HABITAT, POPULATION AND LEAF CHARACTERISTICS OF *Zostera marina* L. ON ROBERTS BANK, BRITISH COLUMBIA

by

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ABSTRACT

The sand and mud flats of the Fraser River foreshore support extensive meadows of the seagrass *Zostera marina* L. (eelgrass). Industrial, residential and recreational developments threaten these valuable foreshore areas. A study was undertaken into the habitat requirements and population and morphological characteristics of eelgrass on southern Roberts Bank, British Columbia to provide information which would help minimize the potentially deleterious effects of such developments on the eelgrass resource.

Water temperatures and salinities and wave motion on southern Roberts Bank all approach the world-wide optima for eelgrass. The upper distributional limit of eelgrass was lower than those of other Pacific Coast eelgrass populations. The sandy nature of the substrate influences "desiccation" which, in turn, controls the intertidal limit of eelgrass growth. Light availability determines the lower distributional limit of eelgrass in other areas. These two factors, the sandy substrate and reduced light availability in the turbid estuarine waters of the Fraser River foreshore, appear to be responsible for the narrow depth range of eelgrass on southern Roberts Bank.

A stratified random sampling technique was used to determine seasonal changes in eelgrass standing crop, turion density and leaf dimensions at five elevations, located at

0.5 m depth intervals, from the upper to the lower limits of eelgrass growth. A pronounced decline in both turion density and leaf standing crop occurred in late summer. Throughout the study period, leaf standing crops and turion densities were greatest at the three intermediate study elevations. Reduced leaf standing crops were found near the upper and lower edges of the eelgrass bed; no significant difference in standing crops was found for these two elevations. Turion densities were also lower near the upper and lower depth limits of eelgrass and a significant difference in turion densities was found between these two elevations, with the lowest turion density recorded near the lower limit of eelgrass. Near the upper edge of the eelgrass bed, turion weights and mean leaf lengths were one-half those of the lower elevations.

A synthesis of the available information indicates that depth-related factors strongly influence certain morphological and population characteristics of eelgrass on southern Roberts Bank.

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1. INTRODUCTION

1.1. Purpose of the Study

Most of the British Columbia coastline is typically precipitous; the shallow protected areas necessary for the successful establishment of seagrass meadows are relatively rare along our coast. The extensive sand and mud flats of the Fraser River Delta support large meadows of the north temperate seagrass *Zostera marina* L. (eelgrass). *Z. marina*, a marine Angiosperm, is a member of the family Potamogetonaceae, subfamily Zosteroideae, genus Zostera, and subgenus Zostera (den Hartog 1970). The importance of eelgrass to invertebrates, fish and waterfowl populations is well-documented in the North American and European literature (Phillips 1975, Thayer et al 1975). In recent years, proposals to develop the tidal flats for residential, industrial and recreational purposes have been increasing. In addition to direct losses of eelgrass habitat, these developments may also have detrimental effects on the remaining eelgrass habitat through alteration of current patterns and water quality, and increased industrial and recreational traffic along the foreshore. To minimize the deleterious effects of various developments on the eelgrass resource of the Fraser River Delta, information is required on the habitat requirements and growth characteristics of eelgrass in the area. The purpose of this study is to provide some of that information.

1.2. Previous Research

In a comprehensive study of the seasonal growth of some seventy taxa of benthic marine plants in Great Pond estuary, Massachusetts, Conover (1958) found that the relations of environmental factors to the growth and distribution of *Z. marina* were not well-defined. High standing crop values of eelgrass were found in those sections of the estuary where salinities ranged from 12 to 32‰, lower values were obtained in areas where the salinity range was 1 to 30‰, and eelgrass was not present in areas having less than 1‰ salinity. Standing crop maxima and minima for eelgrass were associated with the annual maxima and minima of insolation and water temperature. Conover suggests that these two factors, temperature and light, play leading roles in the seasonal growth of eelgrass in Great Pond.

Setchell's scheme (1929) describing various growth, developmental and phenological activities of eelgrass based on 5°C water temperature increments has not been borne out in the recent works of Burkholder and Doheny (1968), McRoy (1969) and Phillips (1972).

Based on information from transplant experiments, Phillips (1974) suggests that the lower depth limit of eelgrass growth in Puget Sound, Washington is determined by light availability. Controlled field experiments in southern California by Backman and Barilotti (1976) confirmed that eelgrass turion density is a function of irradiance received by the plants. A turion is a leafy branch arising from the horizontal rhizome.

In Chesapeake Bay on the Atlantic Coast, Orth (1973) found that the sediments associated with dense stands of eelgrass are more poorly sorted and contain higher fine fractions than the sediments from areas of less dense eelgrass growth. Similarly, Stout (1976) describes a relationship between the occurrence of very fine-grained sands and silts and the presence of eelgrass beds. These sediment characteristics are attributed by both authors to a trapping action by eelgrass. Eelgrass has not been observed growing on sand in previous studies of eelgrass populations on the Pacific Coast.

Phillips (1972) and Stout (1976) describe the habitat factors associated with eelgrass for Puget Sound, Washington and Netarts Bay, Oregon respectively.

Taxonomic classification of the members of the genus *Zostera* has been, to a large extent, based on leaf measurement information and the vertical distribution of the plants. Two forms of *Zostera marina* are recognized on the Atlantic Coast of North America (Setchell 1920, Harrison and Mann 1975) and Alaska (McRoy 1972). A short, narrow-leafed form inhabits the shallow intertidal and upper subtidal zones of these areas. The taller, broad-leafed form is found in the deeper subtidal waters.

Along the Pacific Coast of North America, from British Columbia to California, the shallow-water and deeper-water forms are present but a size shift appears to have occurred. The narrow, short form of the intertidal and shallow subtidal reaches of this area corresponds to the tall, broad-leafed form of the Atlantic Coast (Scagel 1961) and Alaska (Phillips 1972). The tall, wide-leafed form of the central Pacific Coast, often referred to as *Z. marina* var. *latifolia* Morong, has much wider and longer leaves than the typical form (Setchell 1927). Considerable taxonomic confusion exists within geographical areas; leaf length of the larger form *Z. marina* f. *latifolia* described by Outram (1957) for southern British Columbia is the same as that for the short, narrow-leafed form *Z. marina* var. *typica* (*marina*) described by Scagel (1961) for British Columbia coastal waters.

Setchell (1927) felt that the slow rise in water temperature observed for areas inhabited by *Z. marina* var. *latifolia* resulted in a longer growing season which allowed for the full vegetative development of the plant. The typical form of the Atlantic Coast was thus merely an underdeveloped form of var. *latifolia*. Setchell (1927) did not attempt to account for the short, narrow growth form (var. *angustifolia*) of the Atlantic Coast described in an earlier work (Setchell 1920) and makes no mention of the presence of the typical form of the Atlantic Coast along the Pacific Coast. Den Hartog (1970) felt that there was considerable overlap of the upper size limit of the typical form and the lower size limit of var. *latifolia* and regarded the two forms as phenotypes of the taxon, *Z. marina*.

In Humboldt Bay, northern California Keller (1963) found an increase in mean turion length of intertidal *Z. marina* with increased depth but failed to remark on the significance of this relationship in this and in a later paper (Keller and Harris 1966). A similar relationship of increased leaf dimensions with depth was observed by Phillips (1972) in Puget Sound, Washington. He used reciprocal turion transplants across two tidal zones (intertidal and subtidal) and leaf measurements of turions from three broad tidal zones (MLLW, MLLW to LLLW, and below LLLW) to investigate the influence of depth on leaf dimensions. In the United States, mean low water (MLW), the average of all low waters, is the plane which represents Chart Datum on the Atlantic Coast and mean lower low water (MLLW), the average of the lower of the two low waters each day, is the plane for the Pacific Coast (Chapman 1960). Phillips (1972) concluded that the variation in leaf dimensions across tidal zones was attributable to phenotypic plasticity and discounted the validity of varietal distinctions based on leaf measurement information for Puget Sound eelgrass. An increase in leaf length with depth has been reported for other seagrasses (Strawn 1961). An inverse relationship of leaf length and depth for *Z. marina* is reported by Burkholder and Doheny (1968) for Long Island, New York but is not substantiated elsewhere in the literature.

Tidal elevation exerts considerable influence on other characteristics of eelgrass populations. These include reproductive and vegetative turion density, leaf standing crop, biomass and phenology. Studies of eelgrass turion density on the Pacific Coast of North America report conflicting results. Keller and Harris (1966) found that the highest elevation they considered (0.3 meters above MLLW) had the lowest turion density; more significantly, however, their data reveal that turion density decreased above and below mean lower low water (MLLW). This relationship was also reported from Puget Sound, Washington (Phillips 1972) where turion density decreased from MLLW with greater depth and Alaska (McRoy 1972) where subtidal eelgrass density was less than intertidal turion density. Reproductive turion density was also greater in the intertidal zone of Puget Sound (Phillips 1972). Conversely, Stout (1976), working in Netarts Bay, Oregon, found that deep water eelgrass had significantly higher total and reproductive turion densities than shallow water eelgrass. She considered shallow and deep water eelgrass as distinct groups but failed to provide any elevational or morphological information for the two types.

In the same study Stout found that the deep water eelgrass had a much higher biomass per square meter than the shallow water eelgrass. These results do not agree with those of other Pacific Coast eelgrass studies. Phillips (1972) reported that intertidal biomass always exceeded subtidal biomass at his Bush Point, Washington study site and at Alki Point, Washington subtidal biomass only exceeded intertidal biomass from July to September when a large increase in subtidal leaf standing crop occurred. Eelgrass biomass increased from the upper limit of eelgrass growth (0.5 meters above MLLW) to -0.5 meters and decreased gradually thereafter to its lower limit of -2.75 meters in southern California (Backman and Barilotti 1976). Similarly, Keller and Harris (1966) describe an increase in leaf standing crop of intertidal eelgrass from its upper limit of 0.3 meters above MLLW to -0.3 meters and a slight decrease at the lowest elevation (-0.5 meters) they studied.

The influence of tidal elevation, across broad tidal zones, on such phenological events as seasonal changes in leaf and rhizome standing crops, total biomass and turion density is described for Puget Sound by Phillips (1972).

This review of previous ecological studies of *Z. marina* indicates that certain morphological, biomass, and population characteristics of eelgrass are influenced by environmental factors which change with depth. The confusion which exists in the literature as to the true nature of the change in these characteristics with depth can be attributed to:

1. studies conducted over only a portion of the tidal range of eelgrass (Keller 1963, Keller and Harris 1966)
2. studies describing the influence of tidal elevation on only one or two parameters (Burkholder and Doheny 1968, Phillips 1974)
3. studies comparing eelgrass characteristics across broad tidal zones, e.g. intertidal and subtidal (McRoy 1972), shallow and deep (Stout 1976).

Liebig's law of the minimum, that plant yield is dependent on the nutrient present in minimum quantity, has been generally expanded to the broader ecological concept of limiting factors, i.e., that the condition which approaches or exceeds the limits of tolerance of an organism is said to be a limiting factor.

The upper limit of *Z. marina* growth is determined by desiccation of the plant which, in turn, is a function of tidal exposure and substrate composition (den Hartog 1970). The factor controlling the lower limit of eelgrass is light availability (Phillips 1972, Backman and Barilotti 1976). In turbid coastal and estuarine waters, water clarity influences the light environment of eelgrass (Burkholder and Doheny 1968) and, consequently, the photosynthetic activity of the plant. It is reasonable to expect that these two very different limiting factors, light and desiccation, influence the previously described characteristics of eelgrass in different ways as its upper and lower distributional limits are approached.

A study of seasonal changes in total and reproductive turion densities, leaf standing crop and leaf and rhizome dimensions, from the upper to the lower limits of eelgrass growth, provides a means of determining the influence of tidal elevation on eelgrass characteristics. Such a study would also provide insight into the ways in which limiting factors influence the vegetative characteristics of eelgrass near its tolerance limits.

1.3. Objectives of the Study

Considering the purpose of the study, and previous autecological research on eelgrass, the following objectives were established:

1. To assess the seasonal and diurnal changes in environmental factors of eelgrass habitat on southern Roberts Bank.
2. To determine the influence of tidal elevation, from the upper to the lower limits of eelgrass distribution, on eelgrass standing crop, reproductive and total turion densities, and leaf and rhizome dimensions during the growing season.
3. To describe biomass changes of eelgrass during a growing season.
4. To collate the above information to better understand the habitat requirements and growth characteristics of eelgrass on southern Roberts Bank.

2. THE STUDY AREA

The study area, shown in Figure 1, is approximately 20 kilometers south of the City of Vancouver. The geographical location of the study site, adjacent to and south of the Tsawwassen Ferry Terminal Causeway, is 49° 00' N. latitude, 123° 07' W. longitude. Roberts Bank adjoins the southern Strait of Georgia between the main distributary channel of the Fraser River and the Canada-USA International Boundary. The study site is approximately 6 kilometers due south of the mouth of the south arm of the Fraser River. Field reconnaissance and information from aerial photographs and topographic maps were used in the selection of the study site, as shown in Figure 2. A uniform cover of eelgrass from the upper to the lower elevational limits of eelgrass growth, and accessibility, both on foot and by boat, were major considerations in selecting the study site.

