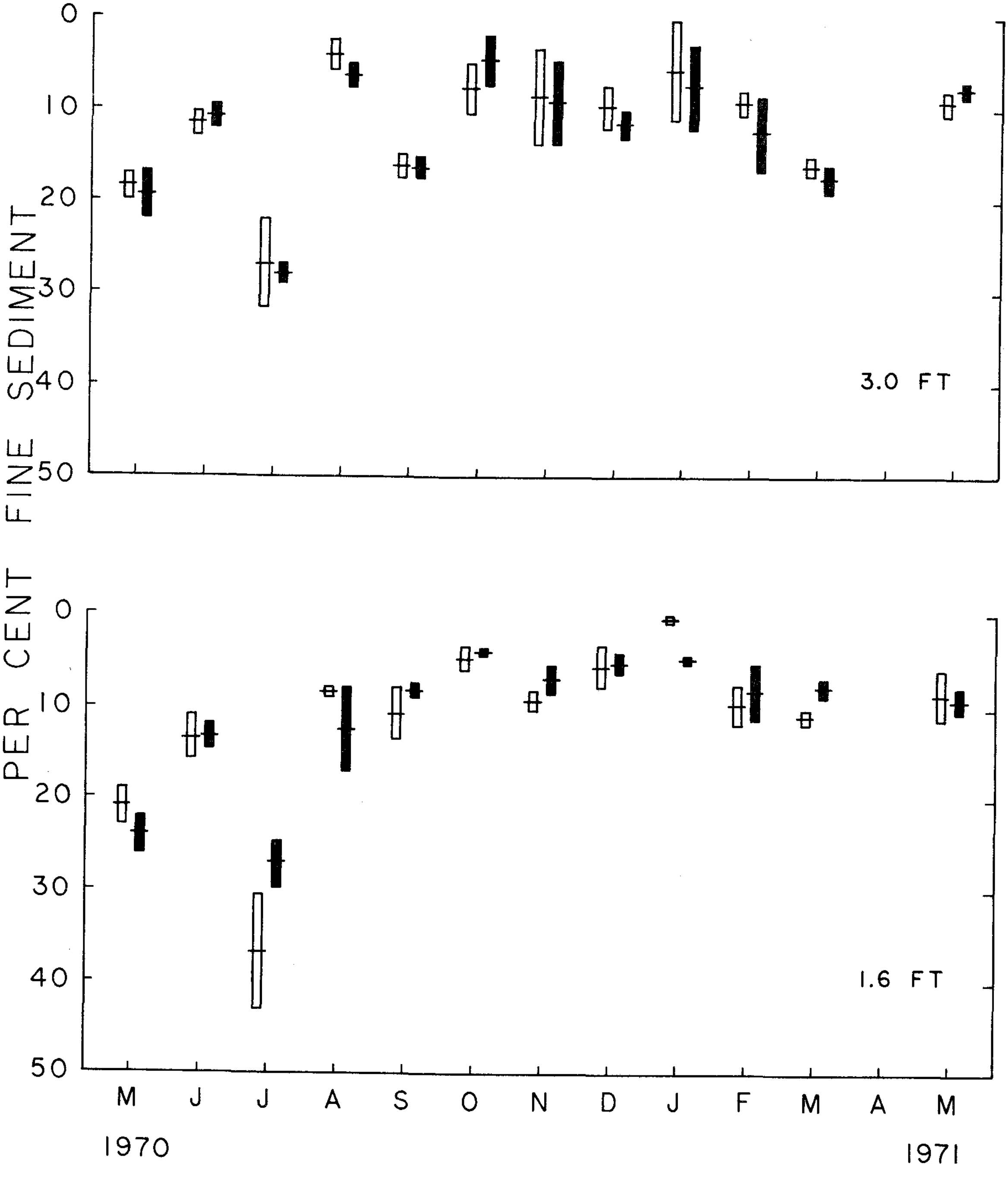

0
10
20
30
40
50
0.0 FT
FINE SEDIMENT
PER CENT
0
10
20
30
40
50
-2.0 FT
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 20. Percentage of fine sediment fraction of samples taken at two intertidal elevations on the transect as shown by the mean (bar) and ±2 x standard error (rectangle) in samples from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


PER CENT FINE SEDIMENT
0
10
20
30
40
50
3.0 FT
1.6 FT
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

The percentage of fines in the second 0.5 cm in depth never exceeded that in the first 0.5 cm, while the percentage of fines in the first 0.5 cm was often significantly greater than in the second 0.5 cm. This was especially true when the percentage of fines was increasing, as for example during September at the 0.0 foot station. The lower stations were quite variable during the winter, while the upper two stations remained relatively unchanged.

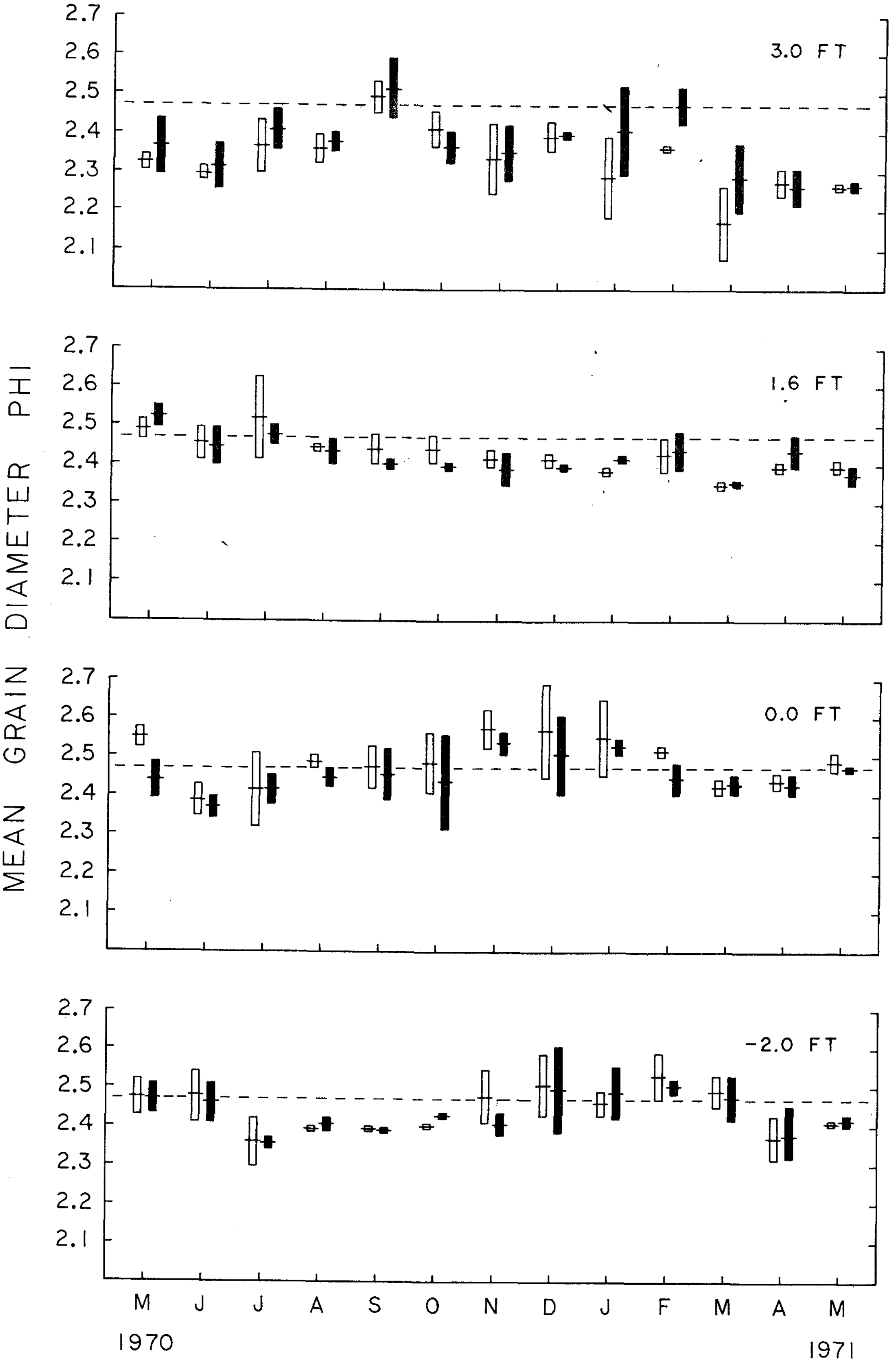
Coarse Fraction

The statistical distributional parameters of the coarse sediment fraction were computed from the settling tube particle size data. Particle size was normalized by conversion of millimeters to phi units, where $\phi = -\mathrm{LOG}_2$ diameter in millimeters. These parameters included the mean particle size, sorting, skewness, and kurtosis, measures defined by Folk and Ward (1957). These analyses did not include the fine fraction.

Mean Particle Size

The variability in monthly samples of sediment from the first and second 0.5 cm in depth was examined at each station (Figure 21). Note that increasing phi values imply decreasing particle size and that 2.47 ϕ is equivalent to 180 microns. Particle size analysis indicated that the sediments at the four stations were clearly composed of fine

Figure 21. Mean particle size in phi units at four intertidal elevations along the transect as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


2.7
2.6
2.5
2.4
2.3
2.2
2.1
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
MEAN GRAIN DIAMETER PHI
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

sand according to the scale of Wentworth (1922). The particle size at 1.6 feet did not change significantly from month to month and showed the least variability within months. The average mean particle size at this elevation ranged between 2.35 and 2.52 phi (0.195-0.177 mm), with little difference in size with depth.

The average mean particle size at the 3.0 foot station varied between 2.17-2.51 phi (0.220-0.177 mm). Mean size of sediment at the surface decreased from 2.32 phi in May to 2.49 phi in September, then increased intermittently to 2.17 phi in March. The second 0.5 cm did not differ markedly from this pattern until January at which time the subsurface sediment grew finer as the surface became coarser.

At MLLW the seasonal pattern was smoother and differences were slight. Particle size was largest in June (2.39 ϕ) and March (2.42 ϕ) and smallest in May (2.55 ϕ) and November-January (2.57-2.55 ϕ). Variation in the average mean particle size of sediment in the second 0.5 cm was generally not significantly different from surface variation. The decrease in size during winter corresponded to the increase in size at the 3.0 foot station and winter was also the most variable period.

The lowest station (-2.0 feet) was rather uniform during the summer and more variable during the winter. The decrease in particle size which occurred from June (2.36 ϕ) to December (2.51 ϕ) at station two was not apparent at station one until November. No significant differences were found with depth.

The smallest particle sizes were recorded in September at 3.0 feet and from November to January in the lower two stations.

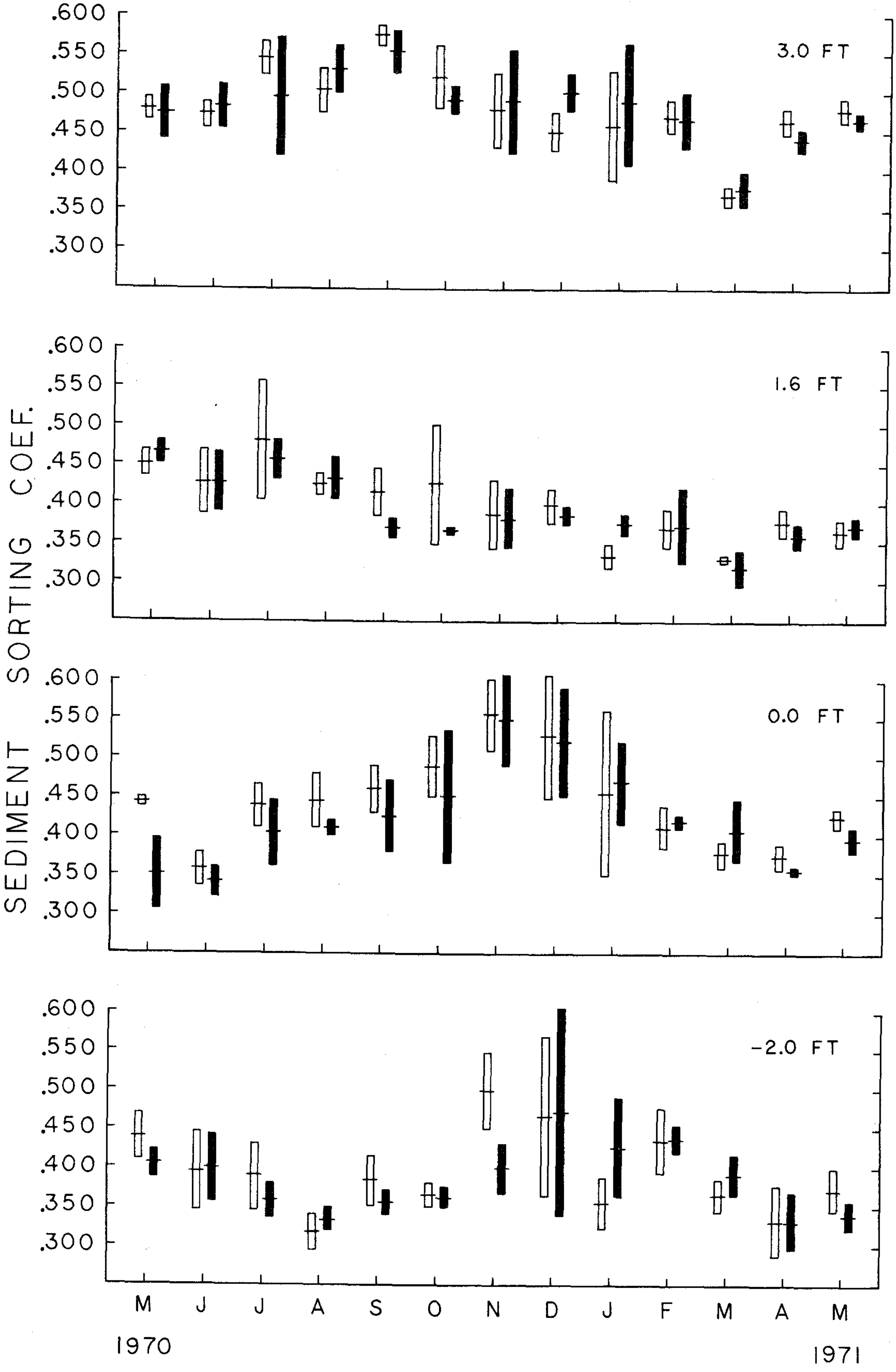
Sorting

The degree of sorting, as a measure of deviation within samples, indicated that the sediment between -2.0 and 3.0 feet was generally "very well sorted," according to the definition of Folk and Ward (1957), as the average mean sorting coefficient ranged between 0.580 and 0.320 (Figure 22).

The pattern of variability in sorting of sediment was found to be an amplification of the pattern of variability observed in the mean particle size. The sediments at 3.0 feet grew less sorted from May (0.480) through September (0.580), then gradually returned to more sorted conditions with a dip during November and December and another in March. Differences of significance were noted between seasons.

Sorting of sediments at 1.6 feet increased significantly and rather uniformly through the year from 0.450 to 0.365. Peak sorting periods at 0.0 feet occurred during June (0.360) and from March through April (0.380). The sediment was more poorly sorted during November and December (0.540). The degree and variation in

Figure 22. Sediment sorting coefficient at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


SEDIMENT SORTING COEF.
.600
.550
.500
.450
.400
.350
.300
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

sorting in the second 0.5 cm appeared to lag behind change in sorting of surface sediments. The initial sediment response to environmental changes in hydrography seemed to be characterized by change in sorting magnitude with increased variability followed by reduced variation during the succeeding month. At each station the average mean sorting values at depth were otherwise similar to that at the surface.

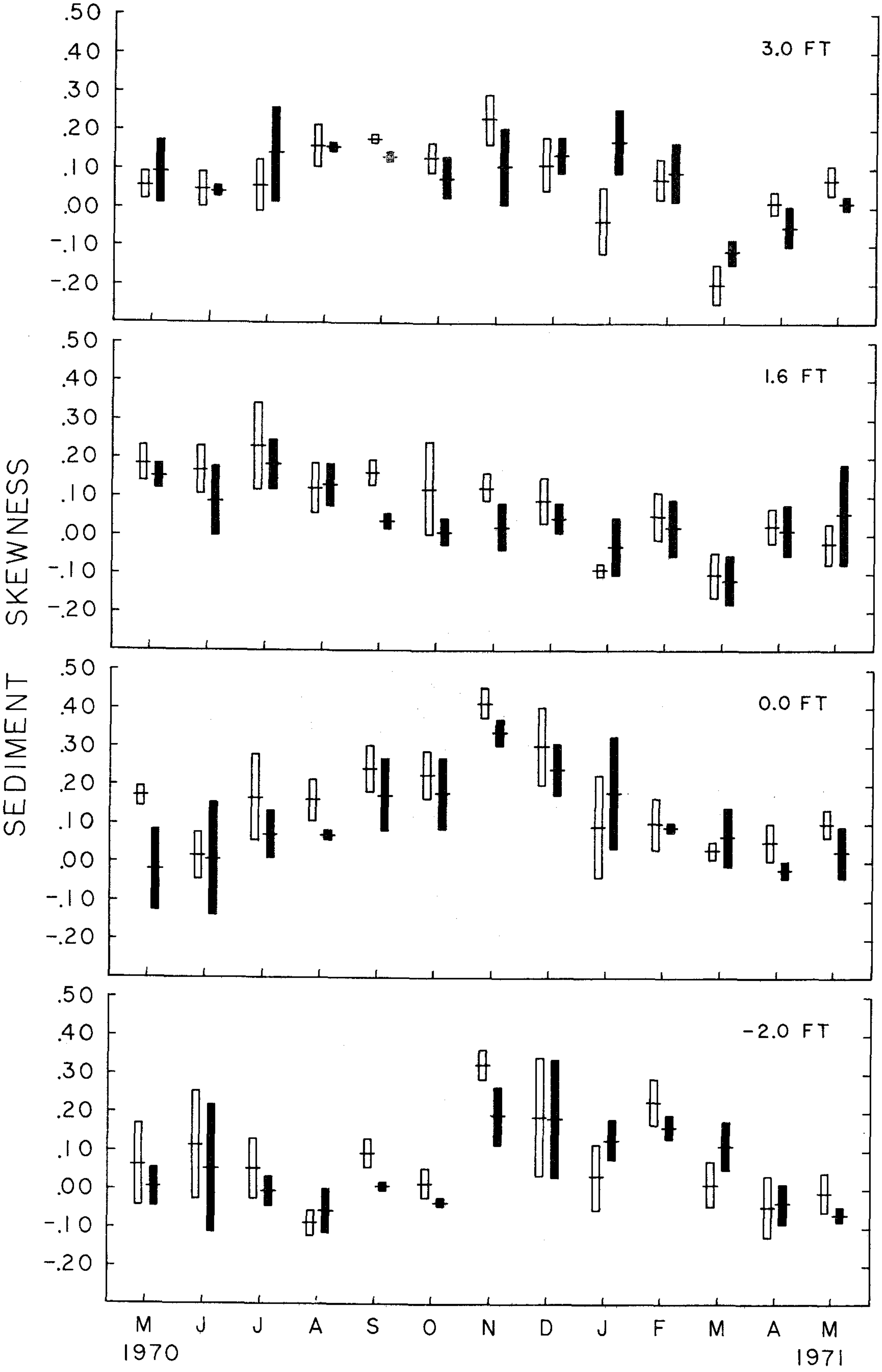
The sediments at -2.0 feet grew more sorted during the summer (0.320), then changed abruptly between October (0.365) and November (0.500) to less sorted sediment.

Sediments were most poorly sorted during September at the uppermost station and during November to December at the lower stations.

Skewness

Analysis of the asymmetry of the coarse fraction indicated that the sediments at all four stations were "nearly symmetrical" (-0.10 to +0.10) or "positively skewed" (0.10 to 0.30) towards finer sediments (Figure 23). The -2.0 and 0.0 foot stations were most positively skewed during later fall and early winter and were relatively symmetrical during the rest of the year. The positively skewed peak at these two stations coincided closely with the period of increased percentage of the fine fraction. This suggested that even if the

Figure 23. Sediment skewness coefficient at four intertidal elevations along the transect as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


3.0 FT
1.6 FT
0.0 FT
-2.0 FT
SEDIMENT SKEWNESS
.50
.40
.30
.20
.10
.00
-.10
-.20
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

measure of skewness was based solely on the coarse fraction, i.e., an open ended distribution, it still indicated the direction of trends where differences are significant.

Sediments at the 1.6 foot level became more symmetrical through the year from more positive-skewed conditions, paralleling the trend towards increased sorting. The station at 3.0 feet remained nearly symmetrical during the summer, but deviated positively during fall and winter and negatively during spring.