The Fraser River Delta is composed of recent sediments several hundreds of feet thick over Pleistocene sediments (Mathews and Shepard 1962). An excellent summary of the geology of the Fraser River Delta is given by Luternauer (Hoos and Packman 1974). Kellerhals and Murray (1969) describe the sedimentary characteristics of the tidal flats covered by eelgrass in Boundary Bay.

Previous vegetation studies of the Fraser River estuary have been largely descriptive and all but two have ignored the submerged vascular plants. General marsh descriptions are provided by Forbes (1972a,b), McLaren (1972)

Fig. 1. Aerial photo mosaic of the Fraser River Delta showing location of the study area.

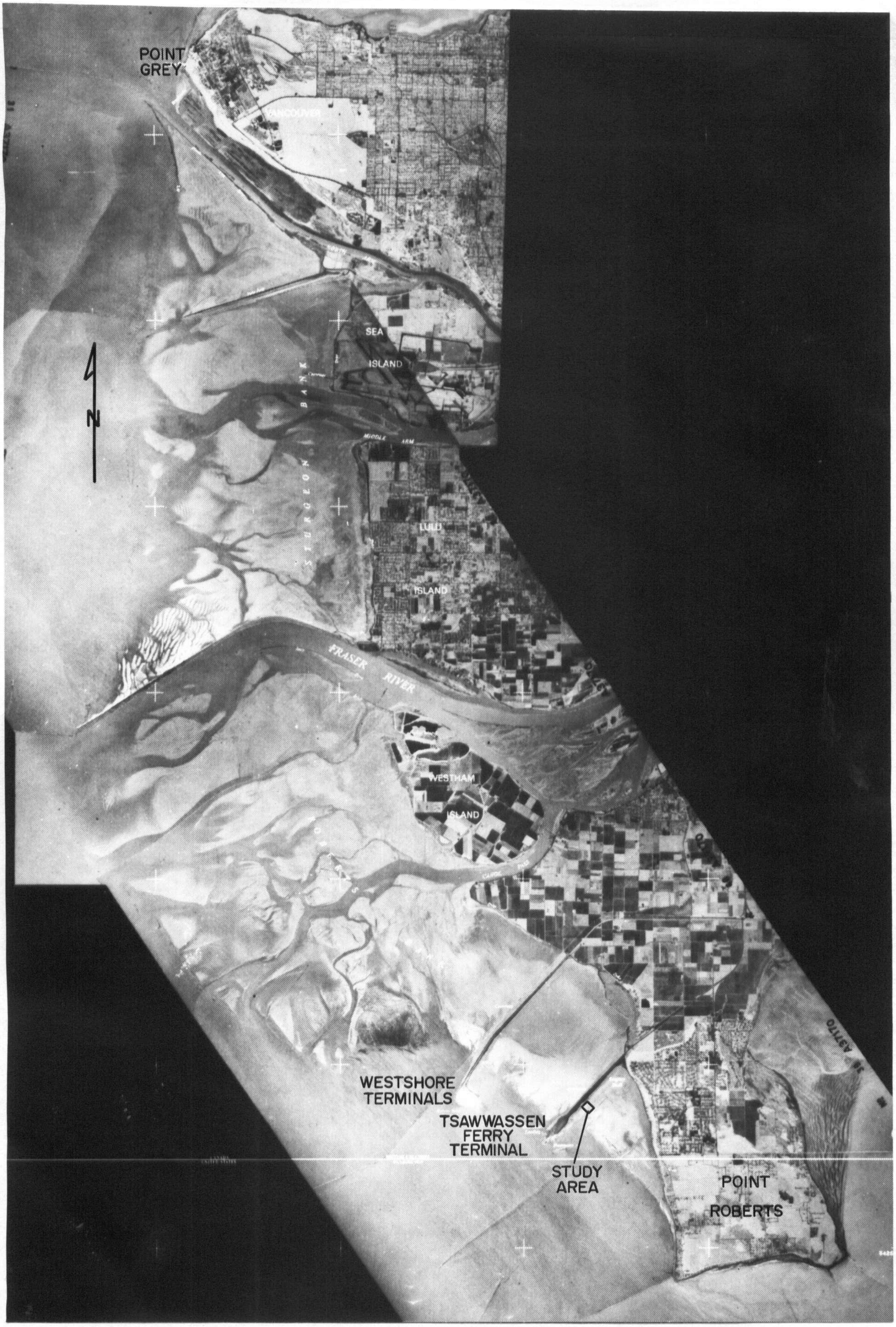
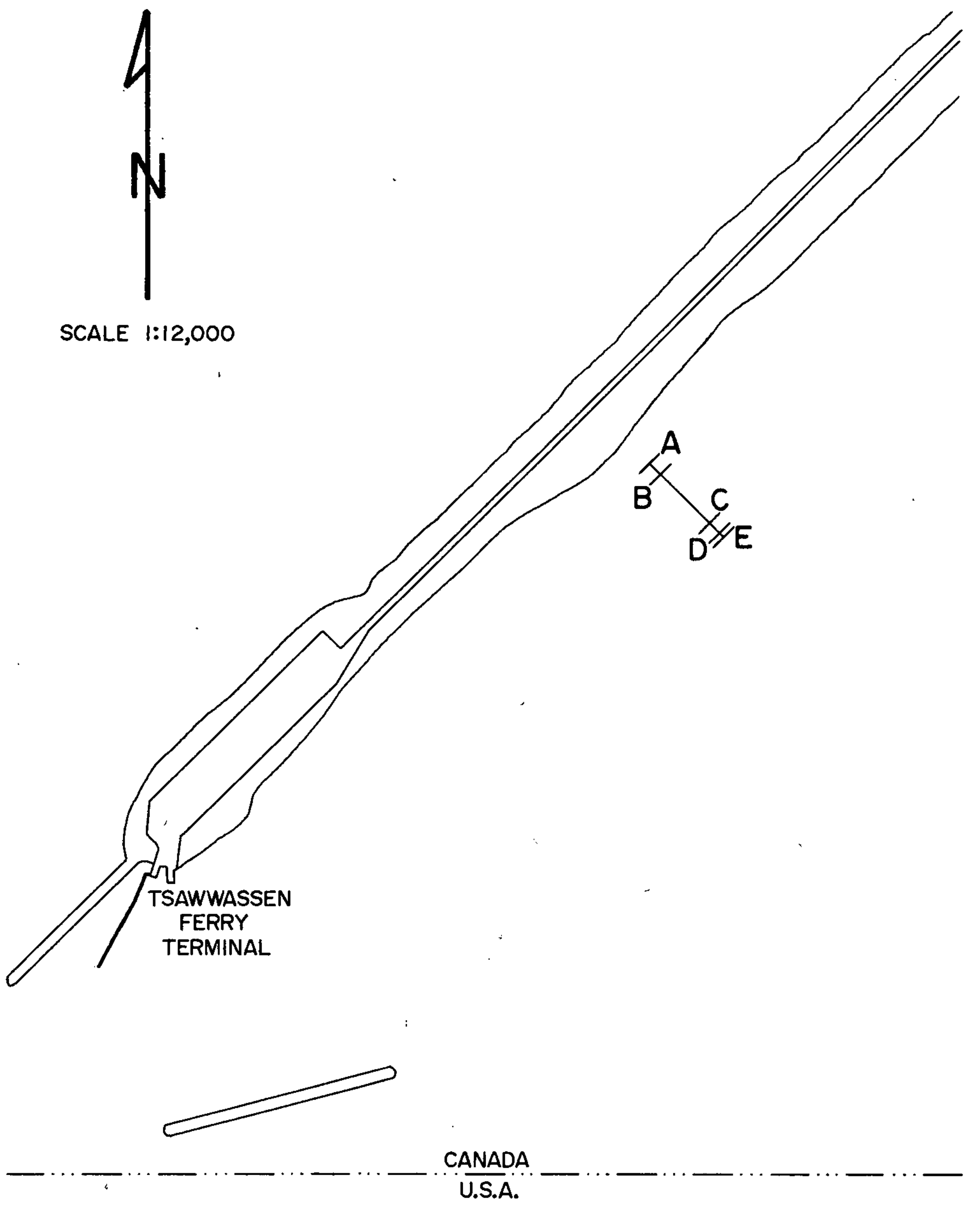

POINT GREY
VANCOUVER
SEA ISLAND
MIDDLE ARM
STURGEON BANK
LULU ISLAND
FRASER RIVER
WESTHAM ISLAND
WESTSHORE TERMINALS
TSAWWASSEN FERRY TERMINAL
STUDY AREA
POINT ROBERTS
N

Fig. 2. Diagram of the study site showing transect locations.


N
SCALE 1:12,000
A
B
C
D
E
TSAWWASSEN
FERRY
TERMINAL
CANADA
U.S.A.

and Hillaby and Barrett (1976). Forbes (1972c) provides rough maps and estimates of eelgrass coverage for the Fraser River foreshore and Boundary Bay. Historical changes in the Roberts Bank eelgrass bed and habitat and population characteristics of Roberts Bank eelgrass are described in an environmental impact assessment of Roberts Bank port expansion prepared for the National Harbours Board, Port of Vancouver (1977) by Beak Consultants Ltd. Yield estimates of the major emergent marsh plants are given by Yamanaka (1975) but information on the submergent vegetation is lacking. Similarly, Burgess (1970) describes the importance of various emergent species to several species of dabbling ducks on the Fraser foreshore marshes. Burgess reports that the physical environment of the tidal marshes exerts strong influences on the composition and distribution of the vegetation.

The estuarine waters adjacent to the Fraser River foreshore are highly stratified (Hoos and Packman 1974), a factor which is strongly influenced by wind and tide-driven currents. Tides in the southern portion of the Strait of Georgia are of the mixed, mainly diurnal type. At the study site the mean tidal range is 3.05 meters; for large tides the range averages 4.69 meters. Mean water level, the average of all hourly observations, is 2.96 meters. During the summer, extreme lower low water associated with the spring tides occurs near midday; in the winter, near midnight. The times are reversed for extreme higher high water (Canadian Hydrographic Service 1976). In Canada, Chart Datum (CD) is the plane of lowest normal tides and is therefore below mean lower low water (MLLW). At the study site MLLW is 1 meter above CD.

Development proposals for areas along the Fraser River foreshore have increased greatly in recent years. The proximity of the Fraser River Estuary to the large and rapidly growing metropolis of Vancouver, the increasing recreational demands of the populace, and the progressive industrialization of the area are all important factors in the encroachment on foreshore lands. Several of the proposed developments are discussed in Hoos and Packman (1974) and Harris and Taylor (1973). The influence of the adjacent urban and industrial areas on the water quality of the lower reaches of the Fraser River is discussed at length by Dorcey (1976).

On southern Roberts Bank recent developments have taken the form of port and causeway construction. The Tsawwassen Ferry Terminal and Causeway were constructed in 1960. In 1970 the Westshore Terminal port facility and causeway were built across southern Roberts Bank. In addition, several power and telecommunication cables have been laid across the intertidal sand flats of Roberts Bank. Current proposals to further develop southern Roberts Bank include a multi-fold expansion of the Westshore Terminal port facility. Depending on the ultimate form of the port expansion, the effects on the eelgrass resource of southern Roberts Bank will vary from slight to considerable.

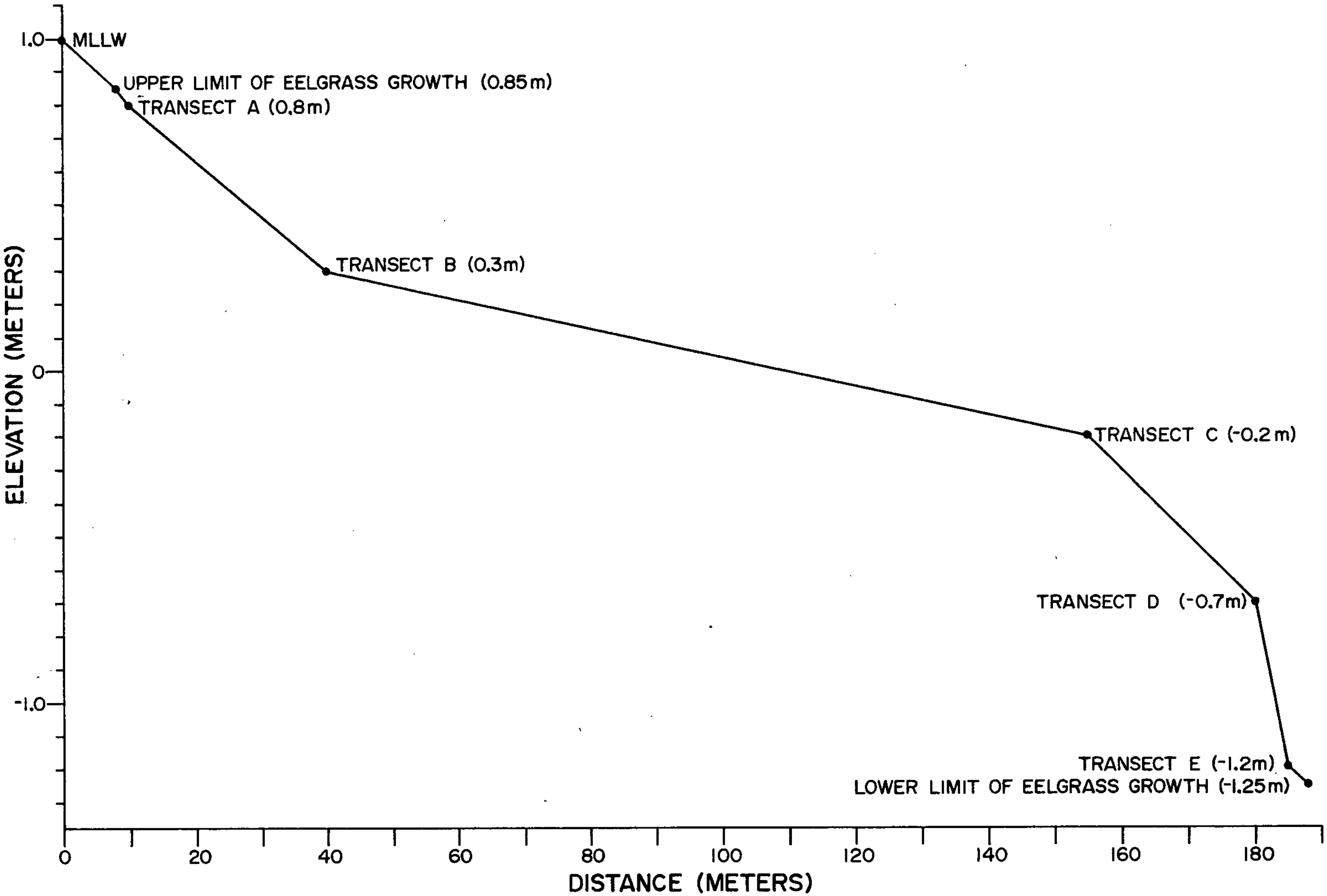
3. ENVIRONMENTAL FACTORS IN RELATION TO EELGRASS HABITAT

3.1. Materials and Methods

Seasonal changes in salinity, temperature and water clarity were determined from measurements made every 2 weeks from April to August 1976 and monthly thereafter to January 1977. Diurnal changes in salinity, temperature, water clarity and light were monitored on four occasions during the study period, corresponding to the spring, summer, fall and winter conditions in the study area. Figure 3 is a schematic profile of the study site. All measurements were taken just seaward of the lower boundary of the eelgrass bed and, with the exception of the diurnal monitoring program, were made between 10.00 and 14.00 hours. Salinity and temperature were measured *in situ*, at the surface and 1.5 meters below surface, with a YSI Model 1486 portable Salinity-Conductivity-Temperature meter. This instrument measures electrical conductivity and temperature and computes salinity from these measurements. The manufacturer lists its accuracy at $\pm 0.1^{\circ}C$ at $-2^{\circ}C$ for temperature and $\pm 0.7‰$ at 20‰ for salinity.

A 30 cm (diameter) Secchi disc was used to measure the transmission of visible light through the water column. The disc was lowered into the water until it disappeared and slowly raised until it reappeared. Secchi depth, a measure of water clarity, was recorded as the average of these two readings. Diurnal changes in photosynthetically active

Fig. 3. Schematic profile of the study site showing transect elevations in relation to Chart Datum.



1.0
0
-1.0
MLLW
UPPER LIMIT OF EELGRASS GROWTH (0.85m)
TRANSECT A (0.8m)
TRANSECT B (0.3m)
TRANSECT C (-0.2m)
TRANSECT D (-0.7m)
TRANSECT E (-1.2m)
LOWER LIMIT OF EELGRASS GROWTH (-1.25m)
ELEVATION (METERS)
0
20
40
60
80
100
120
140
160
180
DISTANCE (METERS)

radiation (PAR) were measured with a LI-COR Model LI-185 Quantum/Radiometer/Photometer equipped with an underwater quantum sensor.

The upper limit of eelgrass growth was determined using predicted tidal information for the Secondary Port of Tsawwassen contained in the 1976 Tide and Current Tables of the Canadian Hydrographic Service. Transect A was established just within the upper boundary of the eelgrass bed and the other four transects were located at 0.5 meter depth intervals with a survey stadia rod. The lower limit of eelgrass growth was determined at the same time. The elevation of transect A was later confirmed using hourly tidal readings from the Tsawwassen Tidal Station for 1976 obtained from the Institute of Ocean Sciences, Fisheries and Marine Service, Environment Canada, Victoria. This information was also used to determine tidal exposure of transects A and B for 1976.

As there was a need for very accurate information concerning tidal elevations, transects A and B were surveyed from Bench Mark "Geod. No. 66-C-045" located in the wall of the Hull Maintenance Building, Tsawwassen Ferry Terminal, on March 12, 1977. A Keuffel and Esser alidade and plane table were used for the survey. There was good agreement ($\pm$3 cm) between the surveyed elevations and those determined from interpolation of hourly tide heights.

A technique similar to that described by Ranwell et al (1974) was used to monitor sediment surface level oscillations within the eelgrass bed. Twenty 2.5 cm diameter and 30 cm long wooden stakes were pushed into the substrate until 10 cm protruded at 10 meter intervals across the eelgrass bed from the upper to the lower limits of eelgrass growth. The length of stake protruding was measured at intervals from July 1976 to January 1977.

Plexiglas tubes 10 cm long (inside diameter 4 cm) were used to remove sediment cores from areas adjacent to the stakes in October 1976, and the upper 5 cm of each core was subjected to various physical and chemical determinations. Carbonate carbon was determined following the gravimetric method for loss of carbon dioxide described by Black (1965). Organic matter content was found by loss in weight on ignition at 550^{o}C (Wood 1975) and was converted to organic carbon content by division with a factor of 1.8 as recommended by Trask (1939). Dry sieving with a set of nested US Standard Sieves (4.0 to 0.1 cm openings) was used to perform the particle size analysis. Approximately 40 g of dry sediment were placed in the top sieve and the set of sieves was shaken on a ROTAP machine for 2 minutes.

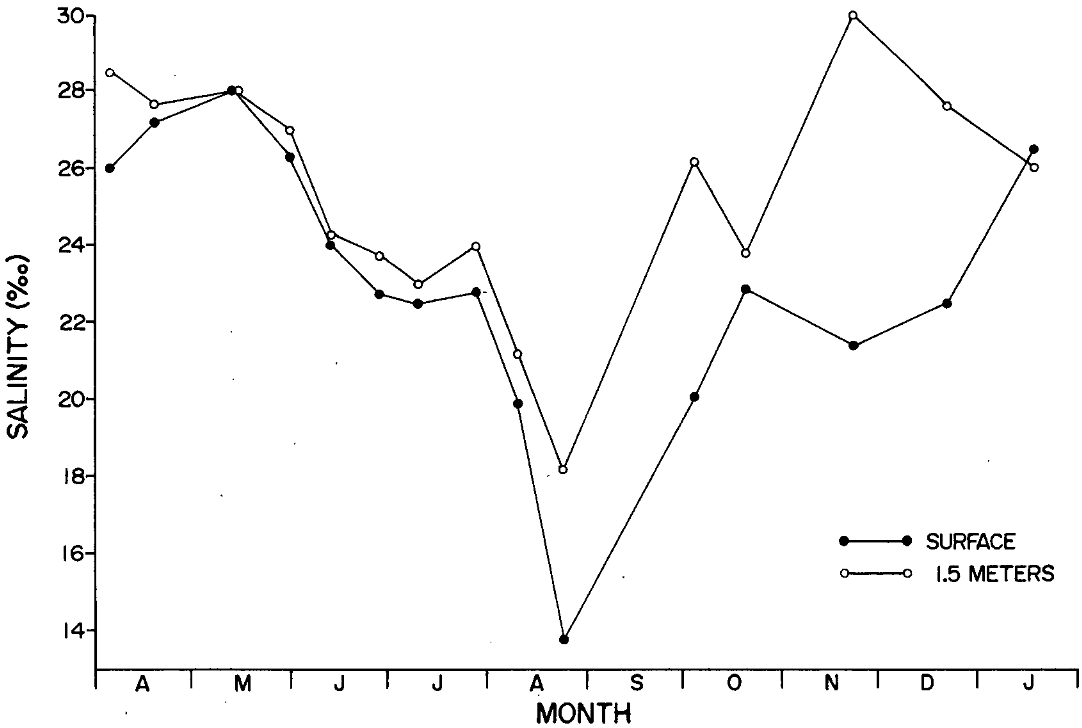
3.2. Habitat Factors

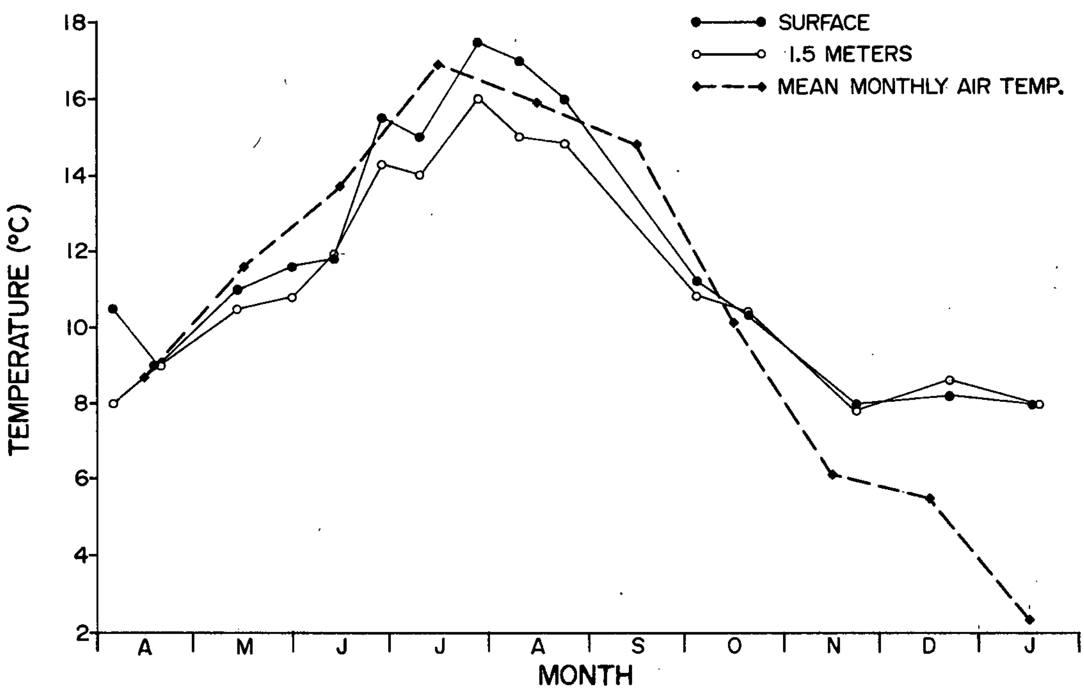
3.2.1. Salinity

3.2.1.1. Seasonal Changes

The 1.5 m salinity (Figure 4) was consistently greater than surface salinity except for one anomalous set

Fig. 4. Surface and 1.5 m salinities and temperatures at the study site and mean monthly air temperature at Vancouver International Airport (Monthly Record, Meteorological Observations in Canada, Atmospheric Environment, Fisheries and Environment Canada, April 1976 to January 1977). Mean monthly air temperature plotted at the midpoint of each month.


30
28
26
24
22
20
18
16
14
SALINITY (‰)
SURFACE
1.5 METERS
A
M
J
J
A
S
O
N
D
J
MONTH


18
16
14
12
10
8
6
4
2
TEMPERATURE (°C)
SURFACE
1.5 METERS
MEAN MONTHLY AIR TEMP.
A
M
J
J
A
S
O
N
D
J
MONTH

of measurements in mid-winter. Surface and 1.5 m salinity differences are on the order of 1 to 2‰ in the spring and early summer, and increase two- to threefold by late summer. The pronounced salinity stratification is maintained until winter.