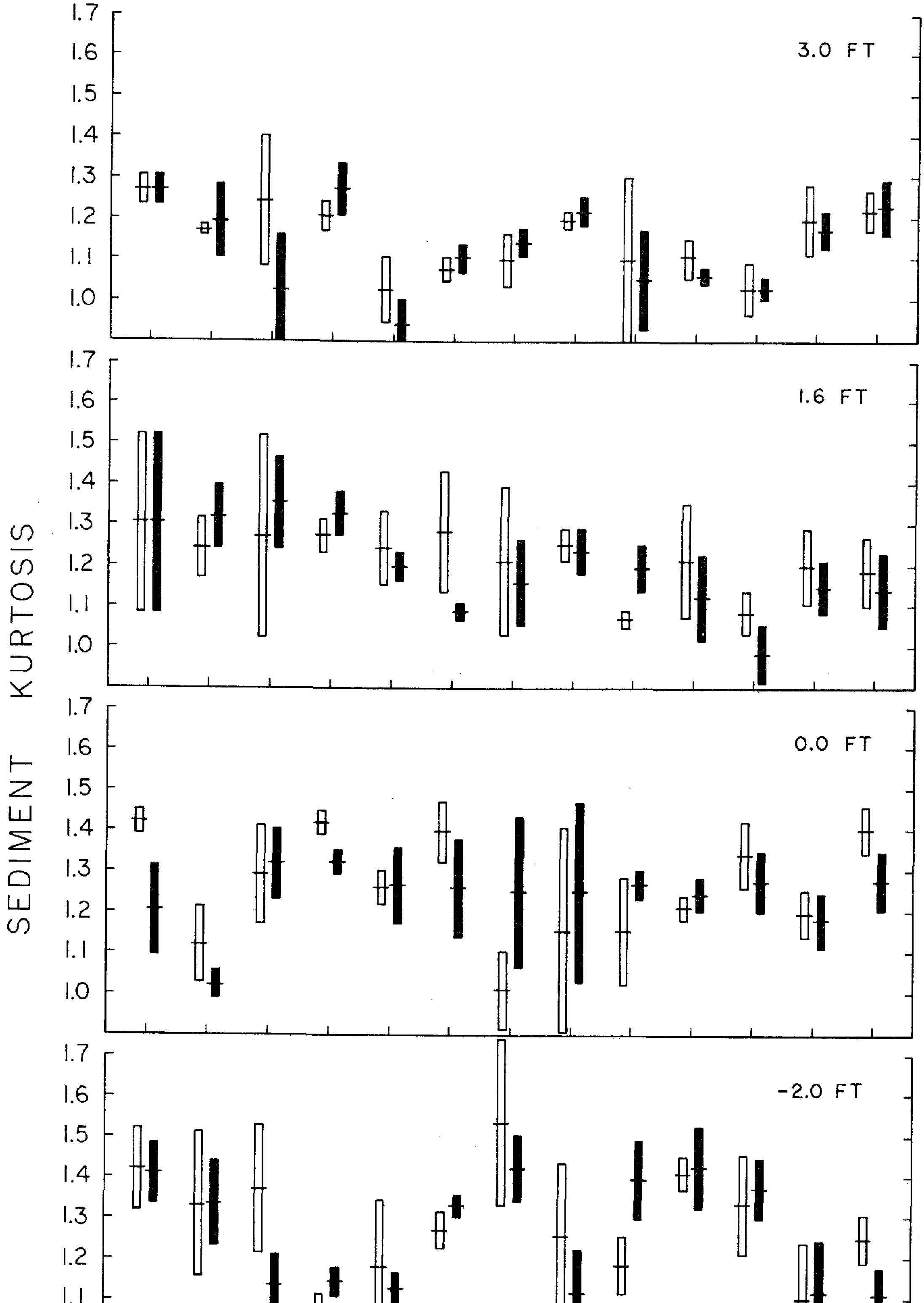
Asymmetry of the sediments in the second 0.5 cm in depth followed that at the surface rather closely, but often lagged behind significant changes in the surface layer.

Kurtosis

Kurtosis is a measure of "peakedness" and normality wherein the degree of spreading at the tails of a distribution are compared with the spread about the center of the distribution. The kurtosis statistic has been used to interpret the origin of mixed deposits (Folk, 1966).

The sediments at all four stations exceeded the kurtosis coefficient characteristic of normal distributions (1.0) and tended towards "leptokurtic" (1.11 to 1.50) distributions, i.e., with coarser and/or finer extremes (Figure 24). Omission of the fine fraction from the kurtosis analysis restricted the usefulness of the measure. However, when the months in which the percent fine fraction was minimal (<10%)

Figure 24. Sediment kurtosis coefficient at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


SEDIMENT KURTOSIS
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

were considered, sediments at the lower two elevations were significantly more leptokurtic on certain instances (February and March) than the two high stations. Nevertheless, it was not possible to consider the genesis of seasonal deposits on the basis of the kurtosis statistic.

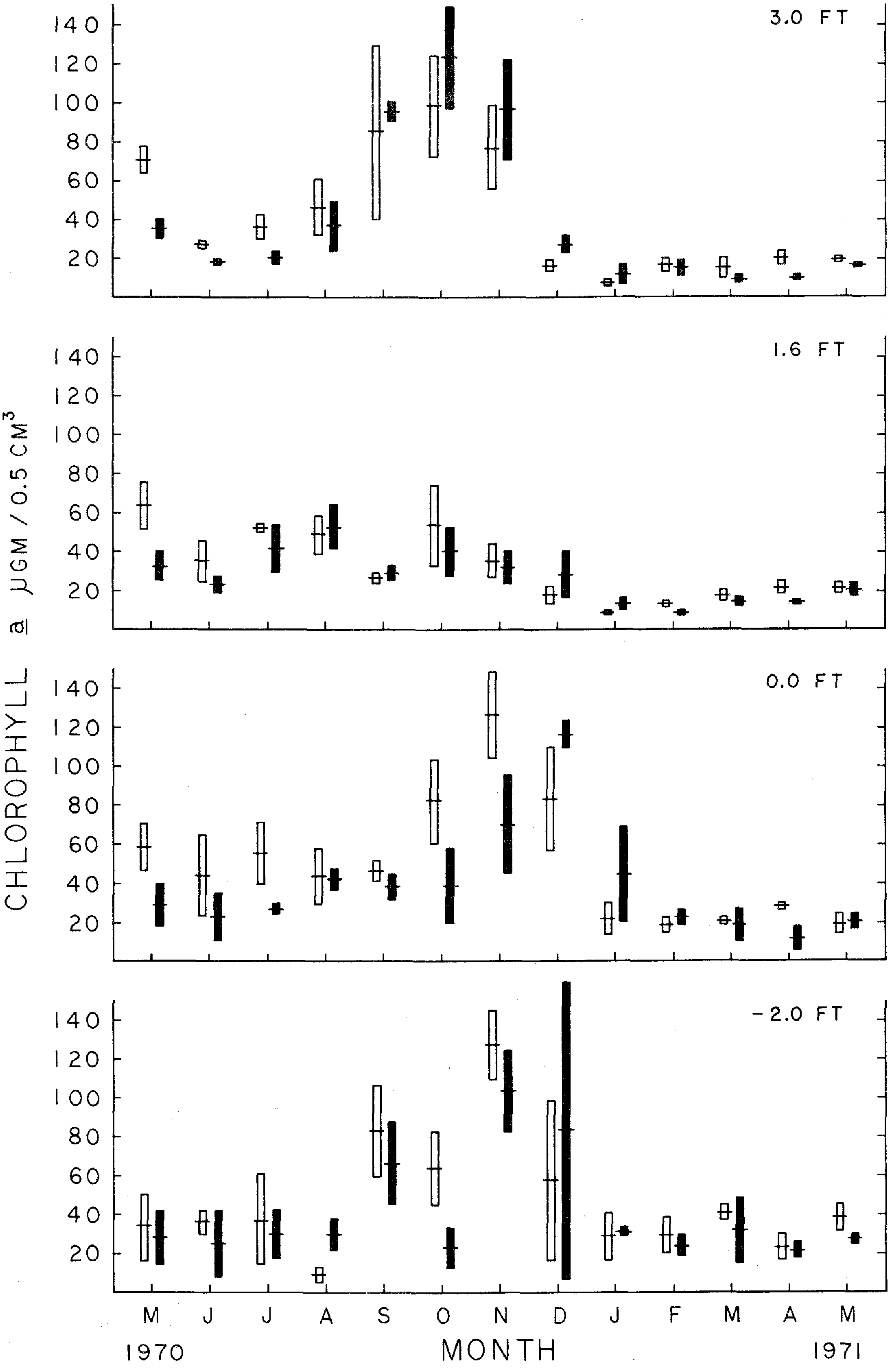
Photosynthetic Pigments

The photosynthetic pigments chlorophyll a, b, c and total carotenoids were compared at four tidal elevations, two depths in the sediment, and at different seasons.

Chlorophyll a

Chlorophyll a was present throughout the year with slightly higher concentrations in the lower intertidal (Figure 25). High concentrations near 100 μgm/0.5 cm^3 of sediment, were evident during the fall and early winter (September through December) at each station except for the 1.6 foot level. Summer, fall, and winter samples at all stations were more variable than spring samples. The first 0.5 cm of sediment tended toward higher concentrations of chlorophyll a than the second 0.5 cm from summer through fall at stations above -2.0 feet, and the reverse occurred during the spring.

Figure 25. Concentration of chlorophyll a in sediment at four intertidal elevations along the transect as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


3.0 FT
1.6 FT
0.0 FT
- 2.0 FT
140
120
100
80
60
40
20
CHLOROPHYLL a μGM / 0.5 CM³
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
MONTH
1971

Chlorophyll b

Chlorophyll b was present only during the period from September through January (Figure 26). The first 0.5 cm in depth appeared to have a larger concentration than the second 0.5 cm during September and October, but smaller during December and January. High surface values near 20 μgm/0.5 cm^3 occurred during November in the two lower stations.

Chlorophyll c

Chlorophyll c was not measurably present every month at all stations (Figure 27). Although present in the lower intertidal at -2.0 feet, chlorophyll c was absent from January through May at the other stations. Concentrations were generally less than 15 μgm/0.5 cm^3 at all tide levels. Larger concentrations were found at the 3.0 foot elevation during September and October, reaching 30 μgm/0.5 cm^3. Chlorophyll c was frequently more concentrated in the first 0.5 cm of sediment and more variable there than in the second 0.5 cm.

Total Carotenoids

The concentration of total carotenoids was generally less than 30 μgm/0.5 cm^3. Higher concentrations, near 50 μgm/0.5 cm^3, were

Figure 26. Concentration of chlorophyll b in the sediment at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.

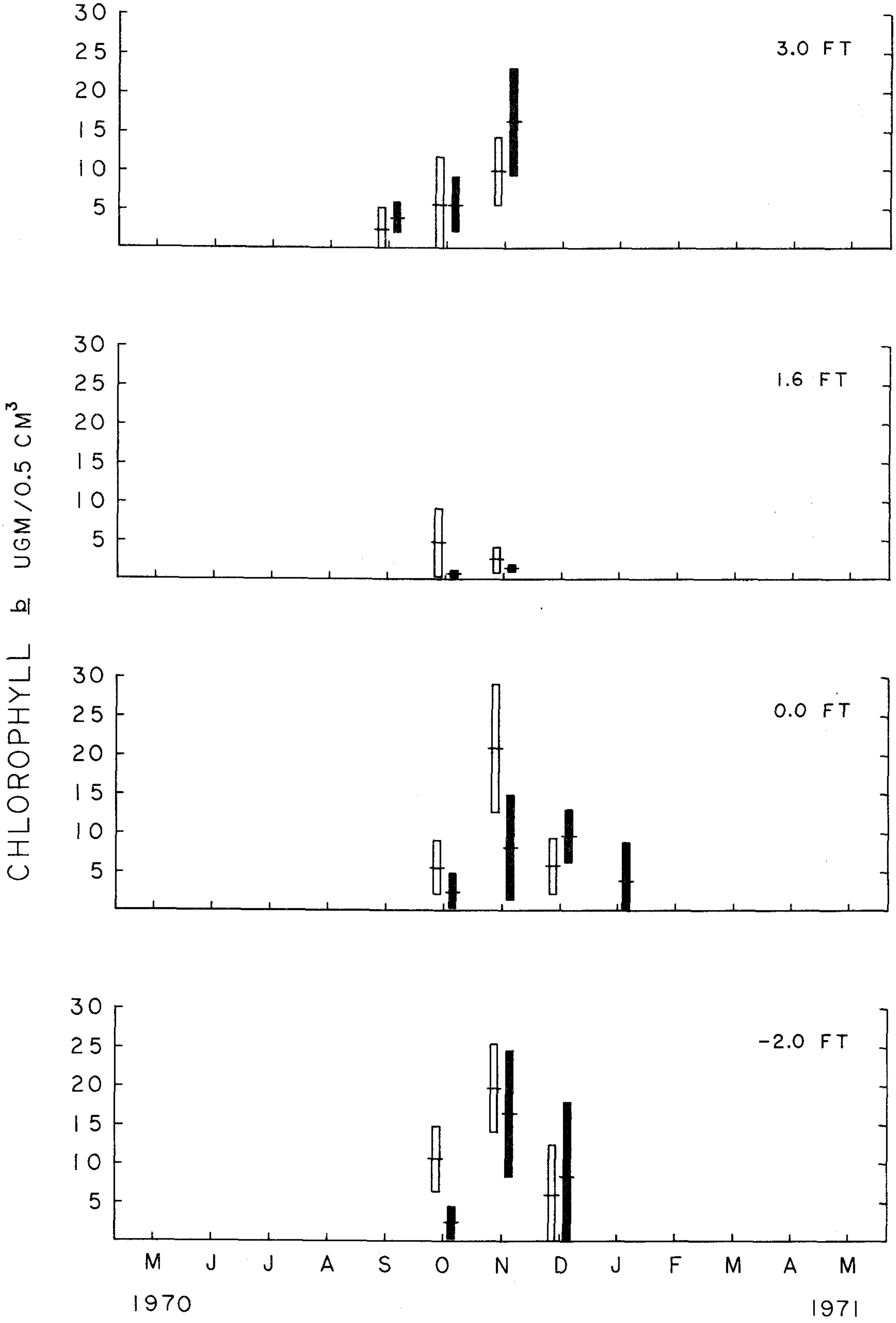
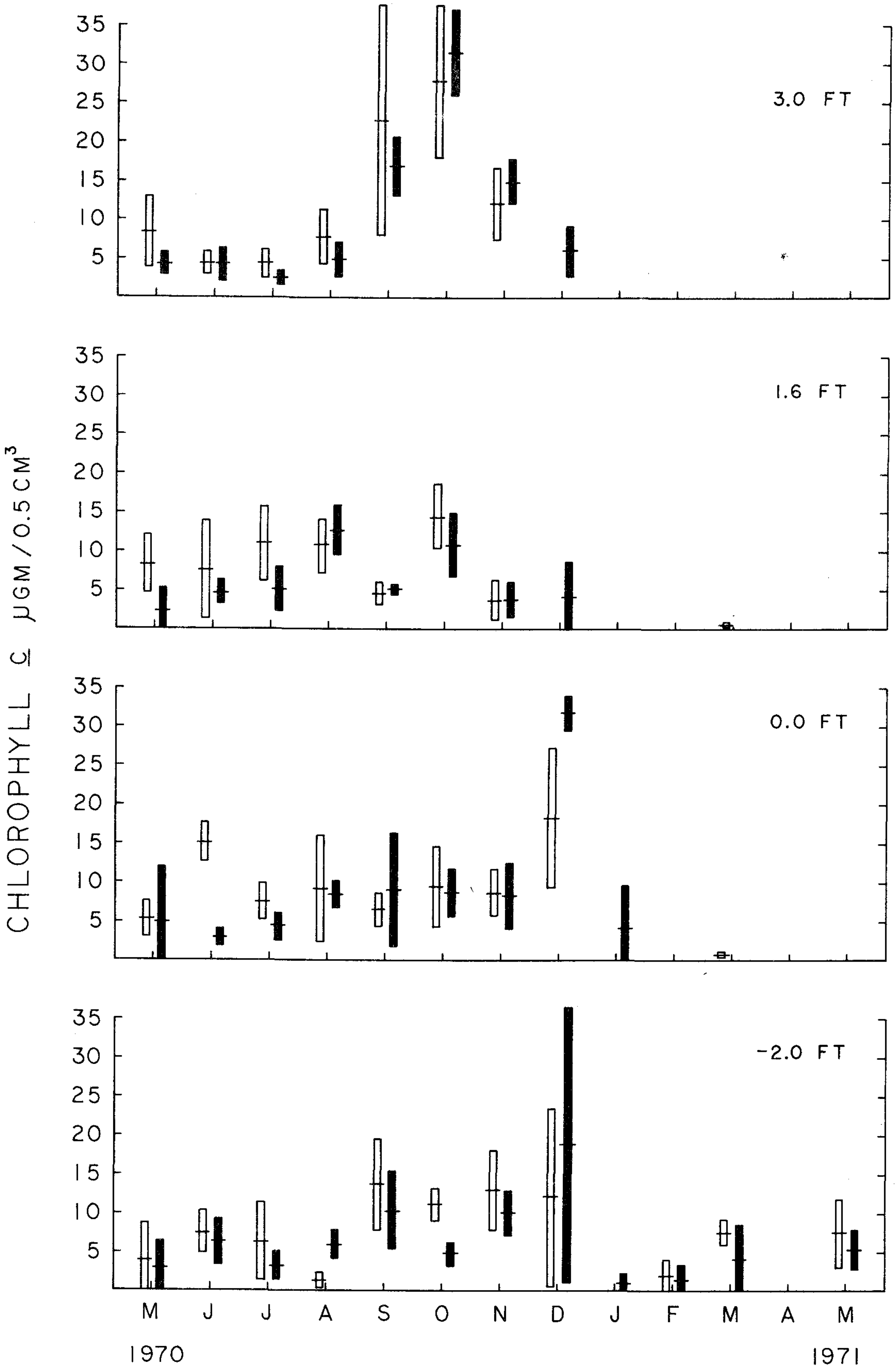

3.0 FT
1.6 FT
0.0 FT
-2.0 FT
30
25
20
15
10
5
CHLOROPHYLL b UGM/0.5 CM^3
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 27. Concentration of chlorophyll c in the sediment at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


3.0 FT
1.6 FT
0.0 FT
-2.0 FT
35
30
25
20
15
10
5
CHLOROPHYLL c μGM/0.5 CM^3
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

found from September through December at all levels except at 1.6 feet (Figure 28). Spring concentrations were generally the least variable, while fall and winter months showed the most variability. The first 0.5 cm commonly contained more carotenoids than the second 0.5 cm in the highest station with increasing homogeneity towards the lower intertidal.

Organics

The total organic content at the four stations examined was similar from one season to the next (10 mgm/Glucose/gm sediment), with the greatest uniformity at 1.6 feet (Figure 29). Large deviations (50 mgm/Glucose/gm sediment) occurred from October to January at -2.0 and 0.0 feet and a slight increase was found from September through November at 3.0 feet. During this period, in October the organic concentration was initially greater at the surface in the lower intertidal. By December the amount in the second 0.5 cm had exceeded the surface concentration. The most variable period was winter.

Sulfides

Variation in total free sulfide content of the sediment was examined with depth at each station. The sulfide concentration increased with lower tidal elevation and with depth within stations (Figures 30 and 31).

Figure 28. Total carotenoid content in the sediment at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.

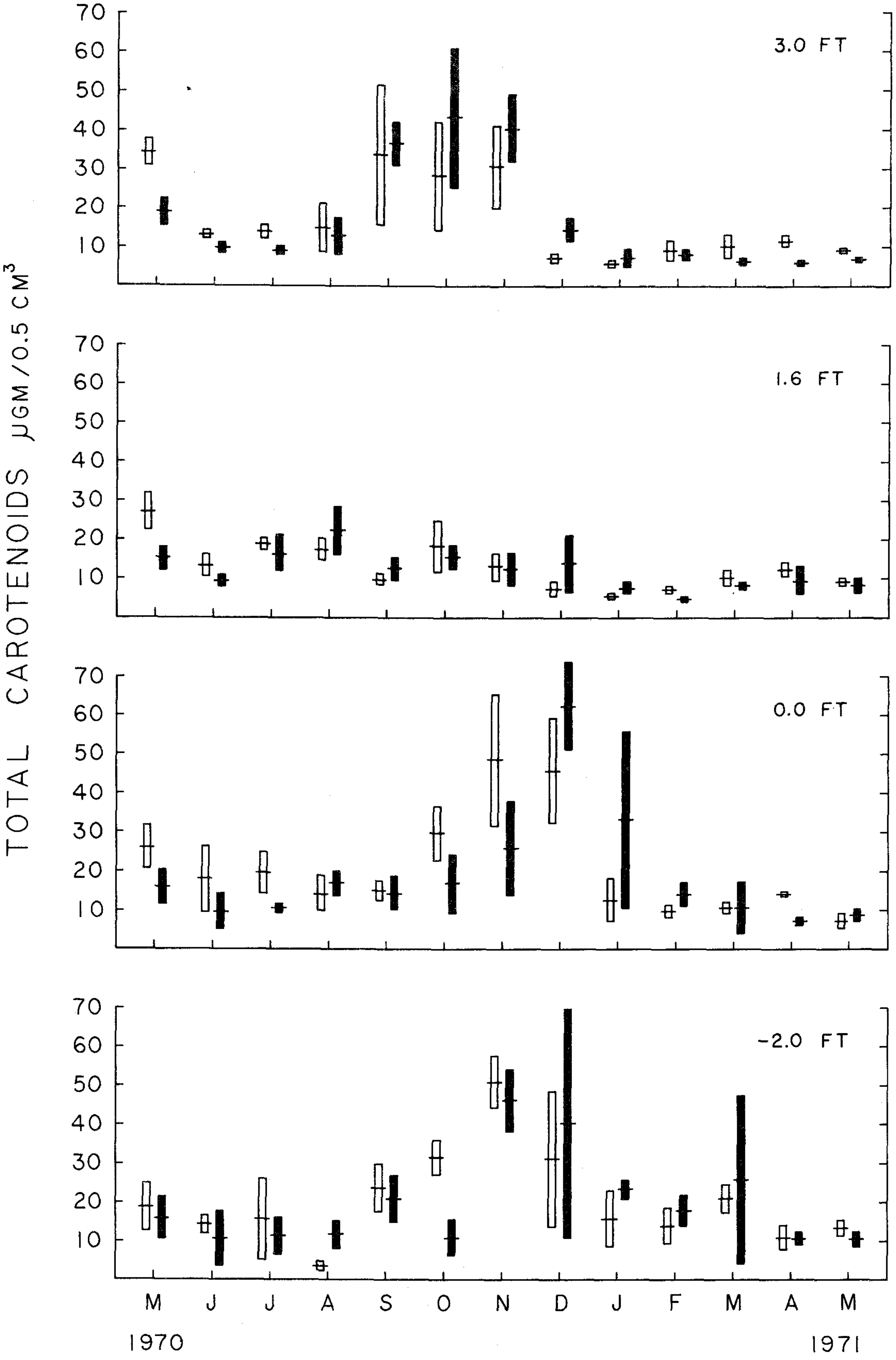

TOTAL CAROTENOIDS μGM/0.5 CM³
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
70
60
50
40
30
20
10
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 29. Total organic carbon in the sediment at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.

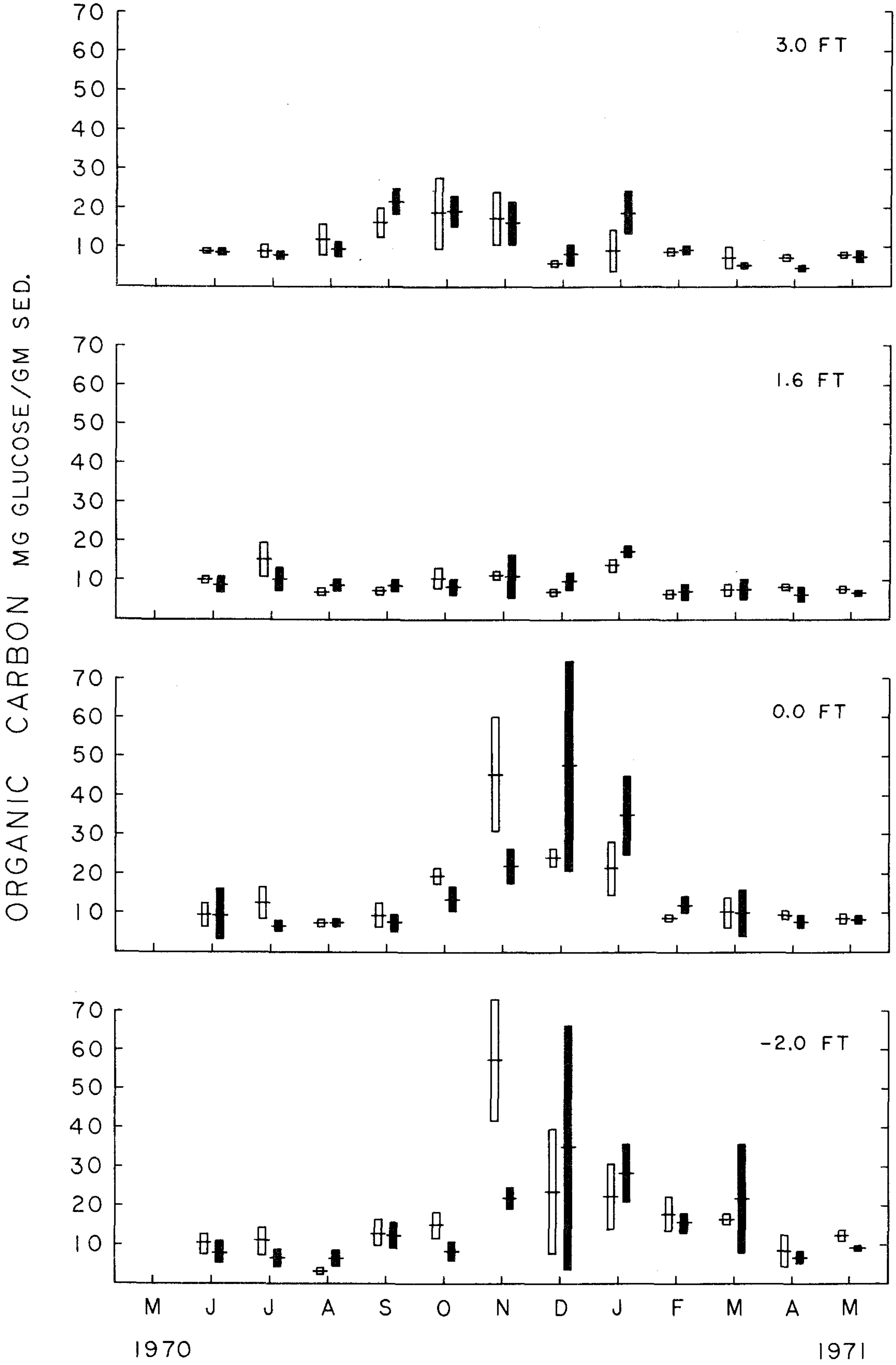

ORGANIC CARBON MG GLUCOSE/GM SED.
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
70
60
50
40
30
20
10
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 30. Total free sulfide content in the sediment at two intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.

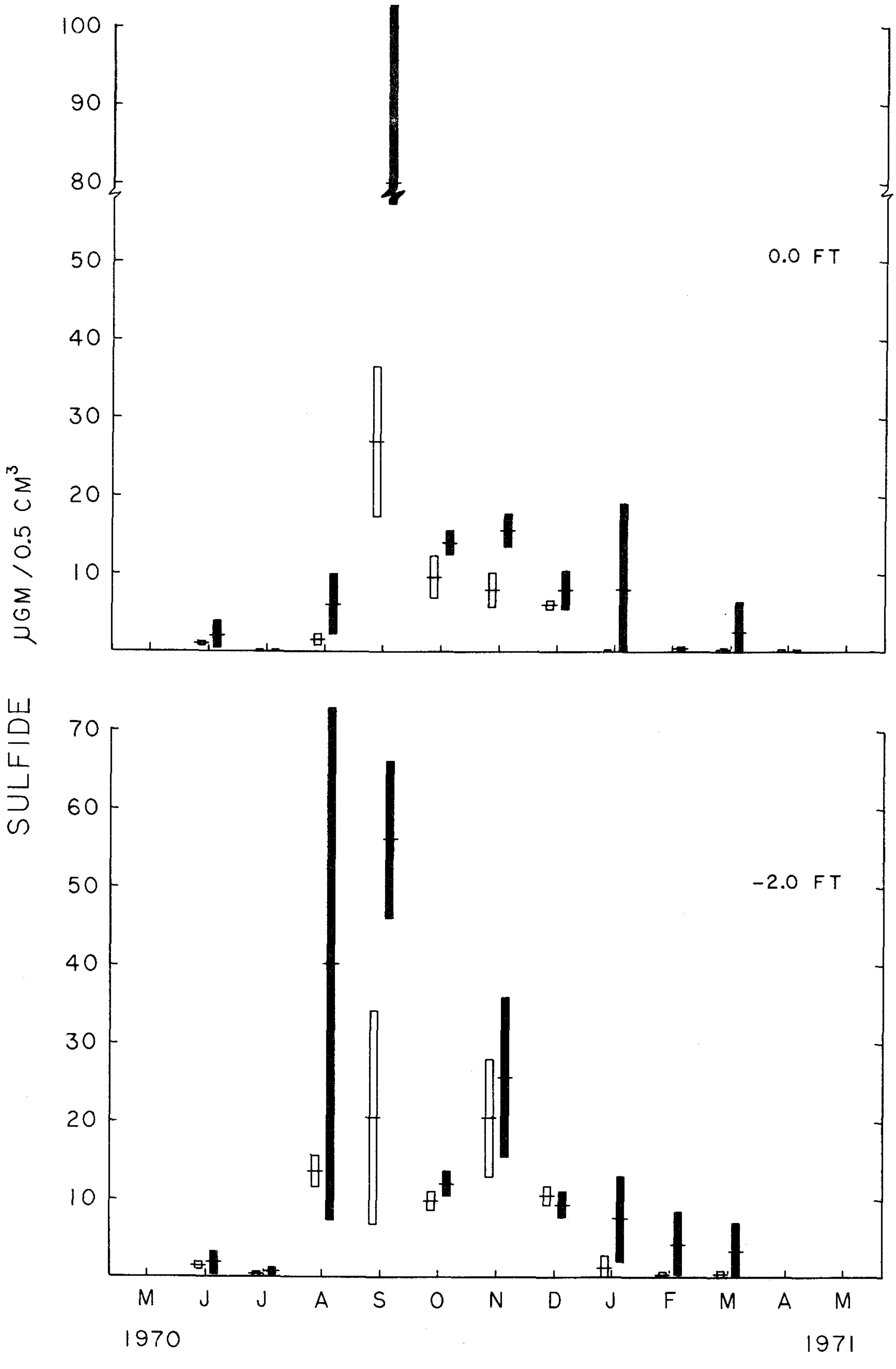
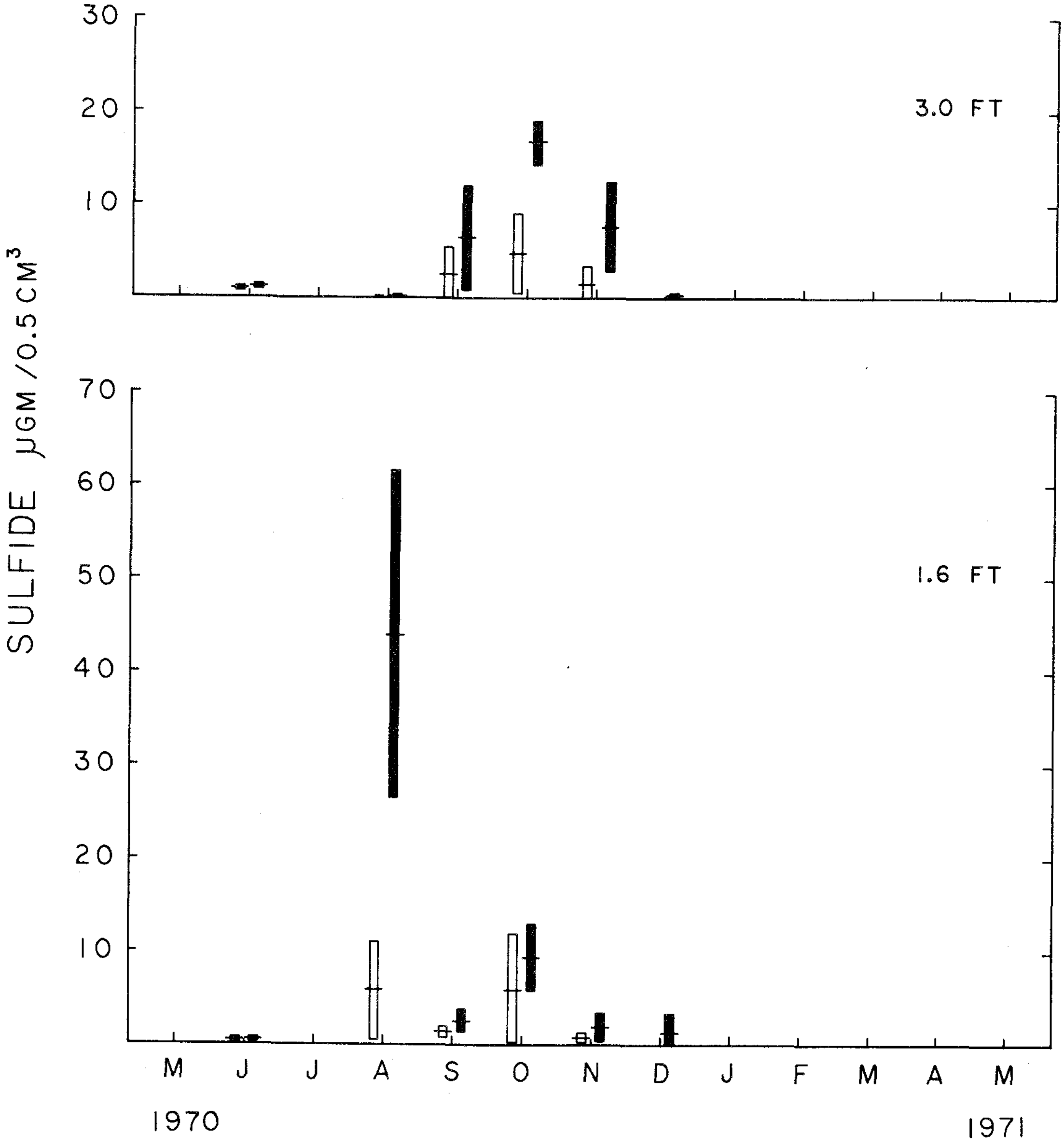

SULFIDE
μGM / 0.5 CM³
100
90
80
50
40
30
20
10
0.0 FT
70
60
50
40
30
20
10
-2.0 FT
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 31. Total free sulfide content in the sediment at two intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm (white) and 0.5-1.0 cm (black) in depth.


SULFIDE µGM/0.5 CM^3
3.0 FT
30
20
10
1.6 FT
70
60
50
40
30
20
10
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Sulfide was found nearly every month in the lower intertidal, but only during August through November in the upper stations. This period was also the time of maximal concentration for all elevations. Surface values at 1.6 and 3.0 feet never exceeded 10 μgm S/0.5 cm^3, while surface amounts as large as 20 μgm S/0.5 cm^3 were common at -2.0 and 0.0 feet. Concentrations as high as 40 to 60 μgm S/0.5 cm^3 were found in the second 0.5 cm from August through Stpember at the lower stations. Note that 2 μgm S/0.5 cm^3 equals 5 μgm S/ml.

Hydrogen Ion Concentration

The average pH of the interstitial water near the surface was compared to low low tide estuarine water (Figure 32). The interstitial water at all stations was generally less alkaline than the estuary. The lower stations were similar to the upper stations during the summer and fall, but were more acidic during the winter, especially at -2.0 feet.

Oxygen

The oxygen concentration of the interstitial water was converted, using standard tables (Gilbert, Pawley, and Park, 1968), to percent of saturation at observed interstitial temperature and salinity conditions. The average percentage of oxygen was then compared to the oxygen content (percent saturation) of the estuarine surface water at

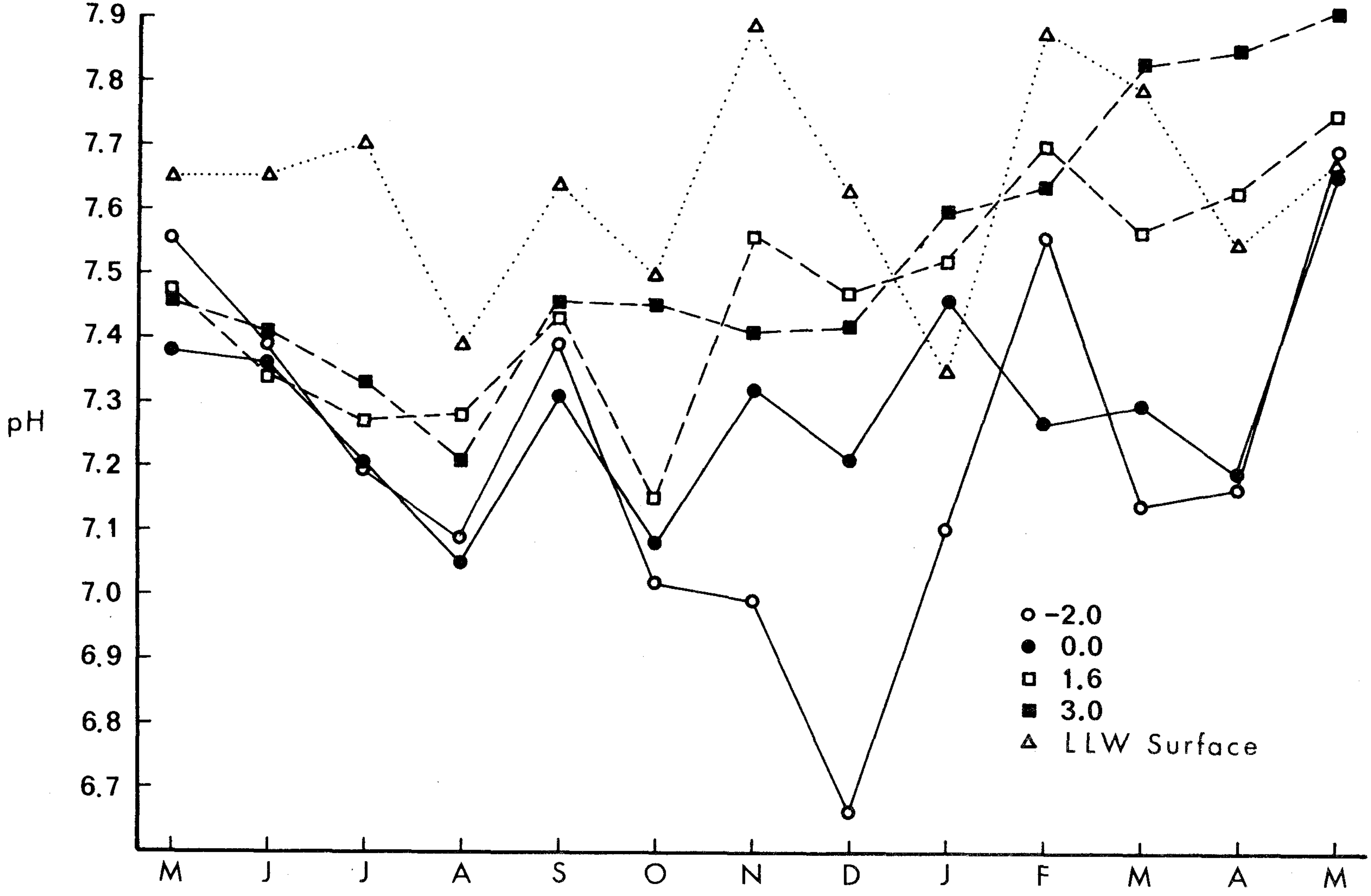


Figure 32. Monthly pH measurements of the surface interstitial pore water at four intertidal elevations along the transect and of the estuary surface water at the corresponding lower low tide. Elevations in feet.

low low tide and at the surface and bottom during the preceding high high tide (Figure 33). High high tide measurements were not taken during the summer. The oxygen content of the near surface interstitial was generally less than 60% of saturation, but became larger from March through May. The lower stations were usually less saturated than the upper stations.

The estuarine water normally contained a greater percentage of oxygen than interstitial water. Low low tide water often contained less than high high surface or bottom water.

The lowest percentages of oxygen for interstitial water were recorded during fall and winter. The spring rise in sediment oxygen lagged behind the rise in low low tide water by several months.

Chlorinity

The interstitial salinity was determined on the basis of chlorinity and converted to salinity for comparative purposes. The salinity ranged between 15 and 35‰ during the year, and the pattern of change at each station was remarkably similar (Figure 34). The highest salinities occurred during the summer (June through September). Salinity decreased thereafter to reach the lowest point in January. During the rainy season the upper stations were more variable than the lower stations, but were otherwise similar and homogeneous.