3.2.1.2. Diurnal Changes

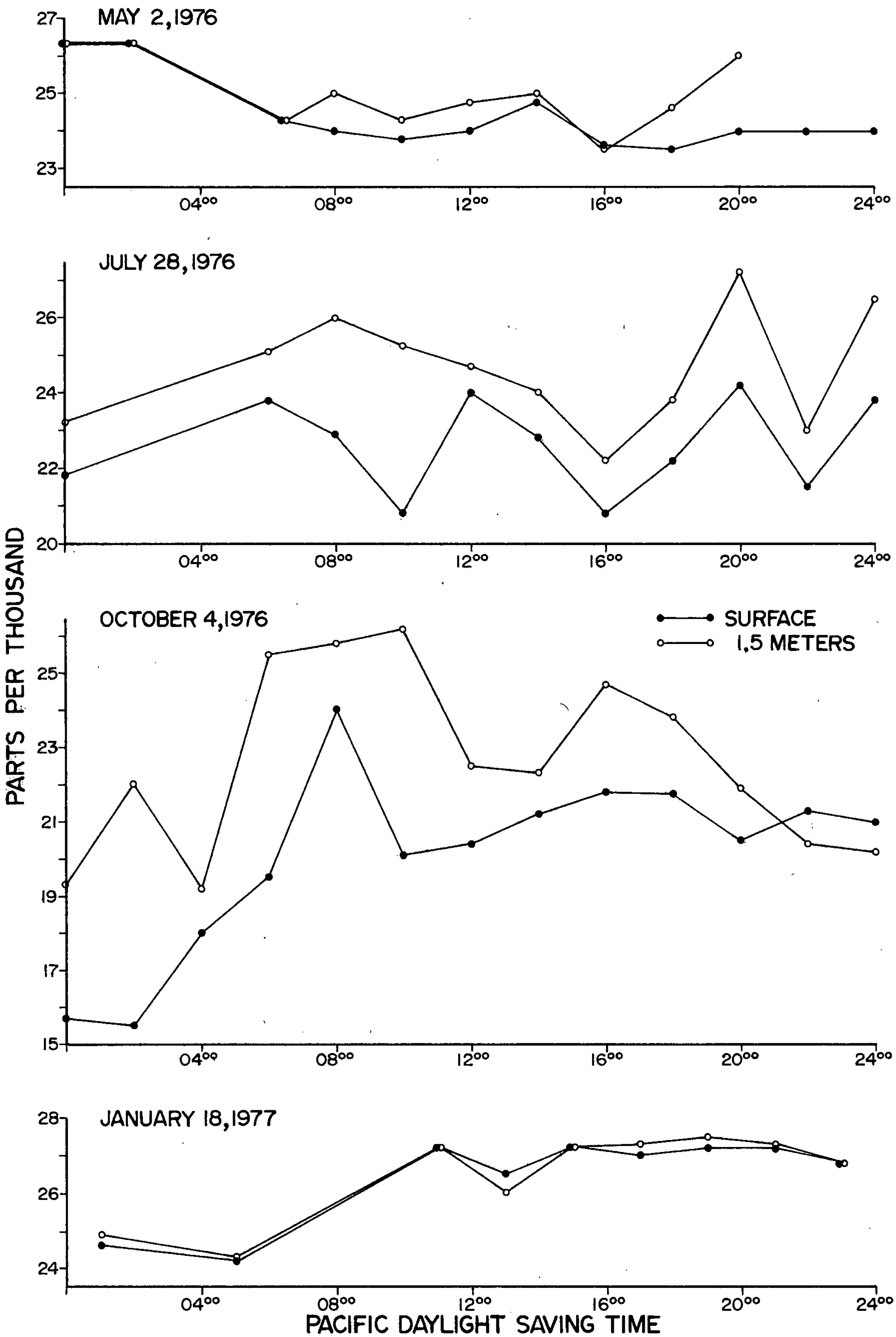
The diurnal salinity measurements of Figure 5 reflect, to a great extent, the pertinent features of the seasonal salinity changes. Observations of May 2, 1976 and January 18, 1977 show that the water column was well mixed in the winter and spring. On July 28, 1976 the higher salinity at 1.5 meters was maintained across two complete tidal cycles. By October the salinity difference of surface and subsurface waters was greater than that observed during the summer.

3.2.2. Temperature

3.2.2.1. Seasonal Changes

Seasonal trends in water temperature resemble salinity in that the thermal stratification apparent in the summer disappears during the rest of the year (Figure 4). The seasonal increase and decrease in water temperature follows the mean monthly air temperature curve for Vancouver International Airport, 20 kilometers north, closely until fall when the curves diverge and the mean monthly air temperature becomes increasingly lower than the sea temperature.

Fig. 5. Diurnal surface and 1.5 m salinities. May 2, July 28 and October 4, 1976. January 18, 1977.


MAY 2, 1976
27
25
23
JULY 28, 1976
26
24
22
20
OCTOBER 4, 1976
SURFACE
1.5 METERS
25
23
21
19
17
15
JANUARY 18, 1977
28
26
24
04⁰⁰
08⁰⁰
12⁰⁰
16⁰⁰
20⁰⁰
24⁰⁰
PARTS PER THOUSAND
PACIFIC DAYLIGHT SAVING TIME

3.2.2.2. Diurnal Changes

Figure 6 indicates that winter and spring surface and subsurface water temperatures were very constant over the 24-hour sampling period. The water column is well mixed during these seasons. In the summer the temperature of the air is warmer than that of the surface water which is, in turn, warmer than the deeper water. The diurnal temperature information for October 4, 1976 illustrates how the warming effect of the sun can influence the temperature relationships of the air and surface and subsurface waters. As the sun rose above the horizon, air temperature increased and surpassed first subsurface, then surface water temperature; a concomitant rise in surface water temperature above subsurface water temperature also occurred.

3.2.3. Light

3.2.3.1. Seasonal Changes

There is an obvious inverse relationship between the seasonal discharge cycle of the Fraser River and the Secchi depth of waters at the study site (Figure 7).

3.2.3.2. Diurnal Changes

Secchi depth measurements and light data collected during the diurnal monitoring sessions show more variability within than between sampling sessions. No trends could be discerned from the information as gathered (Appendix 4).

Fig. 6. Diurnal air temperatures and surface and 1.5 m water temperatures. May 2, July 28 and October 4, 1976. January 18, 1977.

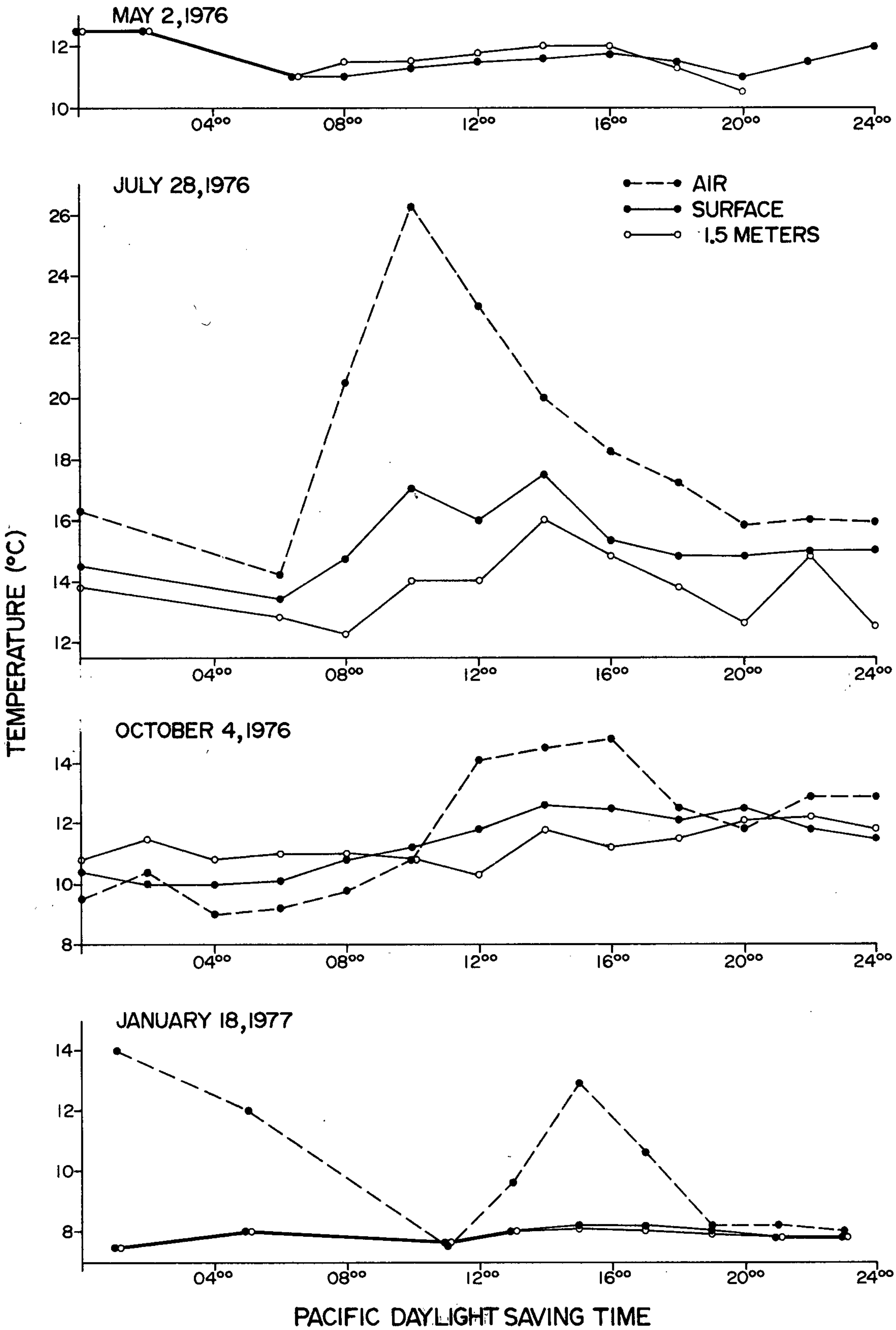
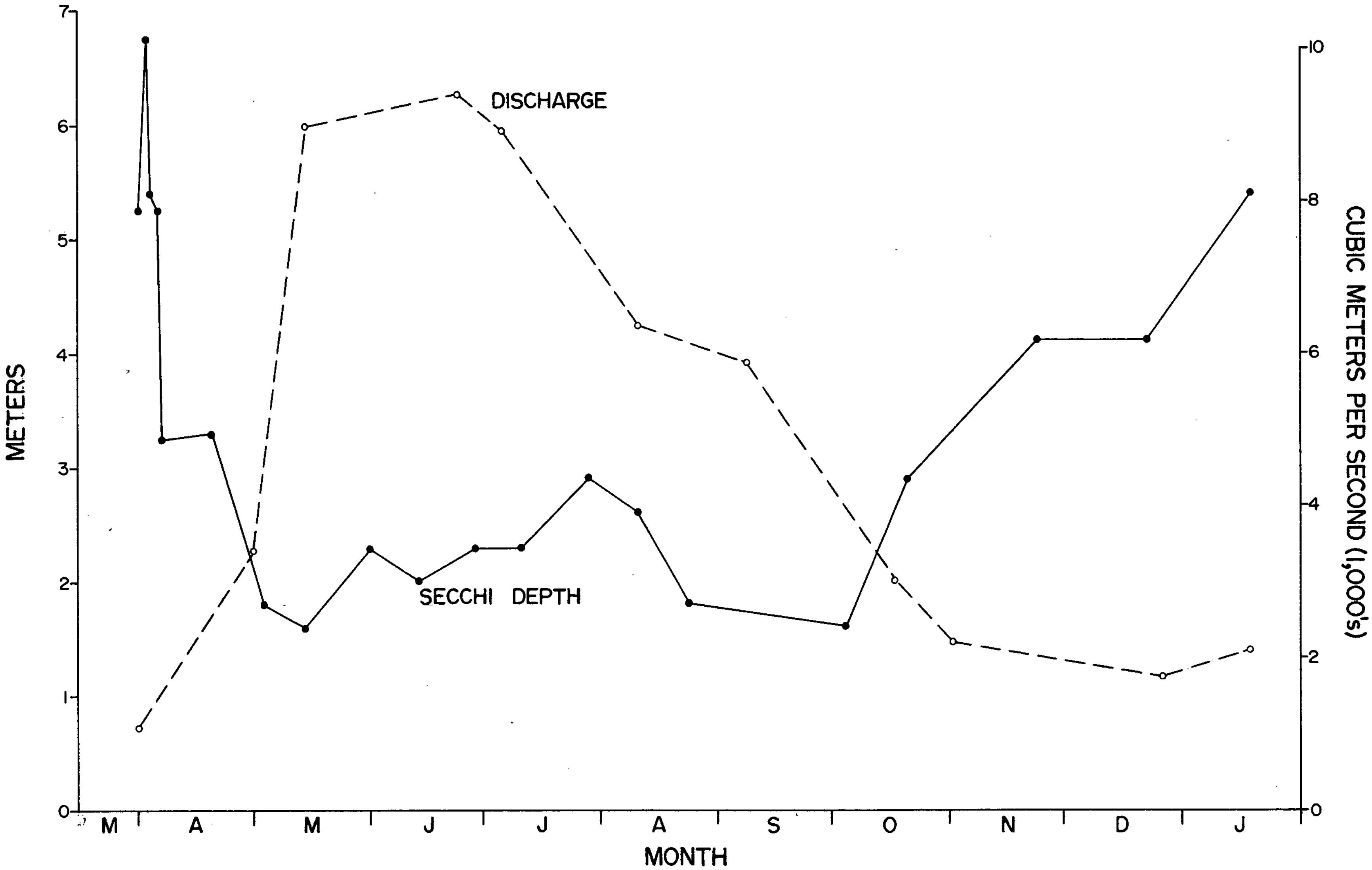

MAY 2, 1976
JULY 28, 1976
OCTOBER 4, 1976
JANUARY 18, 1977
AIR
SURFACE
1.5 METERS
TEMPERATURE (°C)
PACIFIC DAYLIGHT SAVING TIME
04⁰⁰
08⁰⁰
12⁰⁰
16⁰⁰
20⁰⁰
24⁰⁰

Fig. 7. Secchi depth (meters) at the study site and maximum daily discharge (thousands of cubic meters per second) of the Fraser River at Hope, B.C. for each month from March 1976 to January 1977.


DISCHARGE
SECCHI DEPTH
METERS
CUBIC METERS PER SECOND (1,000's)
MONTH
M A M J J A S O N D J
0 1 2 3 4 5 6 7
0 2 4 6 8 10

Atmospheric conditions on the four days selected for diurnal monitoring were highly variable. May 2, 1976 was overcast with periods of rain showers. Morning fog which cleared away before noon, bright sunshine during midday and high clouds by late afternoon occurred on July 28, 1976. October 4, 1976 was sunny with cloudy periods and January 18, 1977 was cloudy with a few sunny periods.