The salinity of the interstitial water was compared to the salinity

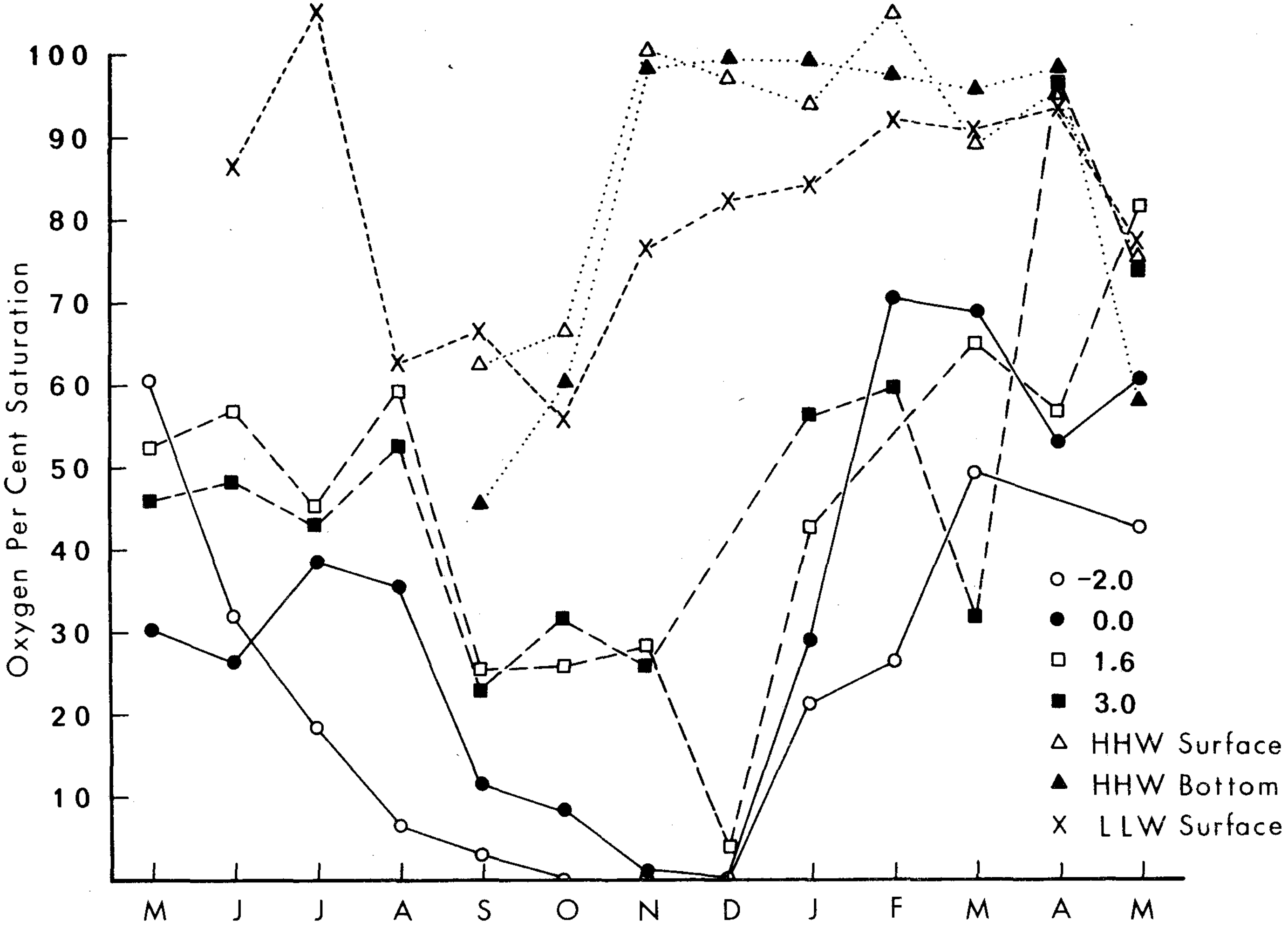
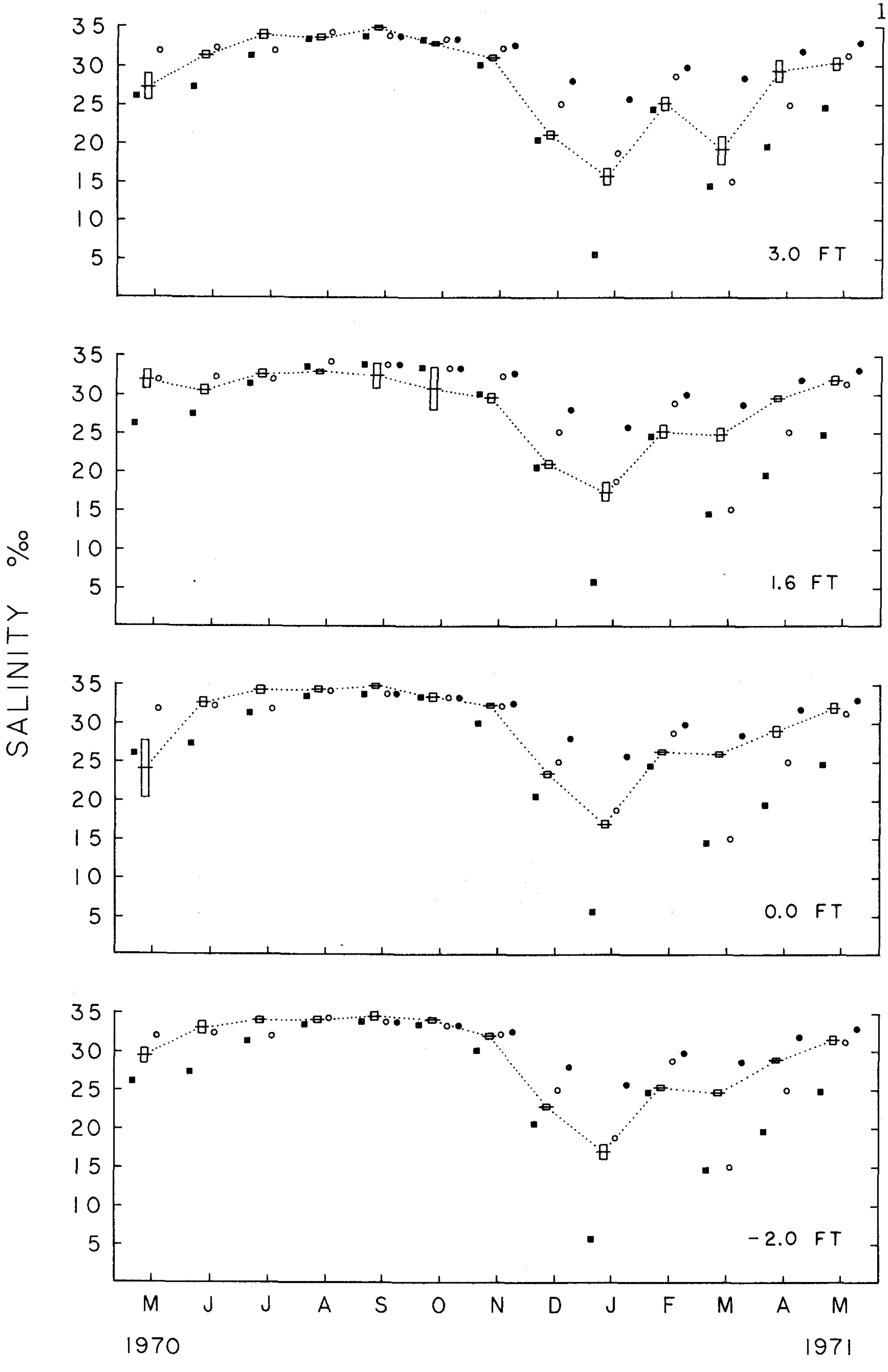


Figure 33. Percentage of oxygen saturation of the surface interstitial pore water at four intertidal elevations along the transect, of the estuary surface at lower low water (LLW), and the estuary surface and bottom at higher high water (HHW). Elevation in feet.

Figure 34. Salinity of the surface interstitial pore water at four elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle), the salinity of the estuary surface at LLW (black square) and surface (blank circle) and bottom (black circle) at HHW.

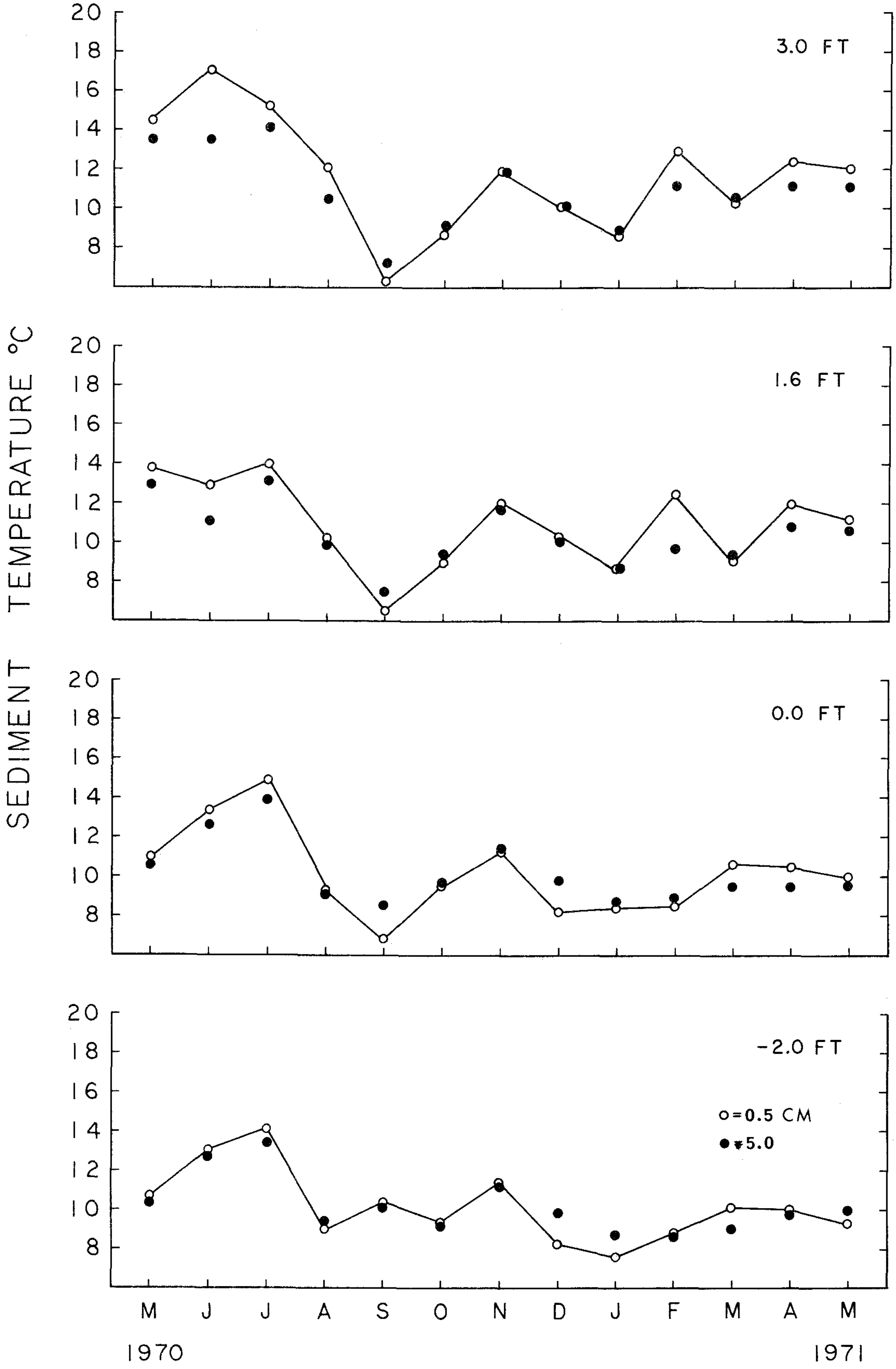

SALINITY ‰
35
30
25
20
15
10
5
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

of the surface and bottom of the estuary measured during the high high tide preceding the low low collecting tide and to the salinity of the estuarine surface water measured during the low low tide collection period (Figure 34). The salinities of the surface and bottom water in the estuary during the preceding high high tide were nearly identical and quite similar to the interstitial values during the summer and fall. Marked differences between surface and bottom measurements occurred from December through April, when the surface water was always less saline than the bottom water. The salinity of the surface water at low low tide off the transect was always less than that of the surface at high high tide, slightly less than that of interstitial water during the summer and very much less (5 to 10‰) than that during the winter and spring. The interstitial water was always less saline than that of the high high bottom water during the period November through April.

Sediment Temperature

The temperature of the sediment at 0.5 and 5.0 cm was recorded in each core prior to sampling, producing six temperature measurements per tidal station. The average temperature at the two depths is given in Figure 35. Although, these data are instantaneous, the intra- and interstation differences followed expected seasonal trends. The upper stations showed the largest differences with depth and season. The instantaneous standard deviation did not exceed 1.6° C and

Figure 35. Instantaneous sediment temperature at 0.5 and 5.0 cm in depth at four elevations along the transect.


SEDIMENT TEMPERATURE °C
3.0 FT
1.6 FT
0.0 FT
-2.0 FT
○=0.5 CM
●=5.0
20
18
16
14
12
10
8
M
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

was usually less than 0.5°C.

Macrophytes

The seasonal change in biomass of the macrophytes *Zostera marina*, *Enteromorpha tubulosa*, *E. intestinalis*, and *Ulva angusta* (?) was studied at the four routinely investigated tidal stations. Large changes in dry weight of biomass were measured (Figure 36). During the summer and fall biomass was maximal, as the dry weight approached 100 gm/30 cm^2, and it was minimal during winter. Maximal biomass was achieved several months earlier during the second summer. The upper stations at 3.0 and 1.6 feet were devoid of macrophytic material by January, yet young *Zostera marina*, 1 to 2 cm in length, were present a month later. The *Zostera* at the lower stations (-2.0 and 0.0 feet) was cropped severely by the black Brant (*Branta nigricans*) during the winter, allowing sediment erosion to proceed.

Two beds of *Zostera* were distinguished on the basis of size of plants and permanence. The permanent mature bed occurred below 0.0 feet, while a second seasonally transitory bed occurred between 3.0 and 0.0 feet.

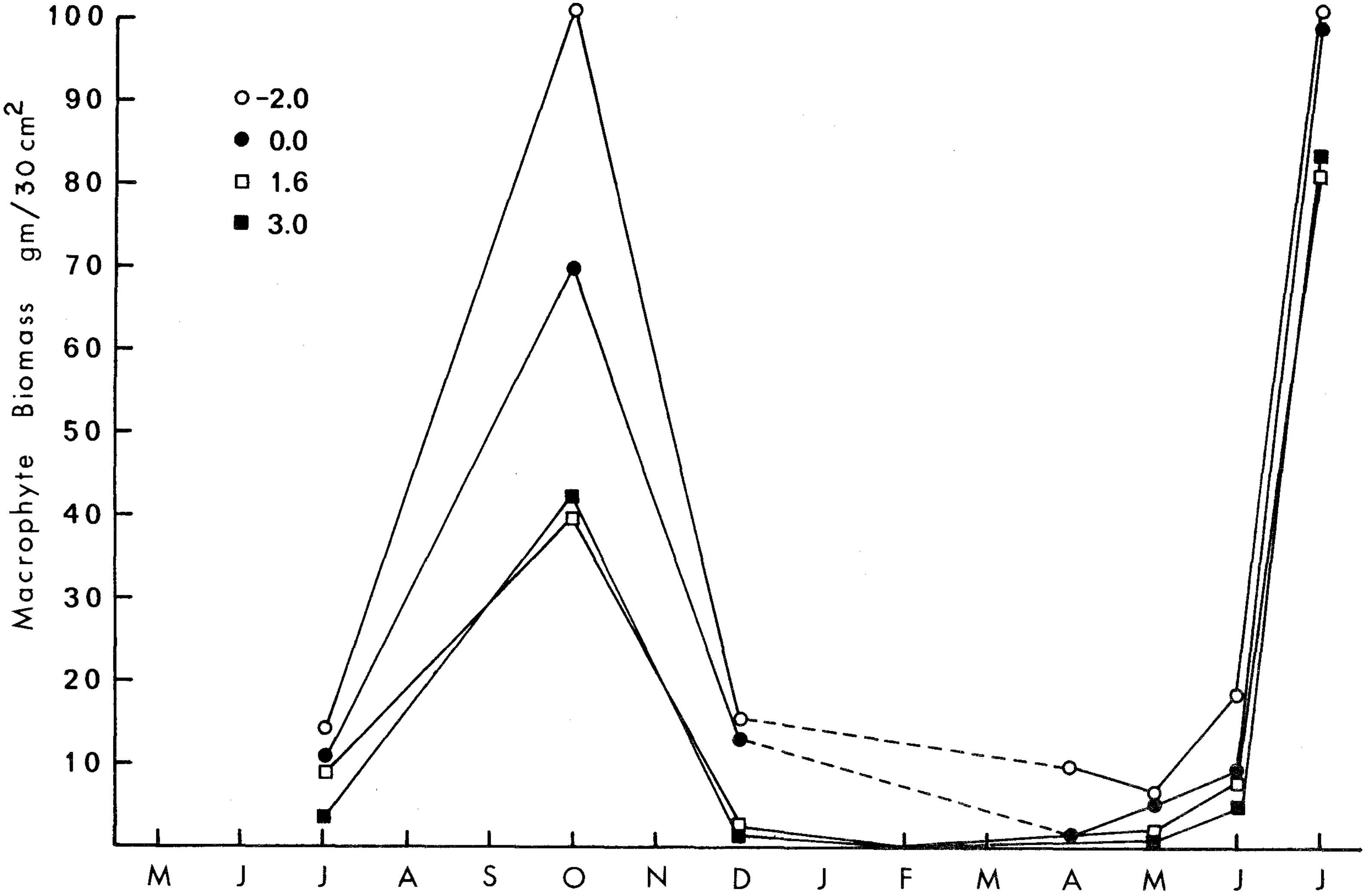


Figure 36. Seasonal change in biomass of macrophytes at four intertidal elevations along the transect.

Temperature-Salinity Tolerance Experiment

Tolerance of Diatomovora amoena to 25 different temperature-salinity combinations was studied in the laboratory. Tolerance was expressed in time as percent survival (Figures 37 and 38). Survival was generally greatest at moderate temperatures (10-18°C) and higher salinities (15-30‰).

The 50% survival level exceeded 12 hours at 15 to 30‰ from 5°C to 20°C, and for 11 hours at 25°C. Survival at 5‰ and 10‰ was less at all temperatures. Fifty percent survival at 5‰ was limited to about 5 hours between 5°C and 15°C and to about 3 hours at temperatures up to 25°C. The duration of survival (50%) at 10‰ was longer at 5°C (15 hours) and 10°C (24 hours) than at temperatures up to 25°C (6-9 hours).

High salinity (15-30‰) increased survival at temperature extremes (5°C and 25°C), while low temperatures (5°C-10°C) increased survival at low salinities (5-10‰).

These data were subjected to a multiple regression analysis and to a test of significance in order to evaluate the linear and quadratic effects of temperature (Tables 3, 4, and 5). The analysis indicated that the linear and quadratic effects of salinity contributed significantly to the variability in survival after 6 hours. The salinity polynomial,

$$Y_{\%\ \text{survival}} = -52.45 + 14.98(S) - 0.34(S^2),$$

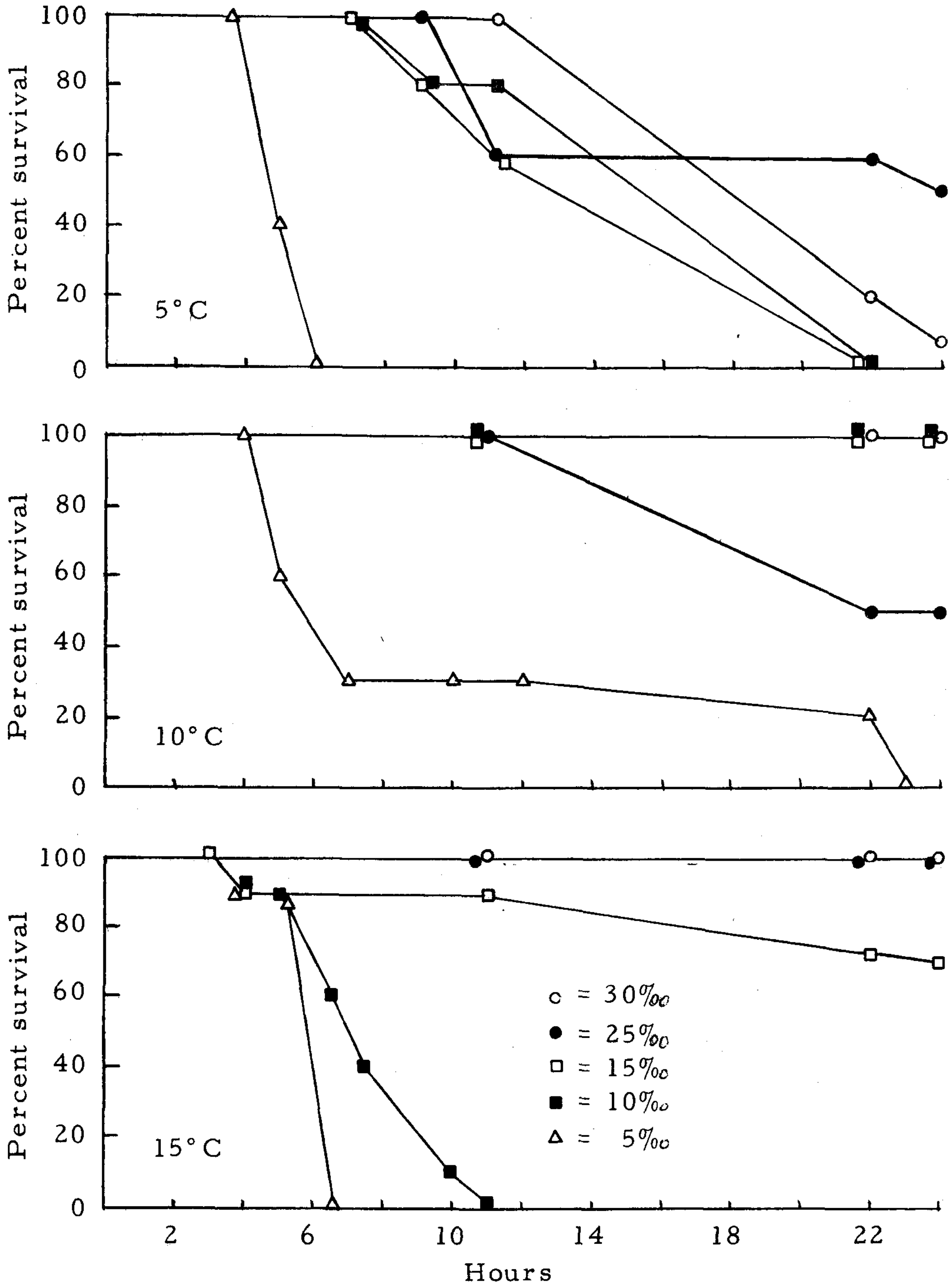


Figure 37. Percent survival of D. amoena at different temperature and salinity combinations.