3.2.4. Tidal Range and Percentage Exposure

At the study site the upper limit of eelgrass growth was 0.85 meters Chart Datum (-0.15 m MLLW) (Figure 2) and the lower limit was -1.25 m CD (-2.25 m MLLW); thus the depth range for eelgrass in this area is approximately 2 meters. Percentage exposures were calculated for the two intertidal transects (A and B) from hourly tidal readings at the Tsawwassen Tidal Station, located 1 kilometer west of the study site, for 1976. Two methods were used. The first method totalled the number of hours during which the study elevations were exposed in 1976 and this total was expressed as a percentage of the total number of hours in 1976. This method indicated that transect A was exposed 1.00% of the year and transect B, 0.034% of 1976. The second, more detailed method entailed direct interpolation of tidal heights between all hourly observations which included but did not encompass the two elevations. This method revealed that transect A had a percentage exposure of 0.936 and transect B was exposed 0.006% of the year. The first method overestimated the percentage exposure of the lower elevation (transect B) by more than fivefold.

3.2.5. Substrate

3.2.5.1. Surface Level Changes

Figure 8 depicts net substrate surface level oscillations observed at the study site within the boundaries of the eelgrass bed. There was an accumulation of sediments until late summer when sediments were transported out of the eelgrass bed. The overall erosion observed during the study period was approximately 2 cm.

3.2.5.2. Physical and Chemical Characteristics

Results of a mechanical analysis of sediment samples collected at 10 meter intervals across the eelgrass bed at the study site are shown in Table 1. The sample taken at the upper edge of the eelgrass bed is better sorted than samples taken at 10, 20 and 30 meters inside the upper edge, which are the most poorly sorted of all. Sorting of samples more than 30 meters from the upper edge increases with depth until just before the lower edge of eelgrass is reached. A moderate decrease in degree of sorting occurs near the lower distributional limit of eelgrass. Fines content (Figure 9) exhibits a similar decline with depth at distances greater than 30 meters from the upper edge and a slight increase near the lower limit.

Fig. 8. Net oscillations of sediment surface levels, July 1976 to January 1977. Mean ± Standard Error.

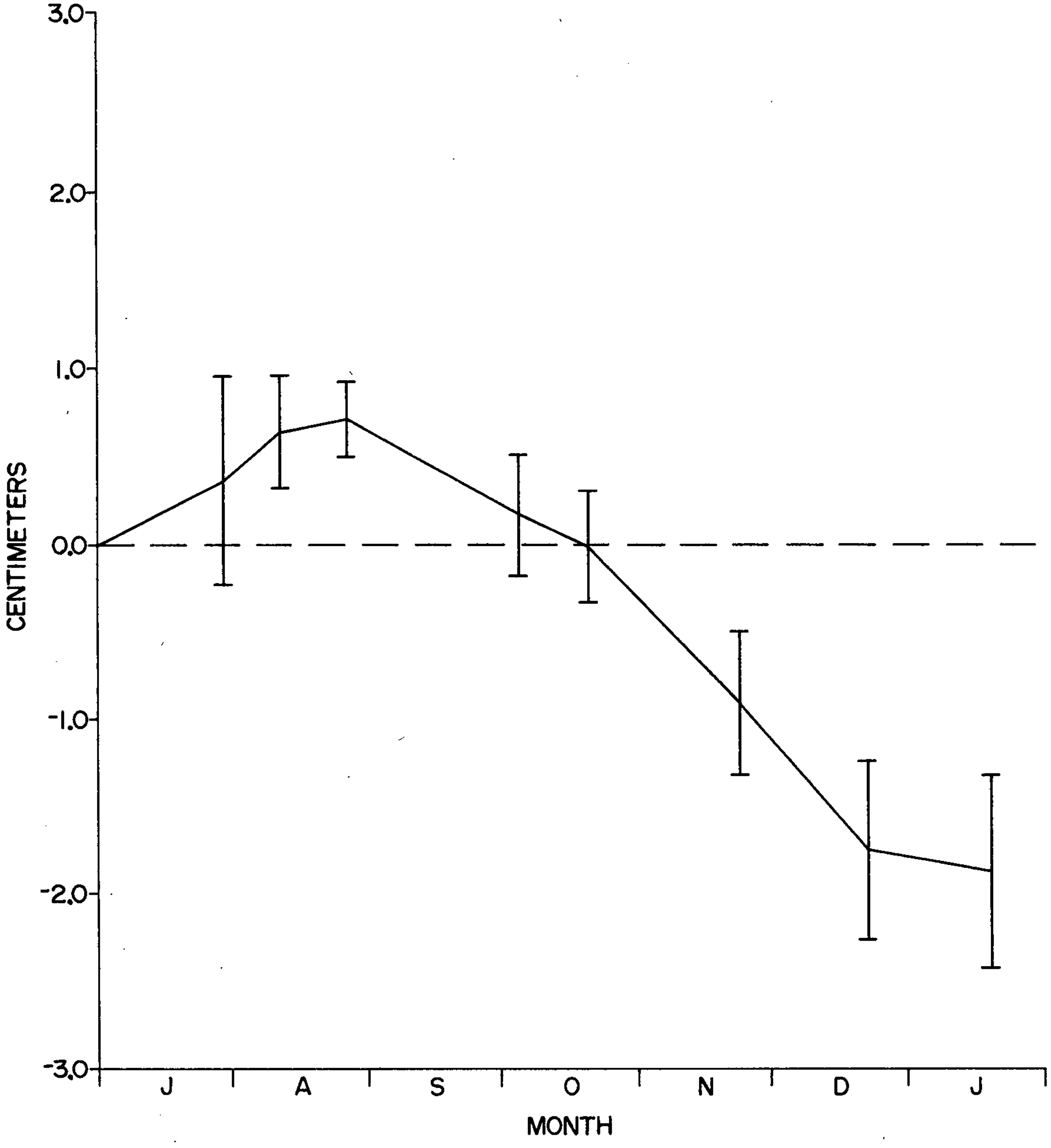
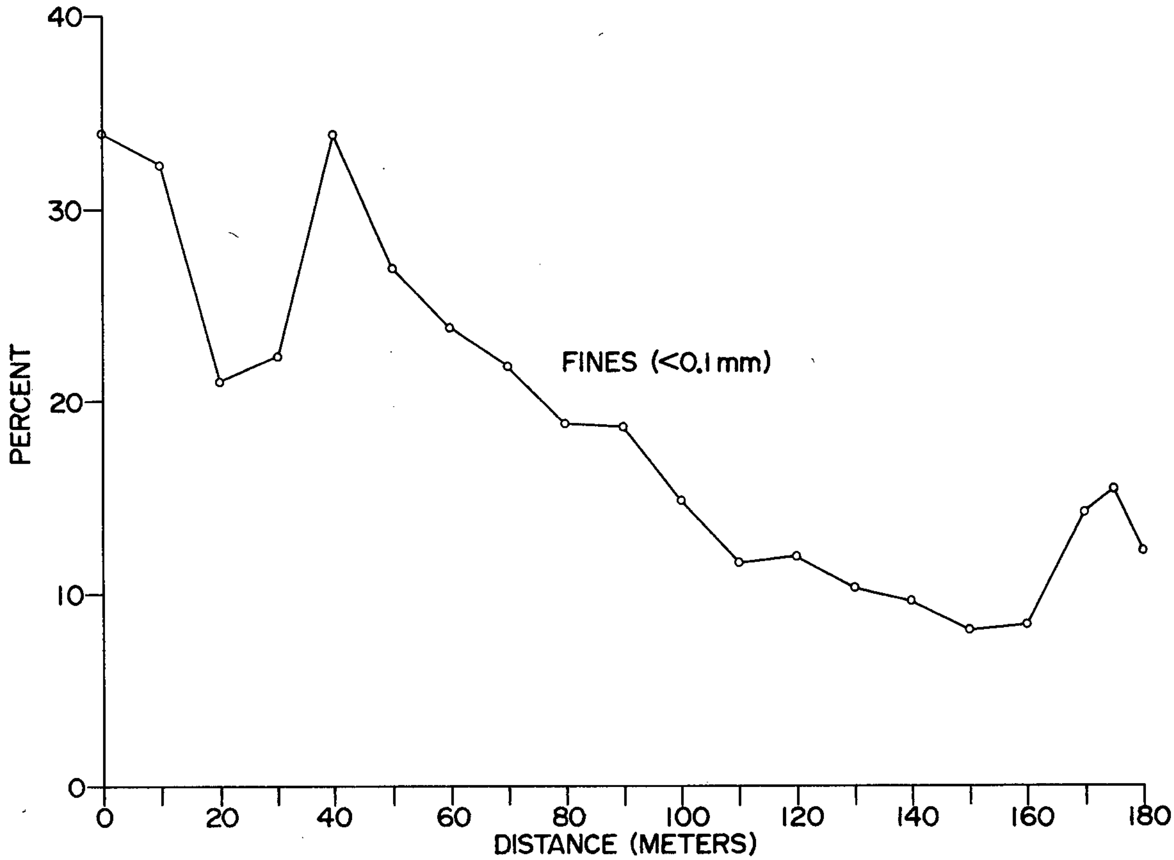
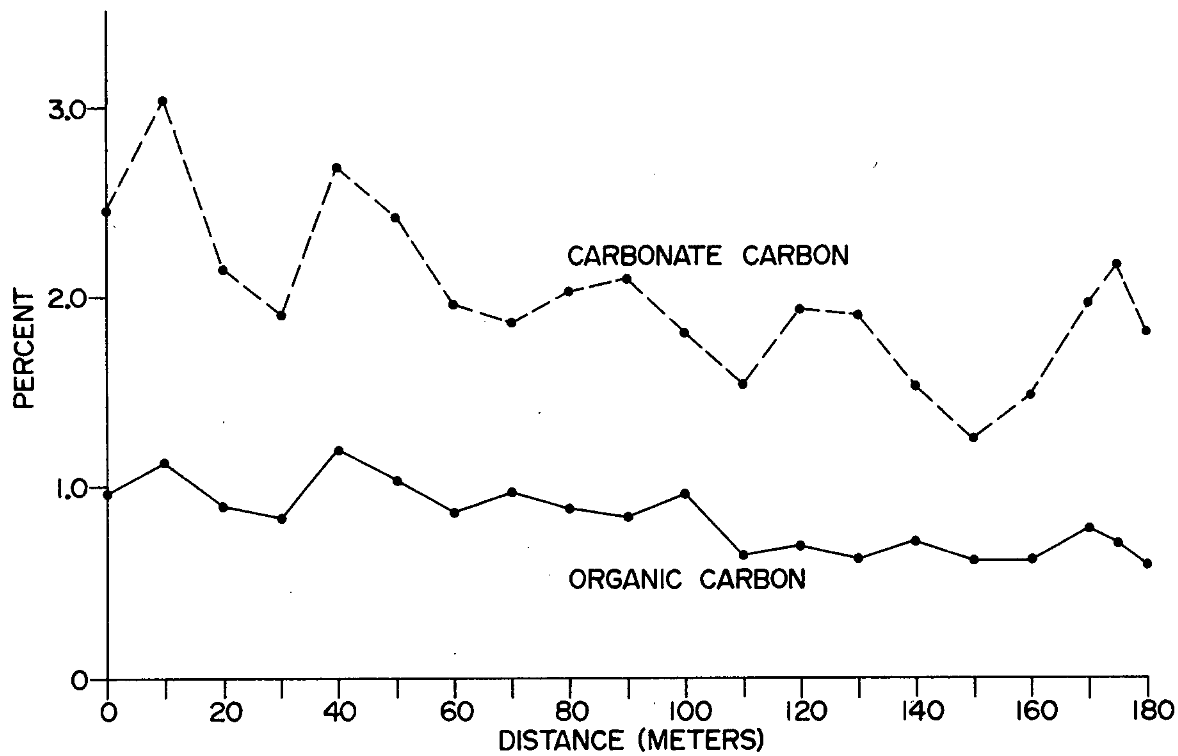

3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
CENTIMETERS
J
A
S
O
N
D
J
MONTH

Table 1. Particle size composition of sediments

	Particle Size (%)				
Distance (m) from Upper Edge of Eelgrass Growth	<0.10 mm	0.10 mm to 0.25 mm	0.25 mm to 0.50 mm	0.50 mm to 1.0 mm	>1.0 mm
0	33.86	57.70	5.11	1.44	1.89
10	32.21	44.03	21.22	1.23	1.31
20	21.06	47.67	27.66	1.78	1.83
30	22.29	43.47	29.55	2.42	2.26
40	33.87	54.22	6.96	1.72	3.23
50	26.78	62.26	5.47	1.08	4.40
60	23.87	66.48	4.58	.88	4.19
70	21.75	69.22	4.85	.66	3.51
80	18.82	71.96	5.30	.64	3.28
90	18.68	69.77	4.75	3.35	3.45
100	14.74	74.25	6.94	.86	3.06
110	11.57	77.61	7.66	6.26	2.53
120	11.89	76.68	8.02	.80	2.61
130	10.31	76.98	8.29	1.36	3.06
140	9.61	80.47	6.88	.65	2.38
150	8.05	79.95	8.61	1.27	2.12
160	8.47	78.80	9.12	1.06	2.56
170	14.17	73.26	7.73	1.34	3.51
175	15.34	70.52	8.90	1.70	3.55
180	12.23	72.36	12.17	1.54	1.69

Fig. 9. Sediment samples taken at 10-meter intervals from the upper to the lower limits of eelgrass growth:
a. Percentage of fines
b. Percentages of organic and carbonate carbon.