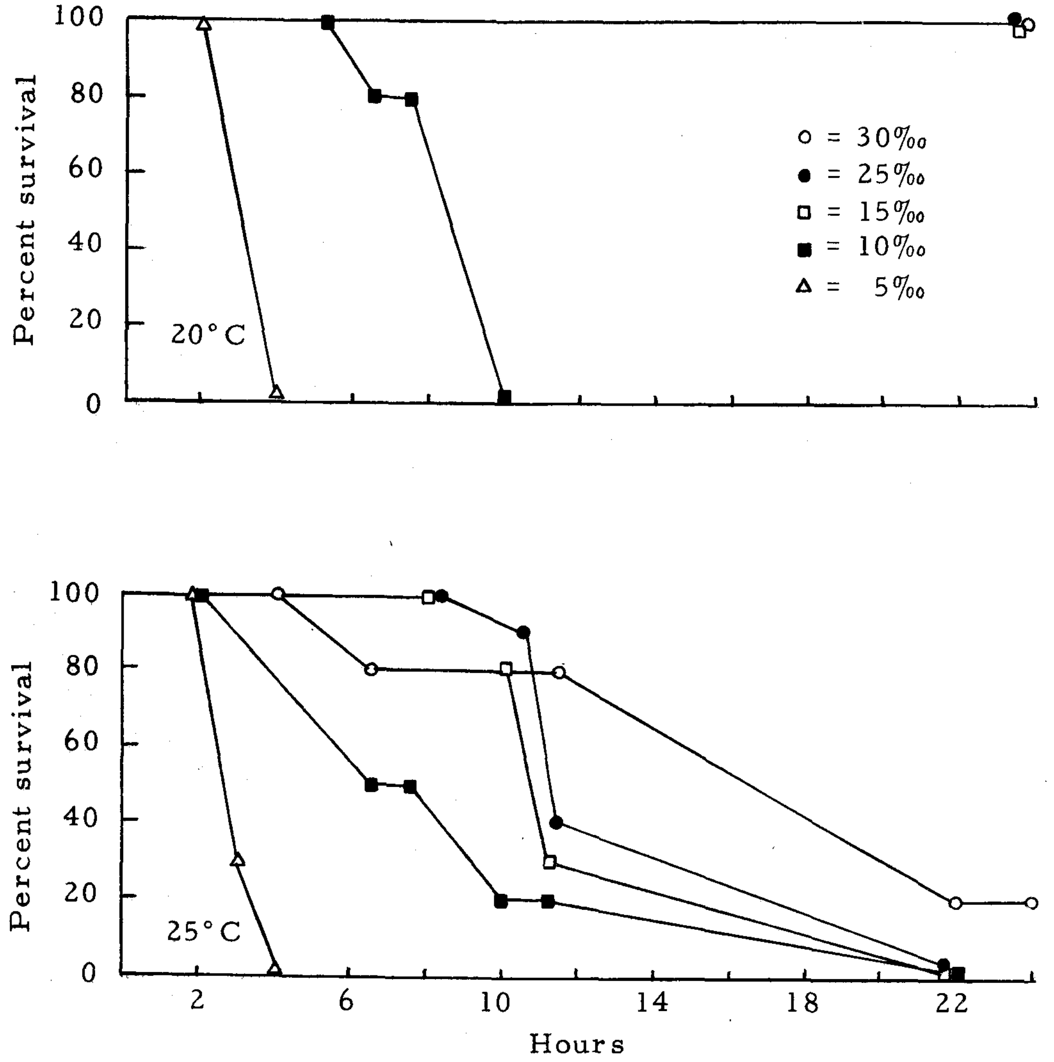


Figure 38. Percentage survival of D. amoena at different temperature and salinity combinations.

Table 3. Statistical analysis of survival of *D. amoena* after 6 hours of exposure to 25 temperature-salinity combinations.

Variable	t-Statistic (19 d.f.)	Significance Level
O	-1.39	n.s.
T	-0.40	n.s.
T^2	7.34	0.01
S	-0.40	n.s.
S^2	-6.78	0.01
T x S	1.31	n.s.

Table 4. Statistical analysis of survival of *D. amoena* after 12 hours of exposure to 25 temperature-salinity combinations.

Variable	t-Statistic (19 d.f.)	Significance Level
O	-0.91	n.s.
T	0.96	n.s.
T^2	2.61	0.05
S	-1.71	0.10
S^2	-2.06	0.05
T x S	0.70	n.s.

Table 5. Statistical analysis of survival of *D. amoena* after 24 hours of exposure to 25 temperature-salinity combinations.

Variable	t-Statistic (19 d.f.)	Significance Level
O	-2.75	0.05
T	3.31	0.01
T^2	2.15	0.01
S	-3.73	0.05
S^2	-1.73	n.s.
T x S	-0.04	n.s.

accounted for 84.7% of the variation. The entire polynomial,

$$Y_{\%\ \text{survival}} = -30.87 - 0.91(T) + 14.08(S) - 0.03(T^2) - 0.34(S^2) + 0.06\ (T \times S),$$

accounted for 88.0% of the variability, of which 3.25% was attributed to temperature.

Analysis of tolerance after 24 hours of exposure showed that the linear and quadratic effects of salinity and temperature contributed significantly to the observed variation and that there were no significant interaction effects. The complete salinity-temperature polynomial

$$Y_{\%\ \text{survival}} = -129.54 + 16.15(T) + 8.73(S) - 0.56(T^2) - 0.18(S^2) - 0.0\ (T \times S)$$

accounted for 59.9% of the observed variation.

The results of the survival data at 12 hours suggested that the time interval between 6 and 24 hours represented a period of transition from a salinity to a temperature dominated response as both the quadratic variables and the linear effects of temperature contributed significantly to variation. The complete salinity-temperature equation,

$$Y_{\%\ \text{survival}} = -35.24 + 3.85(T) + 8.70(S) - 0.21(T^2) - 0.18(S^2) + 0.05\ (T \times S)$$

accounted for 70.6% of the variation.

Initial mortality was primarily due to osmotic stress, while the effects of temperature were indirect, apparently cumulative and acted in concert with salinity. These results are illustrated in Figures 39 and 40. Estimates of survival beyond the ranges of 5-30‰ and 5-25°C should be regarded as predictions. The effect of low temperature in aiding survival at lower salinities, although not significant statistically, was evident in the 6 and 12 hour response surfaces, but was absent at 24 hours.

Sulfide Tolerance Experiment

Tolerance of *D. amoena* to sulfide was examined in the laboratory and the degree of tolerance was expressed as percent survival. Survival in sea water (25‰) at 15°C in concentrations of sulfide ranging from 0 to 45 mg/ml demonstrated limited tolerance to high sulfide concentrations (Figure 41).

At concentrations greater than 3.0 mg S/ml death was almost immediate, while at lower concentrations (1.5 to 0.5 mg S/ml) 50% mortality occurred after 3 to 7 hours exposure. Individuals maintained under the same nitrogen-sparged sea water conditions void of sulfide showed no mortality. The form of the LD-50 curve showed that survival was a non-linear function of sulfide concentration.

Survival at lower concentrations ranging from 0 to 0.10 mg S/ml

Figure 39. Response surface of percentage of survival of Diatomovora amoena at different temperature-salinity combinations after 6 and 12 hours of exposure.

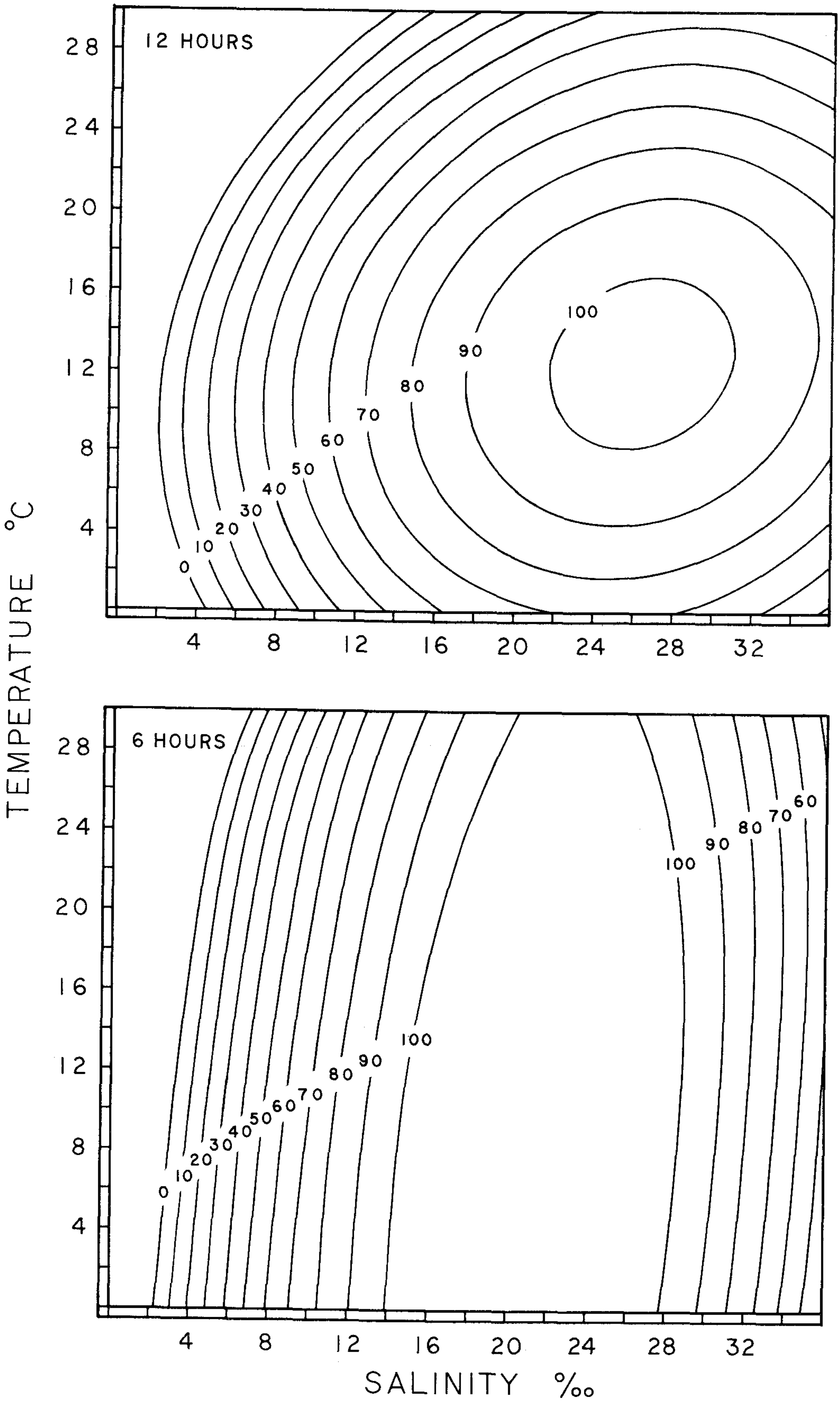
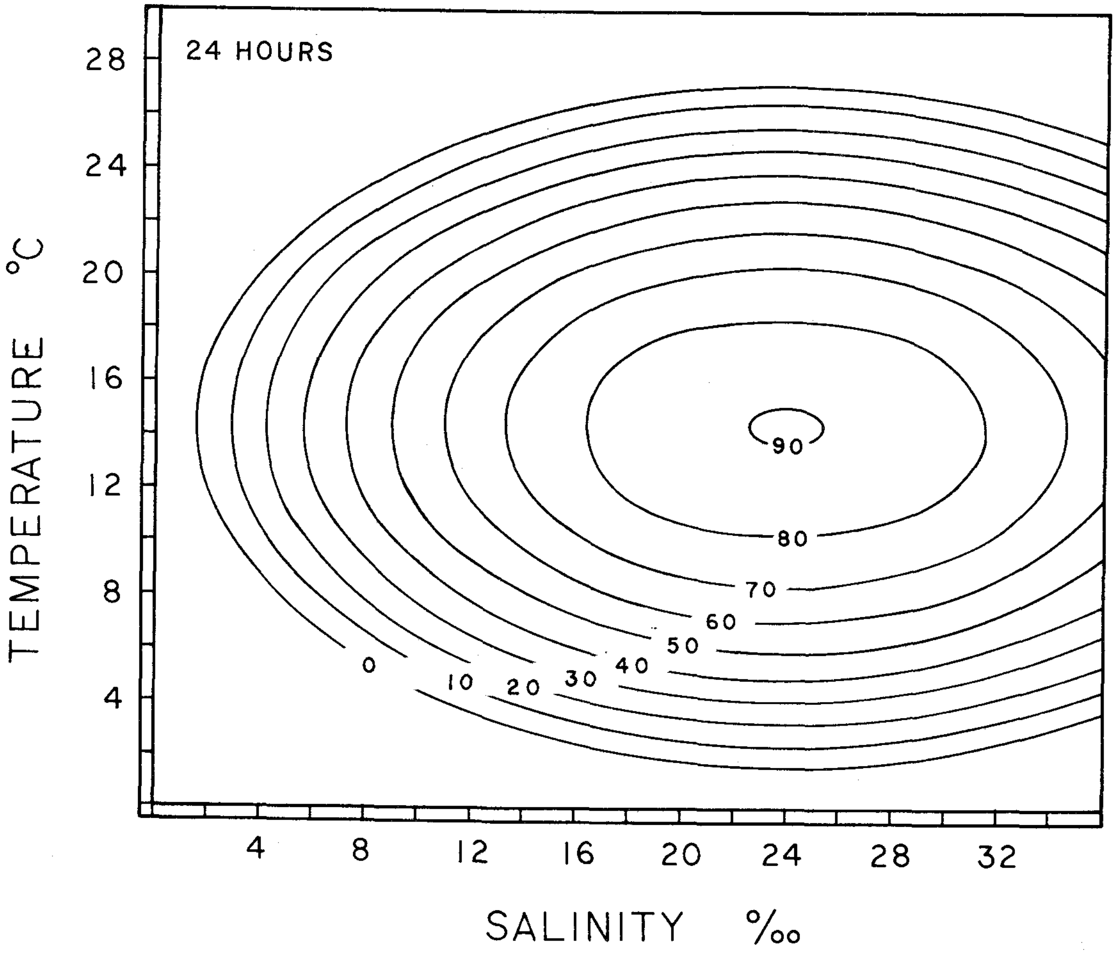

12 HOURS
0
10
20
30
40
50
60
70
80
90
100
28
24
20
16
12
8
4
4
8
12
16
20
24
28
32
6 HOURS
0
10
20
30
40
50
60
70
80
90
100
100
90
80
70
60
TEMPERATURE °C
SALINITY ‰

Figure 40. Response surface of percentage of survival of Diatomovora amoena at different temperature-salinity combinations after 24 hours of exposure.


24 HOURS
TEMPERATURE °C
28
24
20
16
12
8
4
SALINITY ‰
4
8
12
16
20
24
28
32
0
10
20
30
40
50
60
70
80
90

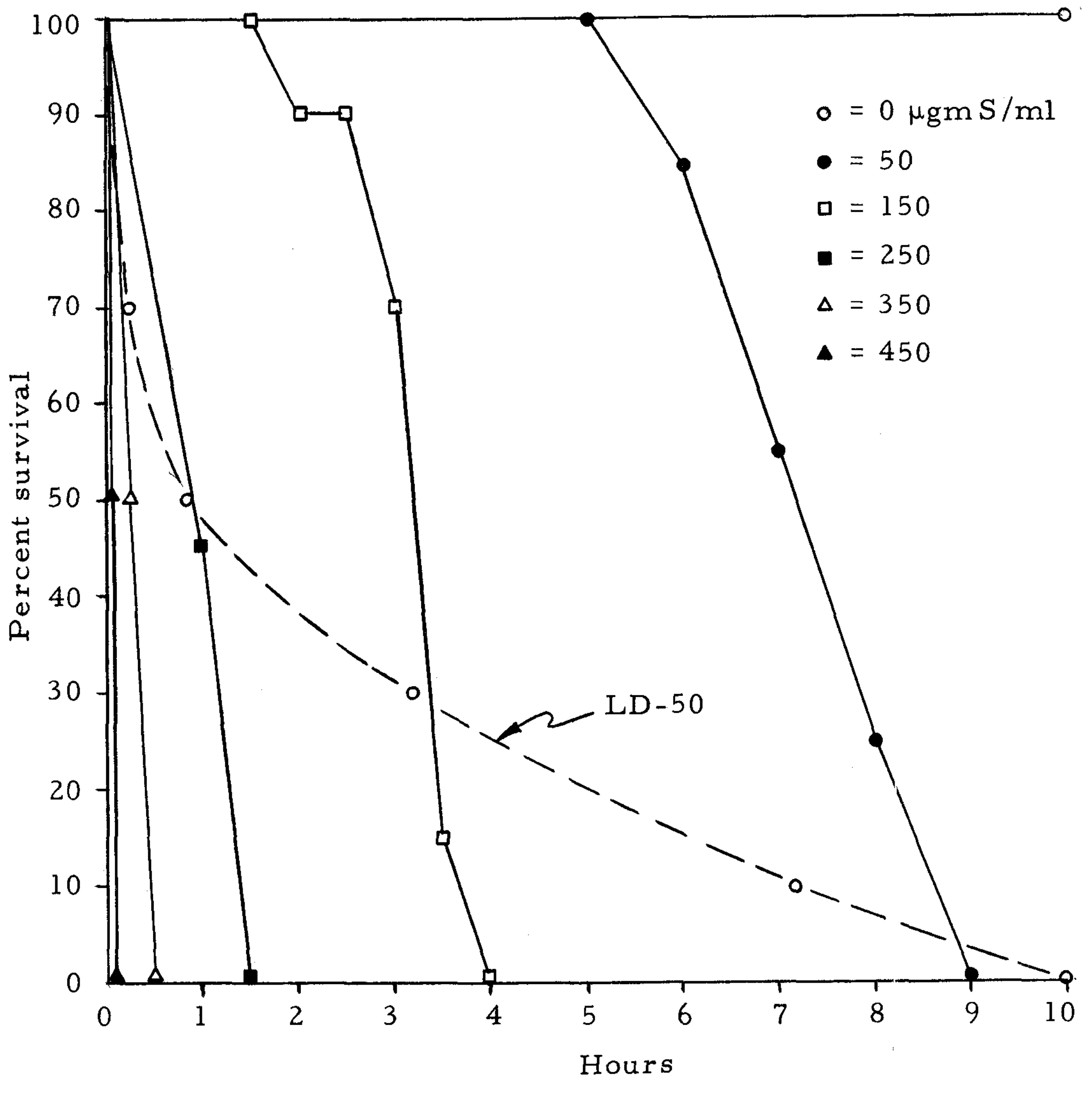


Figure 41. Percent survival of Diatomovora amoena upon exposure to varied concentrations of S at 10°C and 25‰, and calculated LD-50 curve for this data.

was examined at 10°C and 15°C (Figure 42). Survival was generally greater at 10°C, where the 50% survival level exceeded 5.5 hours at all concentrations. At 15°C, 50% survival at the higher concentrations occurred at 3 to 4 hours. At both temperatures survival at 0.0 and 0.01 mg S/ml was nearly 100% for 20 hours. Tolerance to low sulfide concentrations was found to increase with cooler temperatures.

The oxygen content was not observed to increase in any of the experimental flasks. The presence of sulfide reduced the oxygen concentration below the initial nitrogen sparged concentration; 38 mm Hg or 1.65 ml O_2/L to 10-30 mm Hg or 0.43 to 1.28 ml O_2/L in all flasks.

Animal Density

Initial sampling indicated that D. amoena was restricted to the lower littoral zone. Change in animal density was examined with station, depth, and month, and expressed as total number at each tidal level per 2 cm^3 (Figure 43).

The largest densities occurred from September through December and in May, when densities at the 1.6 and 3.0 foot stations usually exceeded those at the -2 and 0 foot stations. Additional samples taken at higher elevations (3.5 and 4.0 feet) during September, December, and June and were void of worms. During October and November specimens were obtained from the overlying algal mat at the two lower stations. Animals were still present in the sediment

Figure 42. Percent survival of Diatomovora amoena upon exposure to varied concentrations of S at 10 and 15°C and 25‰.