FINES (<0.1 mm)
PERCENT
DISTANCE (METERS)
0
10
20
30
40
0
20
40
60
80
100
120
140
160
180


CARBONATE CARBON
ORGANIC CARBON
PERCENT
DISTANCE (METERS)
0
1.0
2.0
3.0
0
20
40
60
80
100
120
140
160
180

The apparent anomaly that the stations located 10, 20 and 30 meters inside the upper edge have lower percentages of fines than adjacent stations and yet are more poorly sorted is explained by the high larger sand fractions (greater than 0.5 mm diameter) of these stations.

Percentage contents of carbonate carbon and organic carbon (Figure 9, Table 2) decline with distance from the upper limit of eelgrass growth. A moderate increase is noted for both near the lower edge of eelgrass.

3.2.6. Waves and Currents

Although current velocities were not measured at the study site, general observations made during the study period indicate only gentle currents occur across the eelgrass bed. Excessive wave action did not appear to be an important factor at the study site as it is protected by the adjacent Tsawwassen Ferry Terminal Causeway and, to a lesser extent, by nearby Point Roberts peninsula.

3.3. Discussion

Zostera marina L. is a euryhaline, eurythermal seagrass which inhabits the shallow, protected coastal waters where suitable substrate is available (Table 3). The salinity, temperature and water motion conditions of southern Roberts Bank are close to the world-wide optima for these habitat factors as indicated by Table 3. The other habitat factors studied, light, substrate and exposure, appear to account

Table 2. Organic and carbonate carbon contents of sediments

	Content (%)	
Distance (m) from Upper Edge of Eelgrass Growth	Organic Carbon	Carbonate Carbon
0	.96	2.45
10	1.12	3.03
20	.89	2.14
30	.83	1.90
40	1.19	2.68
50	1.03	2.42
60	.86	1.96
70	.97	1.86
80	.88	2.02
90	.84	2.09
100	.96	1.81
110	.64	1.54
120	.69	1.93
130	.62	1.90
140	.71	1.53
150	.62	1.26
160	.62	1.48
170	.79	1.98
175	.70	2.17
180	.59	1.81

Table 3. Comparisons of habitat factors affecting eelgrass growth (modified from Stout 1976, and Phillips 1972)

TEMPERATURE	
Range World-wide	0 - 40.5°C
Optimum World-wide	10 - 20°C
Southern Roberts Bank Range	7.8 - 17.5°C
SALINITY	
Range World-wide	Freshwater - 42‰
Optimum World-wide	10 - 30‰
Southern Roberts Bank Range	13.8 - 30.0‰
SUBSTRATE	
Range World-wide	pure firm sand to pure soft mud
Optimum World-wide	mixed sand and mud
Southern Roberts Bank Range	sand to mixed sand and mud
WAVE MOTION	
Range World-wide	waves to stagnant water
Optimum World-wide	little wave action, gentle currents
Southern Roberts Bank	gentle currents, low wave shock
DEPTH	
Range World-wide	MLLW to -30 meters
Optimum Puget Sound	-1 to -4 meters
Southern Roberts Bank Range	MLLW to -2 meters

for the narrow depth distribution of eelgrass on southern Roberts Bank.

Den Hartog (1970) states that the depth attained by eelgrass depends greatly on light intensity and hence water clarity, suspended materials in the water column, etc. The ability of eelgrass to extend to greater depths in other areas of the Pacific Coast having clearer waters (Phillips 1972, Backman and Barilotti 1976) suggests that the turbid water of the Fraser River discharge is responsible for the elevated lower limit of eelgrass on the Fraser River foreshore.

In Florida, Strawn (1961) found that tidal exposure was the major factor influencing the zonation of tropical seagrasses. Based on a sample of six 1-week periods over the year, percentage exposures were calculated for six elevations in Humboldt Bay, northern California (Keller and Harris 1966). These determinations indicated that the upper limit of eelgrass growth (0.3 m above MLLW) was exposed to the air about 15 percent of the time. In my study area, transect A (0.8 m above CD, 0.2 m below MLLW), located just inside the upper boundary of eelgrass, was exposed approximately 1 percent of the time during 1976. If desiccation, and hence tidal exposure, does indeed control the upper limit of eelgrass as postulated by den Hartog (1970) and Keller and Harris (1966), how then can this great disparity in percentage exposure for the upper limit of two Pacific Coast eelgrass populations be accounted for?

The answer lies in the fact that desiccation is determined, to a great extent, by substrate characteristics as well as exposure periods. The only sediment information provided for Humboldt Bay (Keller and Harris 1966) are references to patches of bare mud within the eelgrass bed; the sediment in my study area was sand. The greater water-holding capacity of mud may account for the presence of eelgrass higher in the intertidal zone of areas having muddy substrates. On southern Roberts Bank the sandy substrate limits the exposure tolerance of eelgrass and thereby influences the upper distributional limit of the plant.

Net changes in substrate surface levels observed at the study site are the result of changes in prevailing seasonal winds and wave action. The study site is in the lee of the Tsawwassen Ferry Terminal Causeway and protected from the prevailing northwest summer winds; a depositional environment is thus maintained within the boundaries of the eelgrass bed. During the fall and winter the prevailing winds are from the southeast and the study site receives more wave action. There is a resultant net decrease in sediment surface levels at this time of year.

The high percentage of fines (less than 0.1 mm diameter) and organic carbon and the poorly sorted sediments observed near the edges of eelgrass growth provide strong support for the baffling action of the vertical edge of an eelgrass bed proposed by Orth (1973). Organic carbon content and the percentage of fines was positively correlated ($r = 0.89$) for the samples. Carbonate carbon (largely shell fragments) also had high values near the upper and lower limits of eelgrass growth. Field observations indicated that benthic infauna populations of bivalves were highest near the edges of eelgrass growth. My interpretation of the strong correlation of organic and carbonate carbon ($r = 0.79$) across the eelgrass bed is that the infaunal distribution reflects food abundance (organic carbon) which is concentrated near the upper and lower edges of the eelgrass bed as the nutrient-laden currents are slowed by eelgrass.

Various aspects of the data require further consideration and elaboration to assess the validity of the data as gathered. The salinity, temperature and Secchi depth measurements have the limitation of being "point in time" observations. This limitation becomes even more apparent when the highly variable conditions of the estuarine environment are considered. The diurnal monitoring program was undertaken to, among other things, place the seasonal changes in a better perspective. As noted earlier, weather conditions for three of the four diurnal monitoring sessions were unsettled; the extent to which the variable conditions are reflected in the measurements taken is uncertain and for this reason only general trends were extrapolated from the data.

Sediment samples were collected in October 1976. Figure 8 indicates that the surface levels of the substrate fluctuated during the study period and for this reason it is reasonable to assume that the results of the sediment analyses may have been quite different had the samples been collected at some other time. Future studies on the interactions of sediments and marine angiosperms should include the dynamic nature of the sediments in experimental design considerations.

4. STANDING CROP, TURION DENSITY, BIOMASS AND LEAF MEASUREMENT STUDIES

4.1. Materials and Methods

A stratified random sampling technique was used to determine seasonal changes in eelgrass standing crop, turion density and leaf dimensions at five tidal elevations. Anchor blocks were placed at the upper and lower edges of eelgrass growth and joined by a rope which thus bisected the eelgrass bed (Figure 2). Transect A was established just within the upper edge of eelgrass growth and the remaining four transects were located at 0.5 meter depth intervals across the eelgrass bed. The lowest transect, transect E, was just inside the lower limit of eelgrass and was 2.0 meters below the highest transect.

Fifty-meter long nylon lines, marked at 1 meter intervals, were anchored parallel to the depth contours at 0.5 meter depth intervals. The transect lines were placed in such a way that they were bisected by the rope joining the anchor blocks at the upper and lower eelgrass limits. A random number generator was used to select two numbers between 1 and 50 for each elevation and sampling sites were located along the study transects at these numbers. A 0.25 square meter (0.5 m x 0.5 m) steel quadrat was placed on either side of the transect at each of the two locations and all of the turions rooted within the quadrat were clipped at sediment level and placed in cotton sacks. To avoid the possible effects of increased insolation experienced by areas immediately adjacent to sampled quadrats, only alternate possible sample locations were included, that is to say, sample sites were located at whole meter intervals. SCUBA was used for underwater sampling of the vegetation.

Samples were transported to the laboratory and total and reproductive turion counts were made. Individual samples were then washed for 2 minutes in a portable Hoover washing machine to remove epiphytes and spun for 1 minute in the machine to remove adherent water. The machine proved to be very effective in removing epiphytes from the eelgrass leaves. The weight of the sample after spinning is referred to as wet weight.

Dry weight and organic (ash-free) dry weight determinations were made following the techniques and terminology of Westlake (1963).

Transect E was not established in time for the first sampling session (April 5 and 6, 1976) but an analysis of standing crop (organic dry weight) data from the four 0.25 square meter quadrats collected from each of the other four elevations indicated that transect A had a higher relative variability than the others. The following data illustrate this:

Transect	Coefficient of Variation
A	0.46
B	0.17
C	0.18
D	0.29

The number of samples for transect A was increased to six for the remainder of the study period to reduce sample variability for this elevation.

On April 15, 1976 a program using five different quadrat sizes was conducted to determine the optimum quadrat size for sampling eelgrass. The following figures indicate the effect of quadrat size on relative variability (sample variability relative to the mean of the sample):

Quadrat Area (m^2)	Coefficient of Variation	Percentage Standard Error
1.0	0.27	13.33
0.5	0.33	11.82
0.25	0.22	6.52
0.04	0.56	11.22
0.01	1.90	26.98

Percentage standard errors were calculated by the method of Bordeau (1953). Appendix 6 contains additional information. The 0.25 square meter quadrat had the lowest relative variability and its use was continued for the remainder of the study.

Several attempts were made to sample the root and rhizome components of the vegetation to complement the leaf standing crop studies. The use of a coring device and a post-hole auger met with very limited success due to the sandy nature of the sediments, and underwater digging reduced visibility to nil in a matter of seconds. Consequently the underwater biomass sampling program was dropped; however, intertidal biomass sampling in areas adjacent to transect A was conducted from April 1976 to January 1977 during suitably low tides. Four random samples (0.25 square meter quadrat) were gathered on each collection date. Turions were clipped at sediment level and later enumerated. The sediment was excavated to the lowest root level, generally 20 cm to 30 cm, and sieved through a 0.4 cm metal screen. The root and rhizome material retained by the screen was later hand cleaned and sorted in the laboratory. Dimensions of the longest intact leaf of each turion and random rhizome diameters were recorded for four sampling sessions from August 1976 to January 1977.

Two samples were selected at random from the four collected at each elevation during the six standing crop and density sampling sessions of August 1976 to January 1977. Leaf length and width were measured from the longest intact leaf of each turion. Intact leaves were identified by their rounded tips.

4.2. Standing Crop

Eelgrass samples were collected from each of five elevations on 16 occasions during the period of April 1976 to January 1977 (Appendix 7). A total of 364 quadrats were sampled during the study period for leaf standing crop determinations. All of the statistical analyses follow Zar (1974). Percentage dry weight (of wet weight) and percentage ash content (of dry weight) statistics are illustrated:

	Percent Dry Weight	Percent Ash Content
Determinations	323	343
Mean	12.45	13.98
SD	1.68	4.79
SE	0.09	0.26
Range	9.71 to 18.95	5.58 to 25.72

A three-factor analysis of variance (Zar 1974) with factors A (elevation) and B (time) fixed and factor C (sample location) random was performed on the quadrat leaf standing crop data. The first sampling session was not included in the analysis of variance due to missing information. In addition, one location, representing two samples, was randomly deleted from the transect A data for each sampling session. This was done so that the number of samples for each elevation and sampling time were identical. The analysis of variance calculations were performed on a hand calculator. The following null hypotheses were formulated and tested:

1. Ho: Organic dry weight per quadrat the same for all five elevations
2. Ho: Organic dry weight per quadrat the same for all 15 sampling times
3. Ho: Organic dry weights per quadrat between locations within elevations and times are the same

4. H_O: Organic dry weight per quadrat differences among elevations are independent of differences among times (i.e., absence of A x B interaction)

Table 4 summarizes the analysis of variance for leaf standing crop; an expanded version is presented in Appendix 8.

4.2.1. Temporal Changes

The analysis of variance for leaf standing crop showed that organic dry weight per quadrat was not the same for all 15 sampling sessions. A Newman-Keuls Multiple Range Test was employed to determine between which sampling dates differences existed. Unfortunately, the significance level for this type of test is the probability of encountering at least one Type I error while comparing all the pairs of means. The test was not powerful enough to discern where, among the 15 sampling session means, true differences in organic dry weights occurred. A simpler, although much less sensitive, approach was tried. The means of the 15 sampling sessions were divided into three groups of five and a grand mean, in grams organic dry weight per quadrat, was calculated for each group. The results were:

Sessions	2 - 6	7 - 11	12 - 16
Period	April 18-June 13	June 28-Aug. 25	Sept. 28-Jan. 18
Mean (g)	8.73	8.40	3.42

This information suggests that eelgrass standing crop persists at a fairly high and constant level from late

Table 4. Analysis of variance summary table for mean leaf standing crop (organic dry weight in grams per 0.25 square meter quadrat)

Hypothesis	Calculated F	Critical F	Conclusion
1. Elevation (factor A)	16.55**	$F_{0.01(1),4,70} = 3.60$	Reject H_O
2. Time (factor B)	8.36**	$F_{0.01(1),14,70} = 2.35$	Reject H_O
3. Location (factor C)	3.21**	$F_{0.01(1),70,140} = 1.60$	Reject H_O
4. A x B	1.14*ns*	$F_{0.01(1),50,70} = 1.83$	Accept H_O

spring until late summer. There appears to be a drastic decline in the late summer and early fall period during which more than 50 percent of the standing stock is lost. A low and constant standing stock is maintained during much of the winter. Appendix 7 reveals the same general trends. Figure 10 graphically portrays this seasonal cycle of mid-summer abundance, late summer decline, and reduced standing crop throughout the winter.

4.2.2. Influence of Depth

The analysis of variance conducted for leaf standing crop revealed that organic dry weight per quadrat is not the same for all five elevations (F = 16.55**). Results of a Newman-Keuls Multiple Range Test show that the mean standing crops of the highest and lowest transects (0.8 and -1.2 m respectively) are not significantly different (q = 2.10) from one another. Similarly the standing stocks of the three middle elevations are not significantly different (q = 2.16) from each other; however, they are significantly different (q = 5.11*) from those of the highest and lowest elevations (Table 5).

The differences in leaf standing crops for the five study elevations are shown in Figure 10. The later summer and early fall decline in standing stocks mentioned in section 4.2.1. is very pronounced for the three middle elevations (0.3, -0.2 and -0.7 m). Both the magnitude and rate of decline in leaf standing stock are noticeably less for

Fig. 10. Mean leaf standing crop (grams per square meter) for five elevations (in relation to Chart Datum), April 1976 to January 1977.

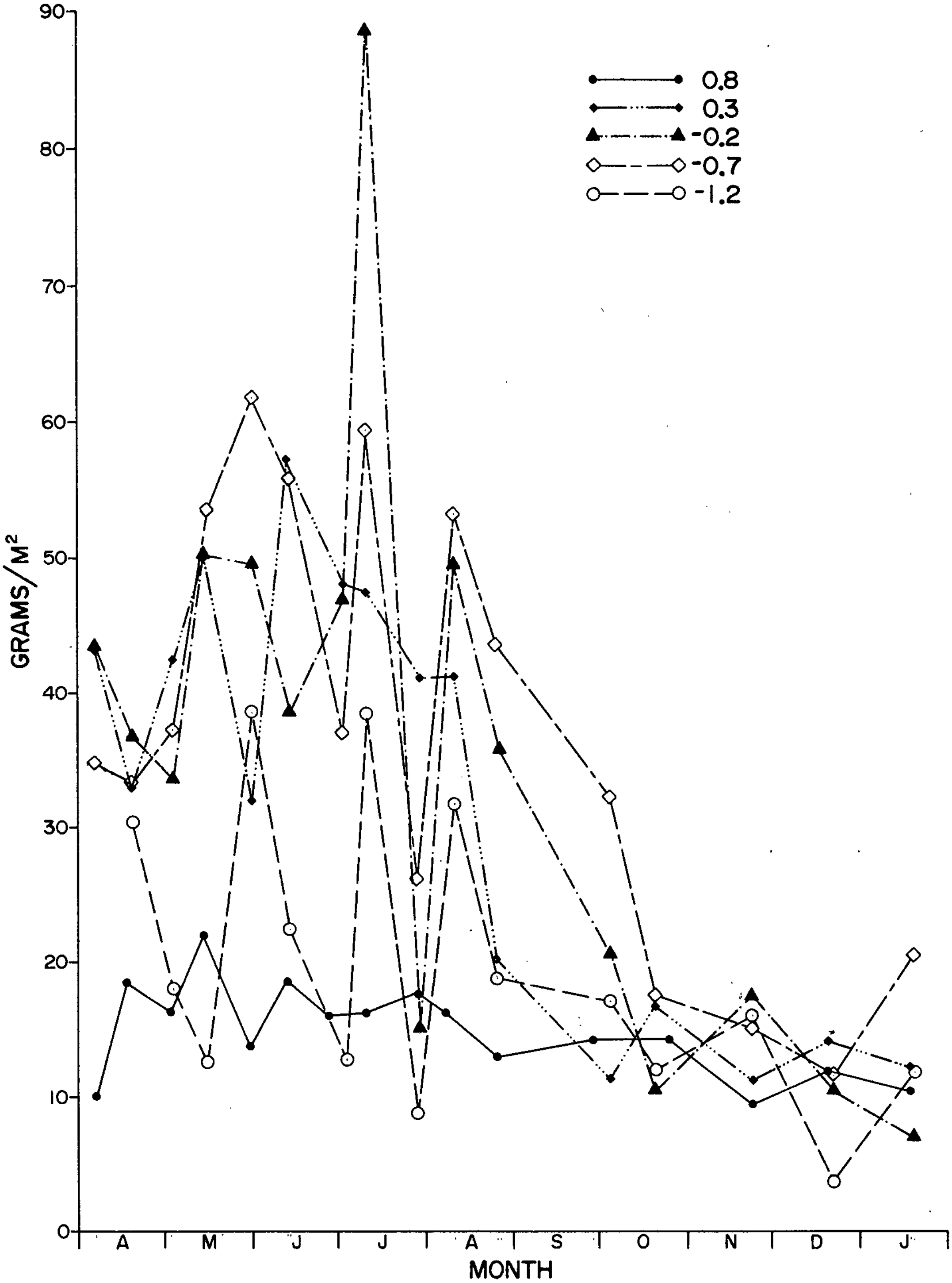

0.8
0.3
-0.2
-0.7
-1.2
GRAMS/M²
90
80
70
60
50
40
30
20
10
0
A
M
J
J
A
S
O
N
D
J
MONTH

Table 5. Newman-Keuls Multiple Range Test for the mean leaf standing stocks (organic dry weight in grams per 0.25 square meter quadrat) at five elevations

Elevation (m)	0.8	-1.2	0.3	-0.2	-0.7
Ranks of Sample Means	1	2	3	4	5
Ranked Sample Means	3.60	4.88	7.98	8.51	9.29

Comparison	Difference	SE	q	p	$q_{0.05,120,p}$	Conclusion
5 *vs* 1	5.69	.61	9.37	5	3.917	Reject H_0*
5 *vs* 2	4.42	.61	7.27	4	3.685	Reject H_0*
5 *vs* 3	1.31	.61	2.16	3	3.356	Accept H_0
5 *vs* 4	0.79	.61	1.30	2	*Do not test*	
4 *vs* 1	4.90	.61	8.07	4	3.685	Reject H_0*
4 *vs* 2	3.63	.61	5.97	3	3.356	Reject H_0*
4 *vs* 3	0.53	.61	0.87	2	*Do not test*	
3 *vs* 1	4.38	.61	7.21	3	3.356	Reject H_0*
3 *vs* 2	3.10	.61	5.11	2	2.800	Reject H_0*
2 *vs* 1	1.27	.61	2.10	2	2.800	Accept H_0

Overall Conclusion 0.8 = -1.2 ≠ 0.3 = -0.2 = -0.7

transects A and E (0.8 and -1.2 m, respectively) which are nearest the upper and lower edges of the eelgrass bed.

4.3. Turion Density

The vegetative axes of eelgrass consist of both horizontal, indeterminate rhizomes and erect annual axes with determinate growth. Clusters of foliage leaves, called turions, arise from both vegetative axes. Reproductive turions are terminal in *Z. marina* (den Hartog 1970) and during the study were differentiated from vegetative turions on the basis of their light yellow-green colour and sympodial branching habit. Total and reproductive turion counts from a total of 338 quadrats (0.25 square meter) were collected from April 1976 to January 1977. A three-factor analysis of variance (Zar 1974) with factors A (elevation) and B (time) fixed and factor C (sample locations) random was conducted on the total and reproductive turion density data.

4.3.1. Influence of Time and Elevation on Total Turion Density

Turion counts were not made on all of the samples from the first and second sampling sessions (April 1976). To facilitate the turion density analysis of variance partial information from the first two sampling sessions were excluded from the calculations. Thus, only the last 14 sampling sessions were included in the analysis of variance.

To further facilitate the analysis of variance calculations data for two of the six quadrats from transect A were deleted at random from each sampling session. Thus, turion counts of four quadrats from each of five elevations sampled on 14 occasions were used in the analysis of variance calculations to test the following null hypotheses:

1. H_O: Turion density per quadrat is the same for all five elevations (Factor A)

2. H_O: Turion density per quadrat is the same for all 15 sampling sessions (Factor B)

3. H_O: Turion density per quadrat between locations within elevations and times is the same (Factor C)

4. H_O: Turion density per quadrat differences among elevations are independent of differences among times (Absence of A x B interaction)

Appendix 9 contains turion density information collected during the study. Table 6 summarizes the analysis of variance for turion density and Appendix 10 presents more analysis of variance information for mean turion density.

Highly significant differences in total turion density existed between elevations and times, and between locations within elevations and times (Table 6). There was no significant interaction of elevation and time on total turion density.

Newman-Keuls Multiple Range Tests were used to determine which treatment means (of five elevations and 15 sessions) were different. Table 7 shows the results for the mean turion densities of the five elevations. Turion densities of the highest and lowest transects (0.8 and -1.2 m respectively) were significantly different from one another

Table 6. Analysis of variance summary table for mean total turion density (turions per 0.25 square meter quadrat)

Hypothesis	Calculated F	Critical F	Conclusion
1. Elevation (factor A)	13.52**	$F_{0.01(1),4,70} = 3.60$	Reject H_O
2. Time (factor B)	8.59**	$F_{0.01(1),13,70} = 2.40$	Reject H_O
3. Location (factor C)	2.345**	$F_{0.01(1),70,140} = 1.60$	Reject H_O
4. A x B	1.393*ns*	$F_{0.01(1),50,70} = 1.83$	Accept H_O

Table 7. Newman-Keuls Multiple Range Test for total turion density (turions per 0.25 square meter quadrat) means at five elevations

Elevation (m)	-1.2	0.8	-0.2	0.3	-0.7
Ranks of Sample Means	1	2	3	4	5
Ranked Sample Means	9.93	13.23	16.89	17.20	19.38

Comparison	Difference	SE	q	p	$q_{0.05,120,p}$	Conclusion
5 *vs* 1	9.45	1.02	9.29	5	3.917	Reject Ho*
5 *vs* 2	6.14	1.02	6.04	4	3.685	Reject Ho*
5 *vs* 3	2.48	1.02	2.44	3	3.356	Accept Ho
5 *vs* 4	2.18	1.02	2.14	2	*Do not test*	
4 *vs* 1	7.27	1.02	7.15	4	3.685	Reject Ho*
4 *vs* 2	3.96	1.02	3.90	3	3.356	Reject Ho*
4 *vs* 3	0.30	1.02	0.30	2	*Do not test*	
3 *vs* 1	6.97	1.02	6.85	3	3.356	Reject Ho*
3 *vs* 2	3.66	1.02	3.60	2	2.800	Reject Ho*
2 *vs* 1	3.30	1.02	3.25	2	2.800	Reject Ho*

Overall Conclusion $\underline{-1.2} \neq \underline{0.8} \neq \underline{-0.2 = 0.3 = 0.7}$