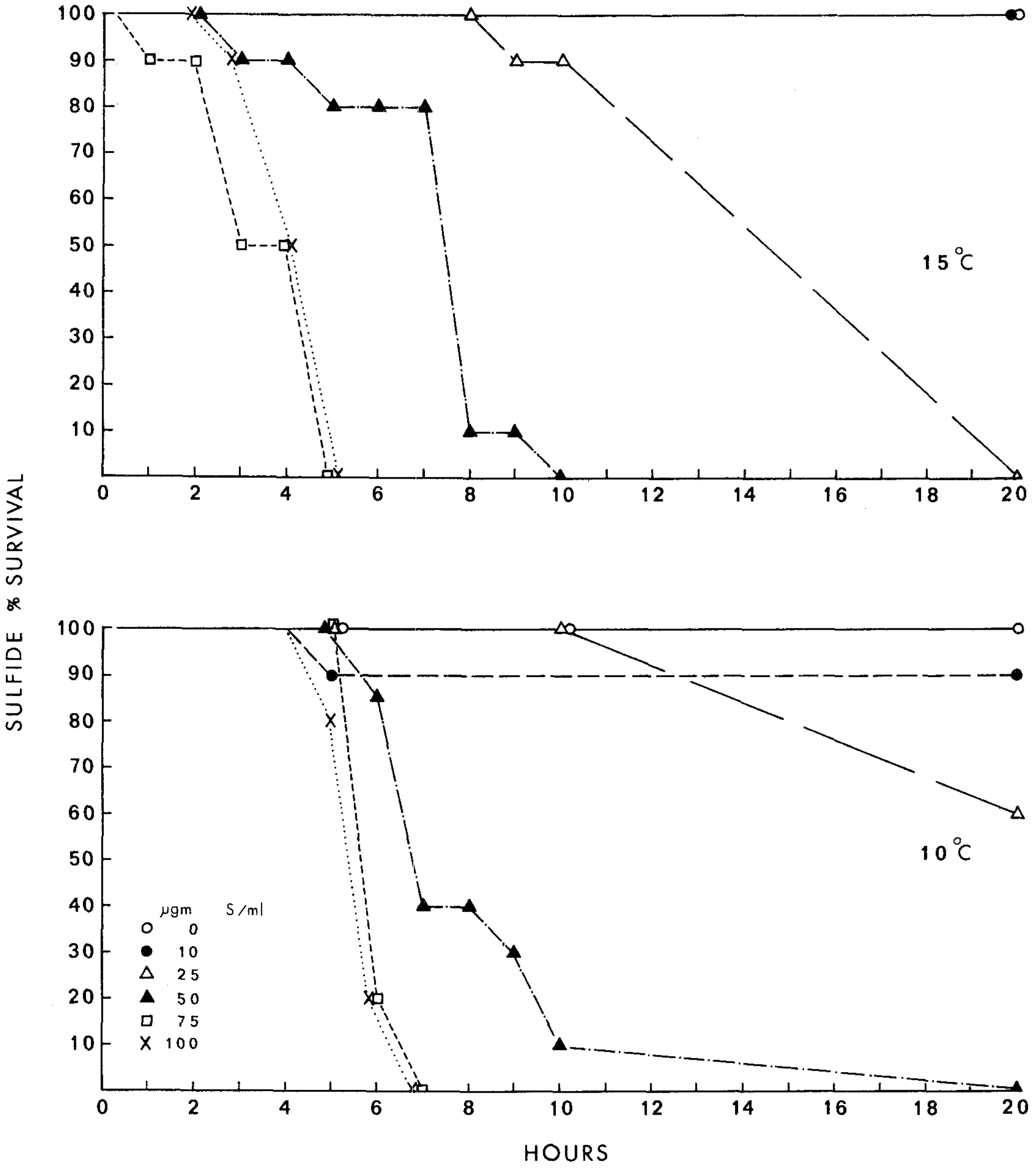
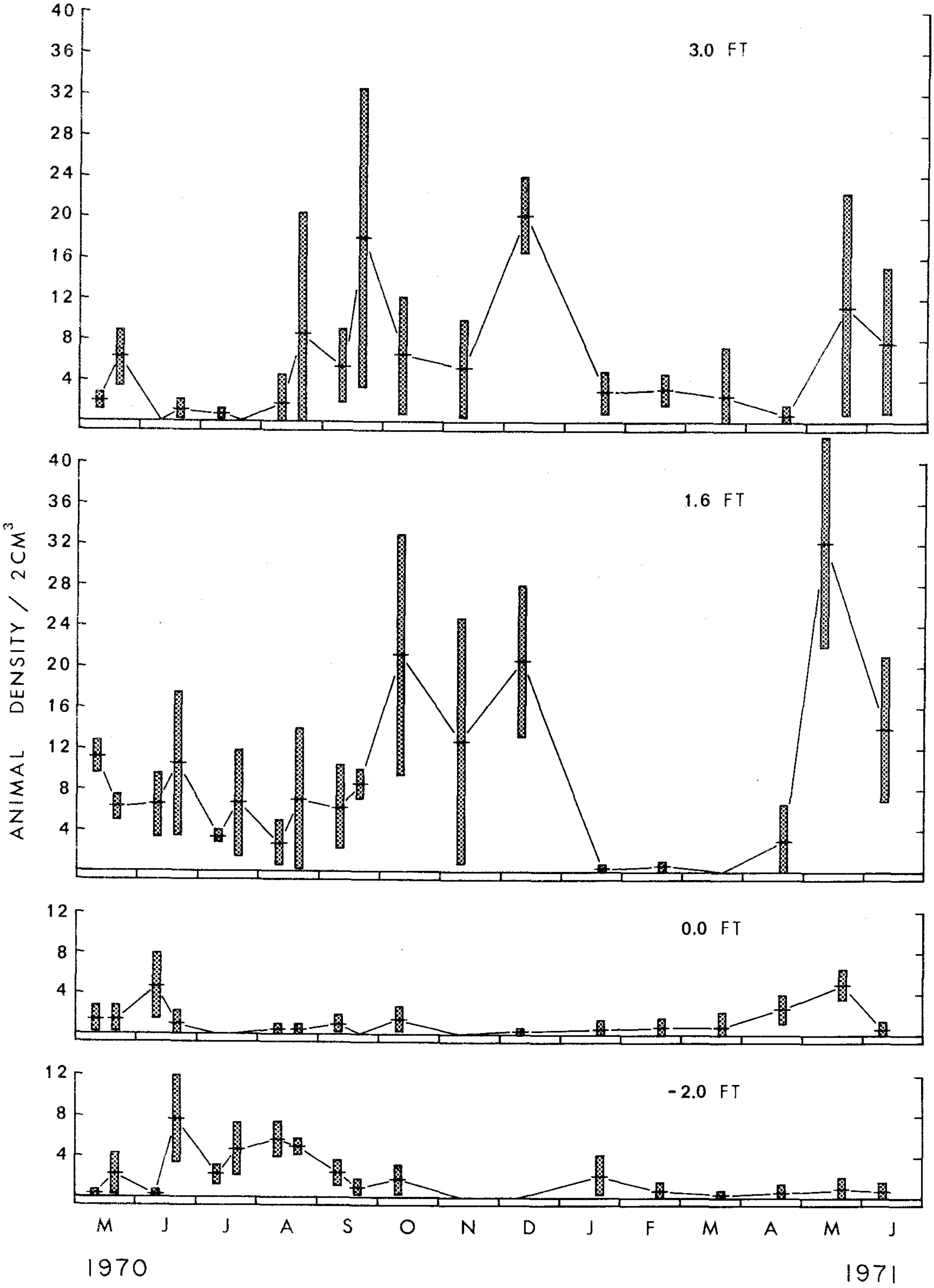

SULFIDE % SURVIVAL
15 °C
10 °C
100
90
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
HOURS
μgm S/ml
○ 0
● 10
△ 25
▲ 50
□ 75
X 100

Figure 43. Density of *Diatomovora amoena* per 2 cm^3 of sediment at four intertidal elevations along the transect, as shown by the mean (bar) and ±2 x standard error (rectangle) from 0.0-0.5 cm in depth.


3.0 FT
1.6 FT
0.0 FT
-2.0 FT
ANIMAL DENSITY / 2CM^3
40
36
32
28
24
20
16
12
8
4
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1970
1971

beneath the mat during October, but were absent in November.

Large adult worms were gravid during summer. The reproductive period was followed in the fall by an increase in density. Density decreased drastically during late winter with only a small number of individuals surviving to maintain the population. The increase in abundance during 1971 preceded that in 1970 by several months.

Correlation Matrix of Data Collected Monthly From All Stations

A correlation matrix of all factors found within the top 0.5 cm of sediment was constructed from monthly data pooled from all stations over a period of one year (Figure 44). The factors were grouped into three categories: 1) biological (factors 5-10), 2) pore water (factors 11-14), and 3) sediment (factors 15-20) and their interactions were investigated. A test of the null hypothesis that the population correlation coefficient ρ between each factor was not different from zero, was applied at the 0.05 and 0.01 levels of significance for r. Only correlations found to be significant at these levels will be discussed. These important relationships were selected on the basis of their having correlation coefficients significantly greater than 0.50.

The significant correlations among the sediment factors (sand elevation, percent fine sediment, mean particle size, sorting, skewness, and kurtosis) reflect their positive interdependence. The

	1 Month	2 Station	3 Replication number	4 Animal density	5 Organics	6 Sulfide	7 Chlorophyll a	8 Chlorophyll b	9 Chlorophyll c	10 Carotenoids	11 Sand salinity	12 pH	13 Oxygen	14 Temperature	15 Sand elevation	16 Per cent fines	17 Mean grain size	18 Sorting	19 Skewness	20 Kurtosis
1 Month																				
2 Station	.02																			
3 Replication number	.01	.97*																		
4 Animal density	.06	.34*	.32*																	
5 Organics	-.04	-.28*	-.29*	-.20*																
6 Sulfide	-.25*	-.34*	-.34*	-.10	.33*															
7 Chlorophyll a	-.32*	-.14*	-.13*	-.13*	.71*	.42*														
8 Chlorophyll b	-.05	-.14*	-.14*	-.10	.72*	.35*	.70*													
9 Chlorophyll c	-.39*	-.01	-.01	-.03	.37*	.25*	.79*	.42*												
10 Carotenoids	-.25*	-.18*	-.17*	-.17*	.77*	.37*	.92*	.70*	.70*											
11 Sand salinity	.02	-.04	-.06	.03	-.02	.02	.03	.00	.02	-.05										
12 pH	.33*	.46*	.45*	.18*	-.30*	-.35*	-.33*	-.27*	-.29*	-.37*	.30*									
13 Oxygen	.30*	.34*	.31*	.11	-.40*	-.53*	-.51*	-.46*	-.40*	-.48*	.02	.43*								
14 Temperature	-.09	.10	.09	-.02	-.07	-.16	-.04	-.04	-.09	-.09	.84*	.36*	.13							
15 Sand elevation	.03	-.28*	-.27*	.04	.20*	.32*	.08	.31	.00	.08	.11	.11	-.14	.01						
16 Per cent fines	.02	-.11	-.11	-.08	.14*	.03	.13	.10	-.00	.09	.91*	.25*	-.04	.80*	.10					
17 Mean grain size	.10	-.04	-.05	.01	-.01	-.03	-.03	-.02	-.05	-.08	.98*	.33*	.02	.82*	.08	.91*				
18 Sorting	.10	-.02	-.04	.02	-.02	-.03	-.03	-.02	-.05	-.09	.98*	.34*	.03	.83*	.08	.91*	.99*			
19 Skewness	-.31	-.07	-.06	-.01	.49*	.29*	.54*	.40*	.33*	.51*	.01	-.30*	-.33*	-.04	.02	.17*	-.02	-.03		
20 Kurtosis	.10	-.04	-.05	.01	-.02	-.03	-.03	-.02	-.05	-.09	.98*	.34*	.03	.83*	.08	.91*	.99*	.99*	-.03	

Figure 44. The correlation coefficient matrix for all stations pooled over months. * = 0.05 level of significance.

biological factors (organics, sulfides, and photosynthetic pigments) are also significantly and positively interrelated by correlation because of their direct and indirect relationship to organic production and to reducing or oxidizing conditions. Significant positive correlations were found among the pore water factors (salinity, pH, oxygen, and temperature). Correlations of interaction also exist between the granulometric and biological factors. Sediment skewness is positively correlated with organics, sulfides, and the photosynthetic pigments, and the percentage of fine sediments is positively correlated with organics. Change in sediment elevation is positively correlated with organics, sulfides, and chlorophyll b. Pore water pH and oxygen are significantly negatively correlated with each of the biological factors, but temperature and salinity correlations are not significant. Pore water salinity, pH, and temperature are positively correlated with most of the sediment factors except for sediment skewness. Correlations of animal density with organics, chlorophyll a and carotenoids were negative, that with pH was positive, and that with sediment factors was not significant.

The numerous positive and negative correlations that were found within and between the biological, pore water, and sediment groups of factors reflect the multiplicity of direct and indirect interactions and support the contention that the tidal flat is a complex interrelated system.

The usefulness of data pooled from all stations for all months may be limited, because correlations assume rectilinear functions and are dependent upon similar variability, including sign. Non-linear relationships were not explored, but the station and month effects of pooling were examined, since moderate station differences and strong seasonality were suggested by the raw data.

Correlation Matrices of Data Collected from All Stations Pooled Over Months

A correlation matrix of data for all factors pooled over a period of 13 months was constructed for each of the four stations. Two other matrices were constructed, one by pooling data from the upper two stations (Figure 45) and the other by pooling data from the lower two stations (Figure 46) under the guidelines and format defined earlier. The latter two matrices will be considered first.

The basic relationships found by correlation of factors pooled for all stations and months (Figure 44) were also found within the correlations of factors found for combined upper and combined lower stations over months. The level of correlation among the biological factors was similar between the upper and lower pooled stations, but the sediment factors were significantly more interrelated by correlation in the lower stations than in the upper stations. The biological-sediment interaction coefficients were unexpectedly more significant

		1 Month	2 Replication number	3 Animal density	4 Organics	5 Sulfide	6 Chlorophyll a	7 Chlorophyll b	8 Chlorophyll c	9 Carotenoids	10 Sand salinity	11 pH	12 Oxygen	13 Temperature	14 Sand elevation	15 Per cent fines	16 Mean grain size	17 Sorting	18 Skewness	19 Kurtosis
1	Month																			
2	Replication number	.00																		
3	Animal density	.04	.02																	
4	Organics	.03	-.08	-.29*																
5	Sulfide	-.31*	-.12	-.12	.27*															
6	Chlorophyll a	-.20*	.04	-.29*	.74*	.42*														
7	Chlorophyll b	-.05	.00	-.18	.73*	.33*	.75*													
8	Chlorophyll c	-.32*	-.04	-.17	.37*	.28*	.72*	.44*												
9	Carotenoids	-.14	.02	-.32*	.79*	.33*	.92*	.73*	.70*											
10	Sand salinity	.10	.04	.35*	-.07	-.02	-.04	-.02	-.06	-.13										
11	pH	.09	.13	.19*	-.17	-.21*	-.20*	-.22*	-.21*	-.29*	.54*									
12	Oxygen	.34*	.17	.17	-.37*	-.56*	-.54*	-.49*	-.44*	-.50*	.08	.37*								
13	Temperature	-.01	.04	.32*	-.05	-.15	-.01	-.00	-.04	-.11	.94*	.53*	.11							
14	Sand elevation	-.13	-.32*	-.04	.24	.35*	.12	.33*	.01	.12	.10	.18	-.16	.09						
15	Per cent fines	.13	.14	.26*	.08	-.02	.09	.09	-.04	.01	.94*	.50*	.05	.90*	.11					
16	Mean grain size	.16	.05	.33*	-.05	-.06	-.07	-.04	-.10	-.13	.98*	.54*	.10	.92*	.07	.95*				
17	Sorting	.15	.05	.33*	-.05	-.06	-.06	-.04	-.09	-.13	.99*	.54*	.09	.93*	.07	.95*	.99*			
18	Skewness	-.12	.28*	-.36*	.54*	.30*	.54*	.44*	.22*	.52*	-.06	-.11	-.32*	-.07	.01	.16	-.06	.06		
19	Kurtosis	.15	.04	.33*	-.05	-.06	-.06	-.04	-.09	-.13	.99*	.54*	.10	.93*	.07	.94*	.99*	.99*	-.06	

Figure 45. The correlation coefficient matrix for the lower two stations (-2.0 and 0.0 feet) combined and pooled over months. * = 0.05 level of significance.

		1 Month	2 Replication number	3 Animal density	4 Organics	5 Sulfide	6 Chlorophyll a	7 Chlorophyll b	8 Chlorophyll c	9 Carotenoids	10 Sand salinity	11 pH	12 Oxygen	13 Temperature	14 Sand elevation	15 Per cent fines	16 Mean grain size	17 Sorting	18 Skewness	19 Kurtosis
1	Month																			
2	Replication number	.01																		
3	Animal density	.08	-.17																	
4	Organics	-.29*	.06	-.10																
5	Sulfide	-.30*	-.11	.24	.12															
6	Chlorophyll a	-.50*	.16	-.01	.67*	.30*														
7	Chlorophyll b	-.06	.10	.00	.62*	.10	.62*													
8	Chlorophyll c	-.45*	.11	.00	.61*	.35*	.93*	.56*												
9	Carotenoids	-.45*	.17	-.05	.69*	.23*	.92*	.59*	.80*											
10	Sand salinity	-.46*	-.03	.13	.24*	.33*	.57*	.19*	.49*	.49*										
11	pH	.07	.20	-.06	-.30*	-.41*	-.39*	-.23*	-.42*	-.33*	-.35*									
12	Oxygen	.30*	-.22	-.11	-.26	-.25	-.36*	-.36*	-.38*	-.31*	.02	.30*								
13	Temperature	-.28*	.15	-.26*	-.11	-.24*	-.06	-.14	-.21*	.00	.24*	-.01	.28*							
14	Sand elevation	.48*	-.59*	.30	-.05	.19	-.12	.12	-.05	-.18	-.01	.14	-.01	-.55*						
15	Per cent fines	-.41*	.00	-.17	.20*	-.15	.20*	-.13	.10	.25*	.33*	-.13	-.04	.41*	-.34*					
16	Mean grain size	-.43*	-.46*	.21*	.37*	.17	.38*	.12	.38*	.30*	.40*	-.47*	-.17	-.10	.32*	.30*				
17	Sorting	-.42*	.54*	.-05	.47*	.08	.52*	.27*	.45*	.47*	.43*	-.25*	-.19	.13	-.51*	.37*	.20*			
18	Skewness	-.54*	-.05	.16	.39*	.20*	.52*	.30*	.44*	.46*	.54*	-.50*	-.20	.07	-.04	.23*	.62*	.56*		
19	Kurtosis	-.31*	-.29*	.13	-.12	-.03	.01	-.11	-.05	.02	.25*	-.19*	.01	.28*	.08	.27*	.32*	.12	.37*	

Figure 46. The correlation coefficient matrix for the upper two stations (1.6 and 3.0 feet) combined and pooled over months. * = 0.05 level of significance.

in the upper stations than in the lower stations. Skewness was correlated with all biological factors at each level. Sediment elevation was correlated with sulfides and chlorophyll b in the lower stations, but not in the upper stations, yet was not significant when pooled over all months for all stations (Figure 44).

The correlations of pore water factors with biological and sediment factors in the lower stations were more similar to the pooled months and stations correlations than to those of the upper stations. The negative correlation of animal density with organics and chlorophyll a in the data pooled over months and stations is attributed to negative correlations in the lower two stations and absence of correlation in the upper stations. The positive correlation of animal density with pore water factors in the lower stations contributes to the positive nature of correlation in the data pooled over months and stations, because the correlation in the upper stations is negative. Animal density was positively correlated with most of the sediment factors in the lower stations, and with sediment elevation and the mean particle size in the upper stations. The latter correlations were not significant in data pooled over months and stations.

The matrices for the pooled monthly data from stations one and two was compared to the matrix for the data for stations one and two combined and pooled over months. Pooling of the lower two stations was justifiable, because little difference in level of significance was found within and between the biological, pore water, and sediment groups of factors between these two stations pooled, and these two stations taken separately. The significance of correlation of animal density with pore water factors for data pooled over stations one and two was largely derived from station two. Animal density is negatively correlated with sediment factors at station one and positively correlated at station two.

The matrices for the pooled monthly data from stations three and four was compared to the matrix for the data for stations three and four combined and pooled over months. The level of significance of correlation among the data of pooled station biological factors was largely due to the level of significance at station four, while that of the sediment factors was due to the level of significance at station three. Correlations with respect to animal density with data of all factors were contributed by station four. Pooling of the upper two stations was less justifiable than pooling of the lower two stations because of these station differences.

Correlation Matrices of Months Pooled over Stations

A correlation matrix was constructed for pooled data from all stations for each month for all factors, in order to evaluate the strength of seasonal effects. The resultant reduction in the number of degrees of freedom was drastic. Insignificant correlations occurred when significant correlations were strongly expected, an effect which may be attributed to small sample size. Only significant correlations at the 0.05-0.01 levels of significance were considered further. Under these circumstances, with a maximal sample size of 16 and 14 degrees of freedom the smallest significant correlation coefficient at the 0.05 level was .497. It was not possible to define a pattern of seasonal effects of factors on animal density, without accepting lower levels of significance. Animal density was largely negatively correlated with organics, sulfides, chlorophyll a, b, c, carotenoids, interstitial salinity, and fine sediment percentage during the period from October through December. Animal density was positively correlated with temperature and pH during this period. No significant correlations were found during January.

The following generalizations are indicated by comparison of the data pooled into matrices:

1. Biological factors are highly interrelated at all stations, but are the least interrelated at station three.
2. Sediment factors are highly interrelated at all stations, but are the least interrelated at station four.
3. Pore water factors are most highly interrelated at station one and two.
4. Biological-sediment interactions are more interrelated at stations one, three, and four than at station two.

5. Pore water-biological interactions are more interrelated at stations three and four, and pore water-sediment interactions are more interrelated at stations two and three.
6. Animal density is more correlated with biological, pore water, and sediment factors at stations one and two, than at stations three and four.

DISCUSSION

System Model

Restriction of Diatomovora amoena to an interstitial mode of life and to the intertidal surface of an estuarine sand flat presented a unique opportunity to explore the relation of an organism to the multi-dimensional interface system it lives in. This system was conceptualized in the manner of Turner and Stevens (1959) as a graphic factor model (Figure 47), where arrows between factors imply relationship and direction. The model does not include all possible relationships (pathways) or operational factors, but does include factors of major significance to near-surface dwelling meiofauna.

The littoral surface in Yaquina Bay is intermittently exposed and submerged by the tide in a mixed semi-diurnal fashion and represents a complex, fluctuating land-sea-air interface.

The principal factors operating in this sytem include tidal processes, insolation, and precipitation. Insolation is represented in the form of light and heat (temperature). Tidal processes are reflected in the beach slope and sediment grain size, and tidal exposure may alter sediment temperature and the overlying estuarine water salinity. Precipitaion determines the estuarine salt content and the availability of groundwater for percolation. Temperature, salinity, light, and particle size may act directly on the distribution and abundance of

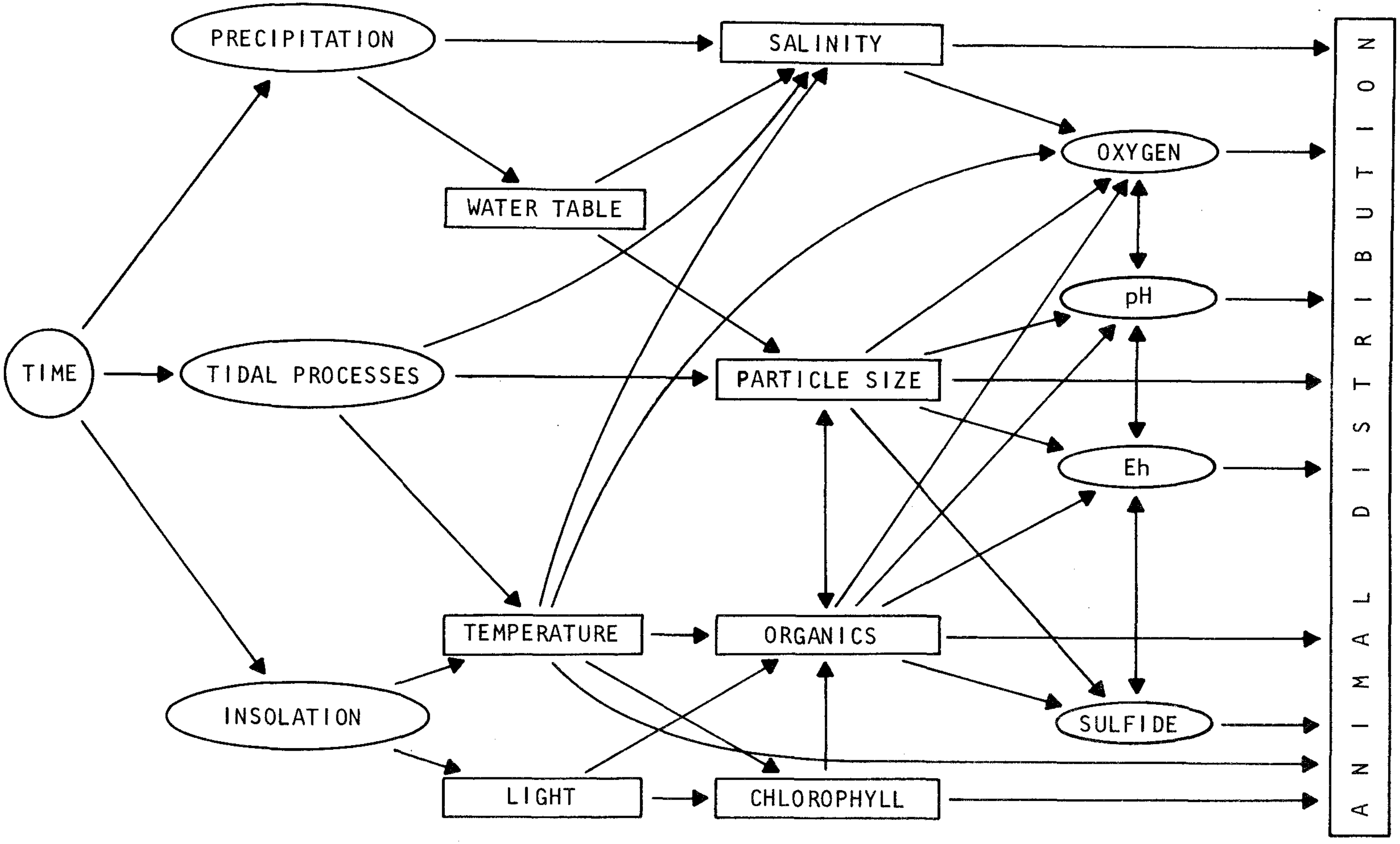


Figure 47. Conceptual graphic factor model of the environmental system controlling distribution of Diatomovora amoena in Yaquina Bay.

organisms in concert with, or indirectly through, other factors. Particle size sets the physical interstitial environment by controlling the pore space, packing, porosity, permeability, capillarity, diffusion rate, and depth of light penetration. Light directly controls autotrophic production (chlorophyll) and indirectly influences the oxidation of organics. Temperature modifies the rate of organic production and the oxygen concentration. Salinity may also modify oxygen content. Organic production may determine the sulfide level, and bacteria may determine the rate of sulfide turnover. The organic-sulfide interaction is reflected in the oxygen content, hydrogen ion concentration, and oxidation-reduction potential.

This suite of factors and their interactions has been assumed to comprise the major environmental mosaic of the acoel flatworm, Diatomovora amoena. The seasonal cycle of the primary input factors (tidal processes, insolation, and precipitation) that control the estuarine littoral system evidently do not vary significantly from year to year. The intertidal environment may, therefore, be considered a relatively stable system even though strong seasonality exists and the timing of seasonal maxima and minima varies.

Sampling Assumptions

The sampling scheme employed in this study assumes that the interstitial environment varies along the slope of the beach and that factors are strongly graded by the rise and fall of the tides over the littoral surface. Environmental gradation, therefore, should bear some relation to tidal exposure and is assumed to be reflected in the distribution of populations.

Restriction of sampling to a single transect and to tidally based stations along the transect restricted information to select tidal levels and to one locality. Sampling is required to measure variability, and an estimate of variance is required to plan sampling. In order to satisfy these conditions, a grid-system is often employed to "characterize" the environment (Cassie and Michael, 1968). A detailed program is then designed on the basis of the grid information. This method usually omits seasonal variation and most meiofaunal studies do not include seasonal information (McIntyre, 1969). Hence, a grid sampling system ought to be employed for a minimum of a year for proper analytical design of the detailed study. Since the objectives of this study included a rigorous analysis of the seasonal variability and interaction of numerous environmental factors, a more inclusive grid-like sampling program was impractical, especially when considering the small interstitial fauna (Lackey, 1961).

The sampling limitations of a single transect are illustrated in Figure 48. Consider a beach of uniform slope with a varied population distribution (dotted lines) and several transects. Inclusion of many transects would enable construction of a response surface.

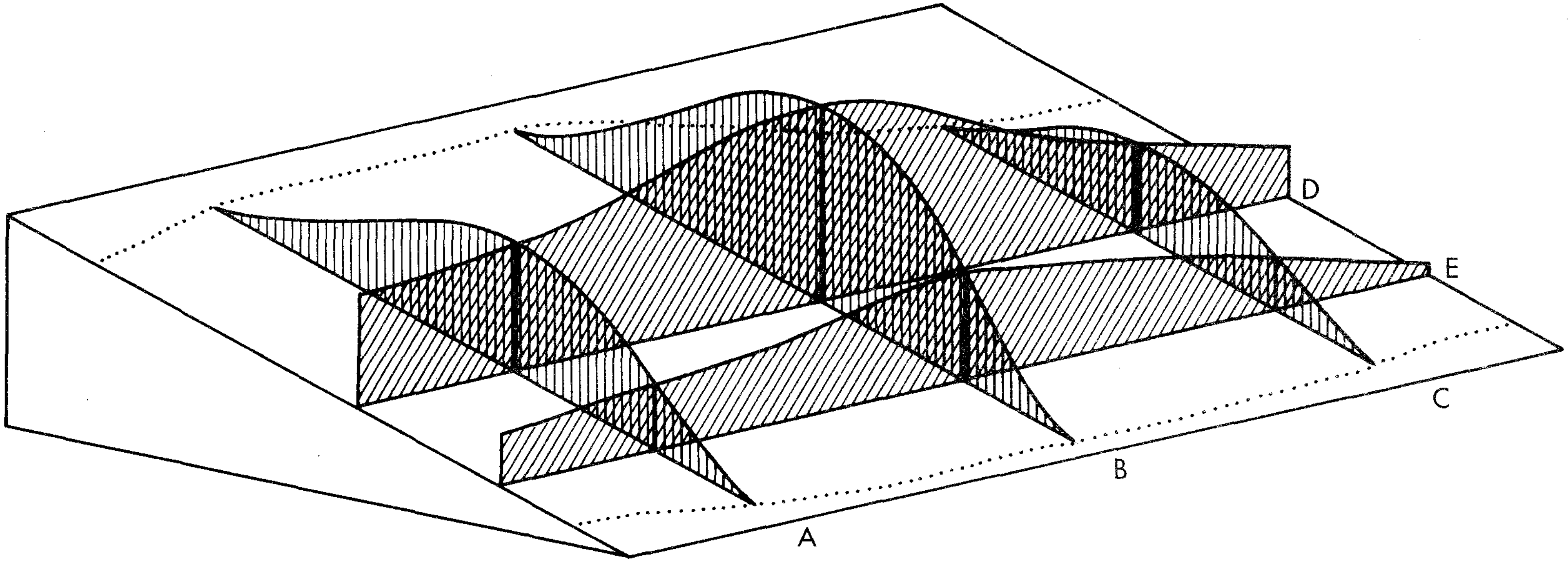


Figure 48. Illustration of conceptual sampling limitations of vertical (A, B, and C) and horizontal (D and E) transects over a beach in relation to the distribution of an interstitial population (dotted lines).

Limitation of sampling to several transects (A, B, and C) or a single transect provides little or no information regarding lateral distribution (D and E). Hence, no estimate of error can be obtained no matter how abundant the replication. Replication of samples along the transect is considered duplication in terms of lateral distribution. Relative seasonal change in distribution along a transect may be considered to reflect changes in the whole population. However, a careful interpretation of magnitude is recommended.

Tidal Processes

Selection of shore stations on the basis of tidal exposure enabled concentration and stratification of sampling. An uncontrollable characteristic of a set of fixed intertidal sampling stations is that they undergo seasonal changes in percent exposure (Figure 5), with percent exposure greater in winter than in summer. This variation, due to the sigmoid nature of the percent exposure curve, differs with tidal level. For example, exposure at the 6.4 ft station in Yaquina Bay varies seasonally ±8.25%, while at the 3.0 ft station seasonal variaation in exposure is only ±6%. Contrary seasonal patterns were found by DeHaan and Zaneveld (1959) in the Netherlands Antilles and were apparently caused by the inverse pattern of seasonal sea level changes in that area. Percent exposure change of fixed station elevations declines at elevations above and below 7.4 feet.

The average annual percent tidal exposure remains almost identical from year to year and implies that once stations are chosen they need only be corrected for wave action, storm surge, sea level, and change in sediment elevation. DeHaan and Zaneveld (1959) were of the opposite opinion in that they found the year-to-year variation in mean tidal level was large compared to daily tidal range.

Abrupt change in exposure near MLW and MHW indicates the significance of the added exposure from HL water to LL water and the decrease in exposure due to LH water. The relative effect of the levels of LH and HL water can be seen in Figure 8. An exposure curve from shores with regular tides, therefore, would be expected to have a less sigmoidal appearance than that in Figure 8. The curves shown by Colman (1933) and Lewis (1964) support this; however, Lewis (1964) incorrectly expected that mixed tides would produce a curve with sharp breaks. The tidal elevations chosen for the sample stations (-2.0 to 3.0 feet) were found to be exposed for significantly different periods of time (Figure 9). The two upper stations differed qualitatively from the lower stations since they encountered two daily periods of exposure during most spring tides.

The daily, fortnightly, and seasonal tidal rhythms alternately expose and submerge the littoral zone and set the pattern for the shore environment. In this manner the estuarine temperature and salinity regimes are strongly controlled by the tides. The fortnightly tidal range (neap-spring cycle, Figure 8), as well as the daily excursion of the tide, is reflected in both the estuarine temperature (Figure 10) and salinity (Figure 11) patterns. This suggests that the flushing and exchange rates of the estuary contribute significantly to the environment of the estuarine intertidal zone. Narrowing of the vertical and horizontal distribution of estuarine interstitial organisms might be expected by reduction of the tidal prism. The high water temperature regime, and by inference, the salinity regime, of the study area is closely related to coastal conditions, as has been shown by Bourke (1969) and Pillsbury (1972).

Under these circumstances the subtidal populations would experience pulses of marine and estuarine temperature and salinity conditions, while intertidal populations would experience the same pulses interrupted by exposure to atmospheric conditions. The daily range in temperature and salinity was often broadest during spring tides and narrowest during neap tides. This pattern became disrupted during winter periods of high river runoff or summer upwelling. Local upwelling not only imparts low temperatures and high salinities along the bay shore at high tide, but may also induce early morning coastal fog, which, from May through August, reduces heating of the shore exposed by low tides occurring in the morning (Figure 9). Insolation was found to be submaximal during this period.

The seasonal effect of runoff on estuarine salinity, although strongly evident at low tides, is still measurable at high tides. Thus, Kulm (1965) and Kjeldsen (1966) were able to correlate precipitation with salinity in Yaquina Bay on the basis of weekly measurements, irrespective of tidal stage.

Groundwater Hydrology

The hydrology of the groundwater is closely associated with the tidal cycle. These two factors ultimately control the dynamics of the interstitial milieu. The precise role of the groundwater is difficult to assess, for the mixing of discharging groundwater and recharging of sea water takes place within the variable matrices of the dynamic sediment system. The intersection of the hydraulic surface and sediment surface occurs just below mean sea level. Elevations below this point generally remain wet through percolation, while elevations above this point are draining. The seasonal and tidal movement of groundwater and beach recharge with sea water is shown diagrammatically in Figure 49. The depth of the hydraulic surface (horizontal lines) controls the volume of sea water entering the sediment above the intersection zone (A) and ultimately controls the pore water salinity. During the summer the cycle is characterized by a low water table (vertical lines), with sea water entering the sediment pores above the intersection zone at high tide (maximal recharge), and with small discharge through percolation at low tide. During the winter the freshwater

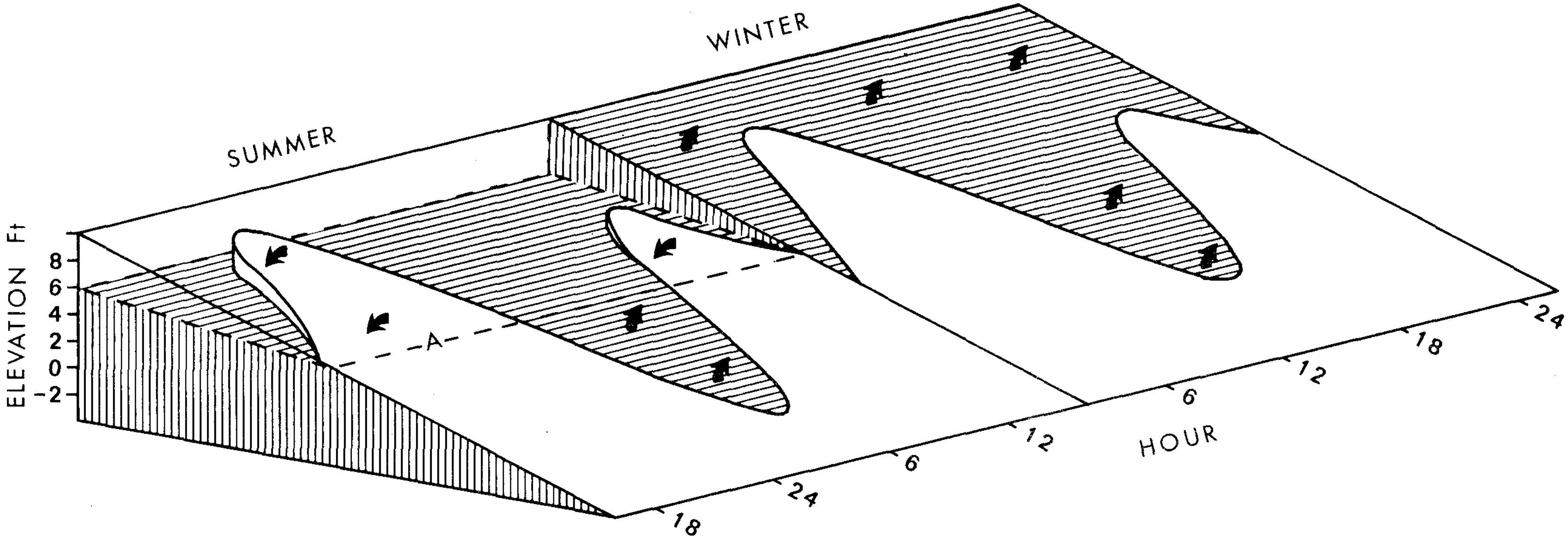


Figure 49. Graphic model of the seasonal variation in depth of the hydraulic surface of the water table (horizontal lines) above the intersection zone (A). The direction of sea water recharge (in) and ground water discharge (out) is shown by arrows. Actual tidal cycles are indicated by curved lines. The clear area indicates the littoral surface wetted by the tide.

hydraulic surface approaches the sediment surface as the water table rises, recharge is minimal, and discharge at low tide is maximal. Significant increases in the amount of daily precipitation during December and January (Figure 21) account for the rising water table and also explain the time of departure of the theoretical water table from the observed water table (Figure 22). As a result, the saline estuarine water present during high tides from December through spring, probably does not enter the pores of the upper beach. Likewise, the very low saline water of lower tides does not enter the discharging lower beach even when it covers it. This cycle protects fauna of the interstitial pore water in the lower beach from lethal low saline conditions during the winter. Summer interstitial mixing is augmented by the entry of sea water into the sediment at higher elevations and by the hydraulic pressure of flooding tides which holds back and elevates the subsurface freshwater near the high intertidal. Thus, interstitial mixing is tidally induced in all planes. These mixing processes are important for the maintenance of a zone of water of buffered salinity below the sediment surface. If mixing did not take place, steeper environmental gradients of salinity, organics, sulfides, etc. within the pore water might be expected.

The pore spaces at exposed elevations below the summer groundwater intersection zone remain permanently filled throughout the year. As the water table rises during the fall, the percolation of groundwater probably accelerates through this zone until the fresh hydraulic surface approaches the sediment surface throughout the beach in the winter. The rate of percolation at the lower stations levels off as the entire beach begins to drain. Hydrologically, the summer and winter beaches are alike in that the sediment pores are filled at high tide, but they differ in that the winter beach may remain filled through the low tide period. The velocity of percolation from the summer beach is assumed to be controlled mainly by the gravitational pressure of the pore water from the immediate upper intertidal. The winter percolation velocity exceeds the summer velocity and is probably controlled by the added pressure of the high freshwater table in the dune.

The combination of abundant rainfall and seasonal coastal upwelling has special significance for the distribution of estuarine interstitial meiofauna on the Pacific northwest coast. Maintenance of the seasonal magnitude of the groundwater hydrologic cycle is dependent upon the seasonal pattern of precipitation. Large seasonal changes in elevation of the water table are normal and contribute to the diluted character of the pore water microhabitat during the winter. An abnormally dry year will cause the pore water beach system to maintain a summer-like saline character throughout the year. The estuarine character of the interstitial fauna, then, can be expected to reflect the groundwater hydrology cycle in this area. The euryhaline nature of D. amoena, shown experimentally, bears this out.

Year-round percolation through the lower intertidal in the study area and winter surface runoff probably contribute a great deal towards the flushing of organics, sulfides, and fine sediments from the shore. The residence time for water entering the upper beach and the rate of down-slope percolation have not been investigated. However, the estimates of summer permeability rates given earlier are suggestive of percolation velocities well below the minimum 1.5 cm/sec threshold velocities for movement of fine sediments.

Grant (1948) investigated aggradation and degradation of exposed beaches and found that higher water tables were correlated with periods of degradation through maintenance of turbulent flow and the dilating effect of groundwater on finer sediments. Emery and Foster (1948) were able to follow the change in groundwater elevation throughout an entire tidal cycle, and found that the rate of flooding of interstices exceeded the draining rate, and that loss of silt could be attributed to groundwater elutriation. These findings explain in part the silt loss observed at the upper station in winter. Shepard (1963, p. 171) notes that wave recharge through sediments less than 1 mm in diameter is negligible for short wave periods, thereby accounting for the low angle of fine sand beaches. Because the beach in this study is characterized by sediments of the above description the effect of wave action on deposition, here, too, should be minimal.

The water content was not examined, as the portion of the beach investigated never exceeded the elevation of the hydraulic grade line. The water content could be expected to vary with the seasonal water table at higher elevations, with the tide during the summer, and with particle size and percent fine fraction in the lower intertidal. Determinations of water content by weight are subject to error by core disruption of sediment thixotropy.

Sediments

The change in sediment elevation along the transect, with winter degradation at the -2.0, 0.0, and 4.5 foot elevations and stability at 1.6, 3.0, and 6.0 foot elevations, can generally be explained by correlation with the seasonal elevation of the groundwater and change in sea level (LaFond, 1938). Winter deposition of sediment in the high intertidal (8.4 feet) is opposite of erosion on exposed beaches as reported by Brunn (1962) and Schwartz (1967) cited by Bird (1969, p. 101), and may be due to absence of wave action, southerly aeolian transport of dune sands, and winter estuarine deposition (Kulm, 1965). Berm formation in the adjacent steeper beach is especially prominent during the fall and winter, while destruction occurs during spring and summer. Expected winter sedimentation coinciding with the upstream transport of sediment in the estuary was not dramatically evident along the transect.

Krumbein (1944/47), Shepard (1963), and Bascom (1951) have shown that wave action, turbulence, and permeability determine the slope and grain size on depositing shores, and that slope is a positive exponential function of particle size. The effect of density on settling velocity is reflected in packing, grain size, and size distribution. These in turn control permeability. Accordingly, the stability of littoral beaches might be governed by a feedback system. Turbulence determines grain parameters, grain parameters determine permeability and slope, and they, in turn, modify turbulence. Variation from steady state (change in beach profile) conditions may be attributed to change in sea level, turbulence, biological activity, and autochthonous organic production. Steele, Munro, and Giese (1970) demonstrated the effect of wave action (turbulence) on change in sediment character.

Deposition of fine sediments during the spring and summer at the lower stations (-2.0 and 0.0 feet) was paralleled by deposition in the upper stations (1.6 and 3.0 feet); however, winter deposition at the lower stations was not repeated in the upper stations which instead eroded. Removal of fine sediments from the upper elevations during the winter and their transport to the lower elevations probably added to the fall-winter in situ deposition observed at the low stations. Much of the fine material is then lost by February. Since the percentage of fine sediment at depth never exceeds surface values, the fines at depth must be derived from surface sediments. Accumulation of fine sediments during the period of September through November in the second 0.5 cm indicates that the percolation velocity or duration of percolation is inadequate for removal of the fine fraction until December or January. At this time the ground water discharge apparently accelerates as the observed water table departs from the theoretical water table, and acting in concert with tidal currents, may have been adequate to remove the critical 180 micron-sized particles from the surface. This cycle is complicated by the anticipated additional silt load coming into the estuary from streams during heavy winter runoff.

An increase in mean particle size of the coarse fraction during the winter at 3.0 feet and decrease in size at the lower stations, fits the pattern found for the fine fraction percentage. The apparent time lag between September and December in attaining the smallest mean particle size from the 3.0 to the -2.0 foot station is also in agreement with the pattern of groundwater percolation.

Gray and Rieger (1971) concluded that sorting and grade seemed to control biomass of interstitial fauna. Wieser (1960) found that the fine sediment content was related to faunal uniformity. The degree of turbulence is reflected in the measure of phi deviation or sorting. Turbulent conditions were apparently prominent at the lower stations only during winter, while turbulence was maintained year round in the uppermost station, with less variability. The annual range in turbulence at low elevations exceeded the rather uniform degree at the upper elevations.

Current velocity may be estimated from the mean grain size (Sanders, 1958). Boaden (1968) pointed out that the 180 micron- (2.47 ϕ) sized particles were the most unstable in terms of threshold velocity (2 cm per second), but were still within the range of the critical diameter for interstitial fauna (200 microns). It is peculiar that a relatively stable system, in terms of input factors, such as an estuarine littoral sediment system, would contain such a supposedly unstable central factor as particle size. The mean grain size in the upper two stations is slightly larger than 180 microns and is equal to, or smaller than, 180 microns in the lower two stations. Since turbulence is likely to suspend particles less than 180 microns, and roll or slide those above 180 microns (Boaden, 1968), the 1.6 and 3.0 foot stations may be considered more stable than the -2.0 and 0.0 foot stations. This contention is supported by the smaller change in sediment elevation at these upper elevations. The seasonal change in mean grain size was rather benign for such a hydrodynamically unstable particle size. When the surmised instability is considered in light of the other grain size parameters and change in sediment elevation, it appears likely that grain sizes near 180 microns were removed from the lower two stations during the winter. This would require minimal current velocities near 2 cm/sec. Surface and bottom velocities an order of magnitude larger than this are common in the channel just off the study site, as described earlier (Kulm, 1965; Neal, 1966). Currents in the range of 30 to 50 cm/sec are available during ebb and flood tides throughout the year. Maximal current velocities often lag behind mid-tidal velocities by 60 minutes. The upper distribution of *D. amoena* at 3.0 feet would be covered by water at the time of maximal tidal velocity. Both sediment and organisms at 3.0 feet would then be subject to transport.

Biological Factors

The grain size distribution of the shore sets the primary conditions of the interstitial environment. Biological activity may significantly alter these conditions. The concentration of photosynthetic pigments, total organics, sulfides, hydrogen ion, and oxygen, reflect biological activity that may directly or indirectly modify distributions of interstitial organisms.

The concentration of the photosynthetic pigments has often been used in estimates of production (Strickland, 1960) and vertical migration of diatoms (Riznyk, 1969), but has been neglected as a factor relating to distribution of interstitial animals. Analysis of the concentration of various chlorophyll and carotenoid pigments contributes to an understanding of the system, and provides clues to the seasonal timing of conditions, distribution with depth and elevation, and relative change. Plant material forms an integral part of the interstitial environment. Chlorophyll a and total carotenoids are present in all plants, while chlorophyll b and c are restricted, in terms of unconsolidated estuarine surfaces, to the Clorophyceae and Bacillariophyceae, respectively. The degradation products of chlorophyll were not measured in this study, as uncertainties still exist concerning technique and interpretation. Estimates of the amount of phaeo-pigments as a percentage of chlorophyll a were made by Riznyk (1969) from sediments in Yaquina Bay near the bridge (1.0 n.m.). Summer values ranging from 12 to 31% and winter values from 4 to 6± were observed in the top 1.3 cm of sediment from low to high intertidal respectively.

The restricted presence of chlorophyll b is correlated with the seasonal presence of deposition and growth of Enteromorpha intestinalis, E. tubulosa, and Ulva angusta (?). The concentration of chlorophyll b actually lagged behind surface algal biomass, as the pigment measured was that of the sediment and not that of the surface algae.

Measurement of sediment chlorophyll makes possible the estimation of the source and quantity of new plant debris entering the sediment system. Seasonal changes also reflect the rate at which newly deposited plant material breaks down.

Seasonal, vertical, and elevational patterns in chlorophyll a and total carotenoid concentrations were so similar that one of the measures could have been omitted. The high fall concentrations coincided with those in chlorophyll b. Chlorophyll c was unexpectantly absent from the upper stations from December through spring, and high concentrations were limited to the 3.0 foot station during the same fall period. Diatoms, therefore, must be either absent or present in very low numbers at the upper stations in winter. However, small concentrations were present throughout the year at the -2.0 foot station. Surface concentrations of pigment usually exceeded subsurface levels during periods of production, while the converse was often true during the winter.

Owing to the shallow depth of light penetration (less than 10%) within sediments from 1.5 to 5.0 mm in depth (Riznyk, 1969; Gomoiu, 1967; Pennak, 1951), the presence of chlorophyll in the second 0.5 cm in depth was unexpected and probably indicated rapid movement of plant debris down into the sediment. Even when the concentrations were corrected for phaeo-pigments, concentrations at several centimeters in depth exceeded surface concentrations in the lower intertidal, but usually not in the mid- or upper intertidal (Riznyk, 1969). Periods of high and low pigment concentrations closely paralleled the groundwater percolation cycle, probably because of flushing of organic material from the sediment during periods of high percolation.

Benthic diatoms form one of the principal food items of

D. amoena, although eggs of copepods may also be ingested (Kozloff, 1965). D. amoena also appears to be non-selective with respect to food diatom species, but this was not established experimentally. Measurement of chlorophyll c may be taken as an estimate of food availability. The gross seasonal pattern of animal density appears to follow the pattern in chlorophyll c even if the observed values are corrected for phaeo-pigments. However, the presence of high animal densities during December and May at the 1.6 and 3.0 foot stations and an apparent absence of chlorophyll c is disarming. The most likely explanation is that the diatom density is actually low and not measurable by the trichromatic method as discussed by Strickland and Parsons (1968, p. 197). The animals may consume other food items or stop feeding at these times if diatom density actually falls to a limiting level. Riznyk (1969) made direct counts of epipelic diatoms in Yaquina Bay and found approximately 200 diatoms/0.1 μgm chlorophyll a/cm^3 at periods of low diatom densities, indicating that diatoms may still be present in the sediment at very low chlorophyll levels.

The measure of total organic concentration included living and detrital material. High winter organic concentrations at lower tidal levels followed the high fall pigment concentrations at the 3.0 foot station. Surface concentrations initially exceeded subsurface amounts during the fall, while winter concentrations were less, suggesting sediment storage of organics. The input of allochthonous material into the sediment system should parallel the pattern of seasonal sea water recharge. Decrease in total organic content in the lower stations during January and February may be attributed to removal through percolation and tidal currents. Oxidation by free oxygen seems unlikely in view of the high hydrogen ion concentration.

The late summer-fall period of high sulfide concentration unexpectantly preceded the highest period for total organic content, but agreed closely with high levels of chlorophyll a and c and carotenoids. When sulfides were present, subsurface concentrations always exceeded surface concentrations.

Both acidic conditions and very low oxygen percent of saturation levels were present at lower elevations during the fall and early winter, and were in close agreement with general reducing conditions. Low levels of pore water oxygen content seemed to follow the low summer levels of oxygen in the estuarine water column. Low oxygen concentrations throughout the water column during summer high tides have been attributed to the presence of coastal upwelled water in the bay (Bourke, 1969). At this time the oxygen gradient across the water-sediment interface is minimal and probably contributes to the slow oxidation of sulfides and to the accumulation of free sulfides near the sediment surface. The strongest inferred oxygen gradient occurred during December, yet it still took several months to effectively oxidize surface sediments. Oxidation of sulfides usually takes place in less than an hour in natural mixed systems (Ostlund and Alexander, 1963). However, surface sulfide oxidation could be expected to be retarded by percolation of anoxic groundwater during low tides at this time. Erosion of surface sediments also contributed to maintenance of reducing conditions. The hydrogen ion concentration was less indicative of the low oxygen conditions at the upper station. In contrast, Brafield (1964) found low summer and high winter oxygen levels in the sediment pore water of an open coastal beach.

The salinity of the pore water near the sediment surface approximated estuary water during the summer and fall. Winter and spring pore water salinities were usually less than estuarine surface and bottom water salinities at high tide, but were greater than the estuary surface water salinity at low tide. The pore water of the lower intertidal is well-buffered against large estuarine changes, and is a product of tidally mixed saline estuary and fresh groundwater. The significant decrease in pore water salinity between November and December is correlated with the time of accelerated groundwater percolation.

The lower intertidal is less buffered against temperature change upon exposure than it is against salinity. Temperatures at depth are less variable with season than surface layers, as has also been reported by Johnson (1965). Winter interstitial conditions are more moderate in the lower intertidal but may approach 5°C and 15‰.

However, Bruce (1928) notes that abrupt changes in temperature of the sediment brought about by a flooding tide may be more important than the temperature range.

Distribution of *Diatomovora amoena*

Tolerance of *D. amoena* to combinations of temperatures and salinities demonstrated that this organism is euryhaline and eurythermal and survives well under the interstitial conditions prevailing near the sediment surface in the estuarine tidal flat studied. Low winter temperatures aid survival at low salinities, and high summer salinities aid survival at temperature extremes. Low temperatures also increase tolerance of this species to sulfides. The adaptation of *Gunda ulvae*, a marine triclad flatwormto estuarine conditions has been described by Pantin (1931). This organism lives in a habitat that is similar to that of *D. amoena*. Schwab (1967) has shown instantaneous incapacitating effects of low temperatures on the acoel *Polychoerus carmelensis*.

The temperature-salinity tolerance experiments facilitated interpretation of acoel distribution in the natural interstitial system. The estuary surface water temperature at HHW and LLW does not go significantly below 7°C and temperatures below 5°C were never observed. Temperatures in excess of 16°C during LLW and 13°C during HHW were rare. The salinity of the estuarine bottom water was rarely less than 16‰ (LLW) or greater than 36‰ (HHW). These values mark the estuarine water temperature and salinity boundary conditions expected in the study area throughout the year.

The temperature and salinity regime of the interstitial water was not monitored as closely as that of the estuarine water. Pore water salinity was not normally expected to go below 15‰; however, heavy rainfall coinciding with low tides may penetrate the superficial layers of the sediment driving pore water salinity to lethal levels near 5‰. Temperatures less than 5°C could occur during winter periods of exposure. The uppermost extent of the acoel distribution, 3.0 feet, would be exposed under extreme tidal conditions for a period of 7 hours. Upper lethal temperature and salinity conditions shown in Figure 39 do not obtain in the overlying estuarine water during submergence. Lower estuarine temperature and salinity conditions that would result in mortality are possible, and occur during winter low tides when the animals are exposed. Combined conditions below 5°C (air) and 5‰ (estuary) were recorded during LLW on December 31 and January 1. These conditions would exist for a maximum of 7 hours with an estimated mortality of 70%, provided that estuarine water penetrates the upper 0.5 cm of sediment. Persistence of these conditions for 12 hours would produce an estimated mortality of 85%, and of 100% in 24 hours.

The buffering effect of groundwater percolation should minimize mortality through increase of pore water salinity. Under normal conditions, excluding direct precipitation effects, no mortality would be expected upon a seven hour low tide exposure to 5°C and 15‰, and a mortality of only 25% would be expected at 5°C and 10‰. However, these conditions would be more detrimental if longer periods of exposure were experienced. It is not known if the mortality effects of longer exposure could be achieved through shorter cumulative periods. The strong decline in acoel density between December 11 and January 26 indicates that one of these mechanisms was working.

Just after the December sample was taken (-1.7 foot tide) and before the tide rose, it rained very hard over the entire exposed sand flat. The water table was already near the sediment surface over much of the beach. The runoff was immediate and moved surface grains down-slope. The salinity of the runoff water at the 3.0 and 1.6 foot stations was 3.16 and 5.07‰ and 3.16 and 4.85‰ just below the surface of the sediment. The sediment temperature was 10°C. The effect of the precipitation and runoff was expected to persist throughout most of the 6 hour period of exposure. A mortality of 75 to 100% would be predicted for that length of time on the basis of the 6 hour temperature-salinity tolerance experiment conducted by the author. The sharp decrease in animal density observed in January may have resulted from the coincidence of a low tide, a heavy rain, and a winter water table-saturated beach. However, whether the low salinity conditions actually persisted through the period of exposure, or even through the tidal cycle, could not be verified. Reid (1932) concluded that the saline conditions would be restored with the flooding tide, but observed that salts may be leached by surface runoff.

Change in animal distribution may also be brought about by other mechanisms. The presumed migration of the acoels up into the overlying algal mat during October and November was evidently in response to the reducing conditions brought on by the exclusion of oxygen from the sediment surface and by the rising sulfide layer. A similar case has been described by Buscemi (1958) involving oxygen depletion of the water near the mud-water interface caused by the respiration of Elodea canadensis. Dense growths apparently inhibit vertical water circulation in this freshwater environment, as the marine algal mat does at the lower intertidal. Sulfide impregnated the lower layers of the algal mat and contributed to its destruction. Portions of the mat were then rafted with the flooding tide and redistributed, usually to the high intertidal, or flushed out the estuary. Acoels were recovered from mid-channel rafts and wrack near the transect in the high intertidal. Gross destruction of the algal mat was brought on by the first runoff freshet during the lower tides. However, the effect of the algal mat, in the form of organics, fine sediments, algal fragments, and reduced conditions continued through December. The migration into the mat and subsequent destruction or translocation of the mat is, therefore, a major cause of the observed low winter population numbers and contributes materially to dispersion in this species.

Vertical limitation of the acoel population to the superficial oxidized 0.5 cm layer of sediment could be attributed to their strong intolerance to the reducing conditions which occur at greater depth. D. amoena is only slightly tolerant of sulfides, but is evidently tolerant of low levels of oxygen.

If the depth of the oxidized layer is assumed to be maintained mainly by tidal mixing during submergence and by oxygen diffusion during emergence, the animals could potentially be exposed to reducing conditions for as long as 7 hours during low tides. Sea water oxidation of sulfide occurs in the order of 20 minutes (Ostlund and Alexander, 1963). In addition, sulfides might be brought to the surface from depths through percolation of groundwater at a rate faster than that of oxygen diffusion.

The survival experiments indicate that these animals could survive the maximal field sulfide concentrations (10 μgm S/0.5 cm^3) found in the first 0.5 cm at the 1.6 and 3.0 foot stations for at least 20 hours, whereas mortality at surface concentrations of 25 μgm S/0.5 cm^3 found in the lower two stations could be 50% after 20 hours at 10°C and 100% at 15°C. One-hundred percent survival at these concentrations is predicted for periods as long as those which actually occur during low tide exposure. The concentration of sulfides present in the second 0.5 cm of sediment would be lethal after 6 to 7 hours.

The presence of sulfide in the sediments is assumed to limit the elevational distribution of D. amoena, but the depth distribution of D. amoena in the sediment can be influenced by sulfides only during summer and fall at the 1.6 and 3.0 foot stations. That the effects of sulfide may be irreversible and, therefore, cumulative in sediment infauna was alluded to by Theede, Ponat, Hiroki, and Schlieper (1969).

The absence of sulfides from the surface and second 0.5 cm of sediment in January and during spring, suggests that other factors limit depth distribution in the sediment at this time.

Hydrographic control of the depth of the reducing layer has been shown by Steele, Munro, and Giese (1970), Fenchel (1969), and Webb and Theodore (1968) for subtidal sediments, while Boaden (1968) found that the disturbance of intertidal surfaces by waves was limited to the top 2 to 4 mm of sediment.

The early increase in abundance of D. amoena during 1971 may be attributed to the generally mild summer, absence of upwelling and coastal fog, a warmer estuarine temperature regime, and exposure to greater heating during low tides. The early increase in algal biomass during the second summer (May, 1971) was probably also an effect of warmer conditions and the absence of upwelling.

Correlation Analyses

Correlation analysis was a useful method of evaluating interaction within and between the biological, pore water, and sediment groups of environmental factors. Pooling of data over months and/or over stations facilitated interpretation of the effects of seasons and elevation on the relationships between environmental factors and the distribution of D. amoena.

The process of pooling over months masks seasonal effects, or assumes that factors will change together in the same direction at a given station during a year. Similarly, pooling of stations masks station differences, or assumes that factors will change together in the same direction during a given month.

Pooling of data over months was more justifiable than pooling over stations for individual months, because the significant correlations between months were not as strongly different in magnitude or sign as were those between the upper and lower stations. Restriction of most of the significant correlations of animal density with environmental factors to the period of October through December indicates either that stations were less different during this period than during the remainder of the year, or that lower levels of significance would have to be accepted. Inspection of correlations among factors other than animal density suggests that the stations were indeed more similar during winter than during other seasons. The negative character of animal correlation with most factors during October through December substantiates the observation that animals were present in large numbers at this time, while the strength of environmental factors such as sulfides, organics, fine sediment percentage, chlorophyll, etc., were decreasing.

The sharp decline in numbers of animals between December and January is reflected in the total absence of any significant correlations during January.

The generally positive character and interrelatedness of significant correlations among the biological, pore water, or sediment factors pooled over months indicate that these factors are fluctuating throughout the year in a similar fashion, but that they may differ in magnitude with station elevation. The greater intensity of correlation of animal density with biological, pore water, and sediment factors in the lower stations may be attributed to small fluctuations in animal numbers and to greater significance within and between sediment and pore water factors at these stations. The reasons for significance of correlation may also differ with elevation. Accumulation of organics, pigments, sulfides, fine sediments, etc. leading towards strongly reducing conditions was not paralleled by large changes in animal density. These conditions leading to a mildly reducing state in the upper stations occurred at a time when animal density was increasing significantly.

The significant correlations found from computation of a yearly matrix were mostly for those factors that were either positive or negative each month, but not mixed. Factors with seasonally mixed correlations determined from the monthly computations were not always significant in the yearly computation.

Although significant correlations were found between animal density and grain size, most workers have concluded that grain size acts indirectly. Schmidt (1969) considers oxygen, temperature, and salinity most important in limiting the distribution of interstitial fauna and Boaden (1968) has constructed an excellent case for pore size. Jansson (1967a, 1968) maintains that water content, circulation, and oxygen availability are more directly related to animal distribution, and Salvat (1967) found meiofaunal distribution well-correlated with oxygen saturation. The oxygen saturation in turn is significantly correlated with the percentage of fine sand, apparently through the rate of pore water drainage (Brafield, 1964).

SUMMARY

1. Seasonal cycles were demonstrated for tidal processes, precipitation and insolation, and these were found to be the principal environmental factors controlling seasonal changes in the intertidal sediment system. These major environmental factors determined granulometry, ground water hydrology and organic production in the tide flat. Interaction of these factors results in a stable annual cycle with strong seasonal changes in interstitial temperature, salinity and other physico-chemical properties.
2. The interstitial physico-chemical environmental cycle exhibits marked differences from that of the estuary water which is also under strong climatic control. High winter precipitation increases percolation of ground water through the beach. Seasonal elevation of the water table controls the stability of the beach and the interstitial water salinity regime, while tidal exposure determines the temperature regime. In summer, the pore water salinity level is the result of mixing of fresh groundwater and high salinity water brought into the estuary at high tide. In winter, the salinity of the interstitial water is buffered from the extremely low salinity of the estuary occurring at low tide by the storage properties of the system.

3. Annual cyclic changes in the time of low spring tides prevent the lower portion of the intertidal beach from being exposed in mid-day during the part of the year when insolation is greatest, thus producing a moderate low tide temperature regime.
4. The environment of the sand flat is strongly graded vertically by the rhythmic movements of the tide and the cycle of ground water percolation. Gradients of environmental factors change with season, with beach elevation, and with depth into the sediment. The beach grades from reducing conditions at low elevations of sediment which are rich in organics, sulfides, and fine particles, to oxidizing conditions at higher elevations, where amounts of organics, sulfides and fine particles are lower. A gradient of oxidizing to reducing conditions was also found with depth in the sediment and this gradient decreased at higher elevations. Heavy groundwater percolation results in reduction of all gradients by leaching during winter.
5. Low water spring tides occur between 0400 and 0800 hours during the summer when the exposed shore would be subject to atmospheric heating. However, morning coastal fog protects the shore from excessive heating. The upper two stations are exposed for a significantly longer period of time than the lower two stations because they are exposed by the HL tide as well as by the LL tide. Lower tidal levels are exposed during the early morning in summer

and early evening in winter. The inversion of time of low water spring tides takes place at the time of the vernal and autumal equinoxes. The occurrence of lowest tides at night in winter causes the shore to be exposed to low air temperatures, which, unlike high temperatures, enhance tolerance of _D. amoena_ to low salinities and high sulfide levels.

6. The annual cycle of insolation, as modified by summer fog, sets the timing of the summer production of plant material on the flat, which in turn sets the level of accumulating organic material and sulfides in the sediment. Seasonal growth of algae occludes the sediment surface from tidal flushing and leads to reducing conditions at the sediment surface in the lower stations during the summer. Density and distribution of _D. amoena_ is influenced by these reducing conditions. Animals migrate upwards into the algal mat and are subsequently lost from the population by the rafting of the mat away from the beach in the fall.
7. The distribution of _Diatomovora amoena_ was found to be limited to the intertidal region between -2.0 and 3.0 feet in elevation and to the surface 0.5 cm depth of sediment. High animal densities (approximately 20 animals/2 cm^3) occurred during the fall, and low densities (approximately 3 animals/2 cm^3) were found throughout the winter. This organism is both euryhaline and eurythermal within the observed seasonal range of salinity and temperature in

the estuary. Heavy precipitation during winter low tides may cause mortality through dilution of interstitial water. The results of tolerance experiments predict that 70% mortality of _D. amoena_ would occur under conditions below 6‰ and 10°C over a period of 6 hours, conditions observed to occur in the sediment during winter periods of extreme precipitation. Low temperatures aid survival of exposure to low salinity and high sulfide concentrations. The increased rate of groundwater percolation reduces the exposure of _D. amoena_ to lethal low winter salinities of the estuary. However, accelerated percolation of interstitial water from depth exposes animals to sulfides. _D. amoena_ is intolerant of sulfide. The results of the tolerance experiments indicate that sulfide concentrations near 50 μgm S/ml are lethal within 6 hours. The levels of sulfide found at the surface during the fall (approximately 20 μgm S/0.5 cm^3) are equivalent to the lethal concentrations found in the experiment, when adjusted on the basis of a porosity percent.

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