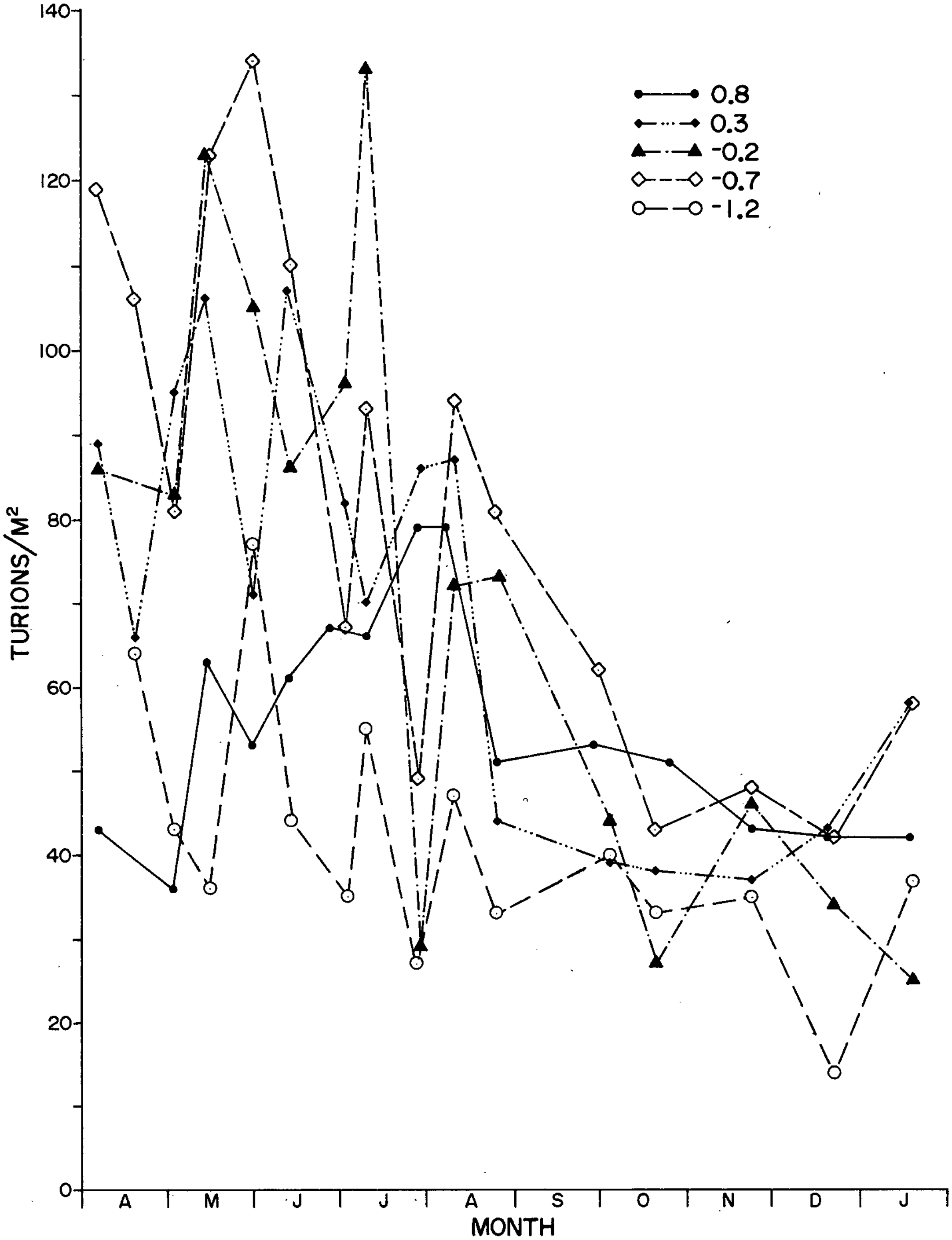
and from the three middle elevations, between which no significant differences existed. The lowest elevations (-1.2 m) had the lowest turion density (40 turions per square meter). Densities for the middle elevations ranged from 67 to 77 turions per square meter. The highest elevation had an intermediate density (53 turions per square meter).

The Newman-Keuls Multiple Range Test gave inconclusive results for comparisons of mean turion densities between sampling sessions. This test often produces ambiguous results for comparisons with large numbers of treatment means (Zar 1974). However, an overall seasonal trend showing a decline in total turion density from summer to winter is seen in Table 8. Summer turion density is halved by mid-winter. Figure 11 depicts the seasonal decline in total turion density for the five transect elevations. The general timing of turion losses seems constant for all elevations; there do, however, appear to be great differences in the rate and magnitude of the decline in density between elevations. Similar winter turion density (approximately 40 turions per square meter) appears to be reached at the same time (October) for all elevations. During the summer the three middle elevations had turion densities twice as great as those of the upper and lower elevations and, consequently, both the rate (turion loss per unit time) and extent (turion loss per square meter) of the observed decline must have been much greater for these middle elevations.

Table 8. Total turion densities (turions per 0.25 square meter quadrat) for fourteen sampling sessions, May to December 1976

Ranks of Sample Means	Ranked Sample Means	Month Sampled
1	22.95	May
2	21.90	May
3	21.05	July
4	20.05	June
5	18.95	August
6	16.55	May
7	15.30	June
8	14.65	August
9	13.00	July
10	11.60	September
11	10.70	January
12	10.15	November
13	9.20	October
14	8.50	December

Fig. 11. Mean total turion numbers per square meter for five elevations (in relation to Chart Datum), April 1976 to January 1977.


0.8
0.3
-0.2
-0.7
-1.2
140
120
100
80
60
40
20
0
TURIONS/M²
A
M
J
J
A
S
O
N
D
J
MONTH

4.3.2. Influence of Time and Elevation on Reproductive Turion Density

A two-factor analysis of variance without replication was performed on the reproductive turion density information (Appendix 11) collected during the study. During the period in which reproductive turions were present (May to August) no significant differences in reproductive turion densities were found between elevations or sampling times (Table 9), but may occur.

However, certain general trends are apparent in the reproductive turion density data of Appendix 11. Peak flowering occurred during June and July. The three middle elevations had a longer period during which reproductive turions were present than had the highest and lowest elevations. Flowering was essentially completed at the highest elevation before it began at the lowest elevations.

4.4. The Influence of Depth on Organic Weight per Turion

To investigate the relationship of organic dry weight per turion and tidal elevation, a simple linear regression equation was calculated for each of the five elevations using the turion density (per quadrat) and standing crop (grams per quadrat) data. The linear regression of organic dry weight (dependent variable) on turion number (independent variable) for the five elevations is presented in Table 10. The equations indicate that the

Table 9. Analysis of variance summary table for mean reproductive turion density (turions per square meter)

Source of Variation	SS	DF	MS
Total	46.97	27	
Elevation	11.13	4	2.78
Time	4.57	5	0.91
Remainder	31.27	18	1.74

To test H_O: No difference among elevations.
Calculated F = 1.60 $F_{0.05(1),4,18}$ = 2.93*ns*

To test H_O: No difference among times.
Calculated F = 0.53 $F_{0.05(1),5,18}$ = 2.77*ns*

Table 10. Linear regression equations of organic dry weight (g) on turion numbers per quadrat for five elevations

Elevation (CD)	Number of Observations	Equation	Coefficient of Determination
0.8 m	88	Y = 0.21 x +0.79	0.57
0.3 m	64	Y = 0.51 x -0.71	0.64
-0.2 m	62	Y = 0.56 x -1.34	0.80
-0.7 m	64	Y = 0.45 x -0.06	0.68
-1.2 m	60	Y = 0.53 x -0.57	0.78

regression coefficient (slope) of the best fit regression line for the highest elevation (0.8 m) differs from those of the other elevations.

An analysis of variance procedure was used to test the significance of each of the regressions. The null hypothesis H_O: $\beta = 0$ was rejected for all five elevations as highly significant differences existed for each (Appendix 12).

The next statistical procedure employed was an analysis of covariance testing for significant differences between the regressions of the five elevations. The null hypothesis that the slopes of all five regressions (for five elevations) were equal was rejected due to the highly significant calculated F value (Table 11). A Newman-Keuls Multiple Range Test was used to determine which slopes were different from which others. Table 12 reveals that the slope of the best fit regression line for the highest elevation (0.8 m) exhibits a highly significant difference from the slopes of the regressions for the other elevations. My interpretation is that the turions of the highest elevation have a much lower foliage (per turion) than is found at the lower elevations. Using the same data the following calculation taken from the leaf standing crop and turion density analyses of variance is recorded.

	Elevation (m)				
	0.8	0.3	-0.2	-0.7	-1.2
Organic Dry Weight (g)	3.60	7.98	8.51	9.29	4.87
Turion Density	13.23	17.19	16.89	19.37	9.93
Organic Dry Weight (g) per Turion	0.27	0.46	0.50	0.48	0.49

Table 11. Analysis of covariance summary testing for significant differences between slopes of linear regression lines of organic dry weight on turion numbers for five elevations

Regression	Number of Observations	Regression Coefficient	Residual SS	Residual DF
Elevation (m)				
0.8	88	0.21	96.98	86
0.3	64	0.51	586.75	62
-0.2	62	0.57	489.28	60
-0.7	64	0.45	524.51	62
-1.2	60	0.53	182.83	58
Pooled			1880.35	
Common		0.45	4669.32	

Calculated F = 12.62**

$F_{0.01(1),4,300} = 3.38$

Conclusion: Reject $H_0: \beta_{0.8} = \beta_{0.3} = \beta_{-0.2} = \beta_{-0.7} = \beta_{-1.2}$

Table 12. Newman-Keuls Multiple Range Test for differences between slopes of linear regressions of organic dry weight on turion numbers for five elevations

Elevation (m)	0.8	0.3	-0.2	-0.7	-1.2
Ranks of Regression Coefficients	1	3	5	2	4
Ranked Regression Coefficients	0.21	0.51	0.57	0.45	0.53

Comparison	Difference	SE	q	p	$q_{0.01,300,p}$	Conclusion
5 *vs* 1	.36	.032	11.42	5	4.603	Reject H_0
5 *vs* 2	.12	.038	3.11	4	4.403	Accept H_0
5 *vs* 3	.07	.042	1.55	3	*Do not test*	
5 *vs* 4	.05	.041	1.15	2	*Do not test*	
4 *vs* 1	.32	.027	11.66	4	4.403	Reject H_0
4 *vs* 2	.07	.042	1.70	3	*Do not test*	
4 *vs* 3	.02	.046	0.41	2	*Do not test*	
3 *vs* 1	.30	.037	8.12	3	4.120	Reject H_0
3 *vs* 2	.05	.044	1.21	2	*Do not test*	
2 *vs* 1	.25	.033	3.38	2	3.643	Reject H_0

Overall Conclusion of Slopes $0.8 \neq 0.3 = -0.2 = -0.7 = -1.2$

4.5. Biomass

Intertidal eelgrass biomass was sampled during low tides from April 1976 to January 1977. Sampling sessions were undertaken at approximately 1-month intervals and were conducted during very low tides when the intertidal eelgrass was exposed. The results of the biomass sampling program are contained in Appendix 13. Percentages of above and below substrate parts were constant from April to July 1976 (Table 13). A drastic decline in intertidal leaf standing crop in August 1976 greatly altered the ratio in subsequent samplings. Rhizome standing crop did not appear to change during the sampling period.

During the spring and early summer the leaf standing crop was about two-thirds and the root and rhizome standing crops about one-third of the total biomass. By late summer and fall the above and below substrate portions each constituted about 50 percent of the biomass.

4.6. Leaf Measurements

Leaf length and width were measured on the longest intact leaf of each turion collected during the regular standing crop and turion density sampling sessions from August 1976 to January 1977. The information is summarized in Table 14. There is a general decline in leaf width from August to January for all five elevations. A similar decline in leaf length is apparent for the same period but there is

Table 13. Percentages of above substrate (leaf) and below substrate (roots and rhizomes) standing crops, April 1976 to January 1977

Date	Percentage Above Substrate	Percentage Below Substrate
16.4.76	61.9	38.1
15.5.76	72.7	27.3
12.6.76	67.2	32.8
10.7.76	64.4	35.6
7.8.76	42.1	57.9
24.8.76	49.8	50.2
25.10.76	56.1	43.9
23.11.76	47.3	52.7
17.1.77	53.0	47.0
Mean	59.3	40.7

Table 14. Leaf measurements for five elevations, August 1976 to January 1977

		Elevation (m)				
		0.8	0.3	-0.2	-0.7	-1.2
Leaf Length (cm)						
August	Mean	54.9	104.3	102.8	99.9	94.5
	SE	5.53	20.0	9.37	8.03	8.25
September	Mean	56.0	71.4	80.7	87.9	69.8
	SE	4.09	8.51	9.65	7.90	9.56
October	Mean	55.0	59.3	49.7	69.3	70.3
	SE	5.67	8.11	11.23	9.40	8.30
November	Mean	39.3	42.6	54.7	40.5	60.7
	SE	3.45	6.79	5.71	4.63	7.85
December	Mean	39.6	45.6	42.7	55.0	54.0
	SE	3.43	4.30	5.72	6.90	11.37
January	Mean	31.6	29.6	41.4	41.0	42.6
	SE	3.89	2.61	3.91	2.23	2.96
Leaf Width (cm)						
August	Mean	0.61	0.69	0.60	0.66	0.66
	SE	0.022	0.058	0.029	0.031	0.036
September	Mean	0.58	0.62	0.65	0.60	0.56
	SE	0.027	0.029	0.027	0.026	0.041
October	Mean	0.51	0.57	0.61	0.56	0.55
	SE	0.028	0.028	0.040	0.039	0.031
November	Mean	0.53	0.56	0.49	0.46	0.56
	SE	0.021	0.043	0.020	0.019	0.029
December	Mean	0.52	0.54	0.54	0.57	0.52
	SE	0.025	0.022	0.033	0.025	0.037
January	Mean	0.50	0.40	0.52	0.58	0.58
	SE	0.025	0.017	0.020	0.016	0.023

a striking dissimilarity between the highest elevation (0.8 m) and the others. In August, mean leaf length for the highest elevation is approximately one-half that of the other elevations. By January, mean leaf length for the upper elevation has been reduced by 40 percent; however, mean leaf length for the other elevations has declined by about 60 percent. Mean winter leaf length (of the longest intact leaf on each turion) appears to be the same for all five elevations and thus the lower elevations experience a greater and more rapid change in mean leaf length during the fall. There appears to be a time lag associated with increasing depth for the observed changes in mean leaf length. In August the 0.3 and -0.2 m elevations had the greatest mean leaf length, in September the -0.2 and -0.7 m elevations, October the lowest two elevations, and by November the greatest mean leaf length was observed at the lowest elevation.

Table 15 shows the same seasonal decline in leaf length and width of samples collected adjacent to the 0.8 m elevation for the biomass determinations (August 1976 to January 1977). Disregarding the anomalous readings (Vide Table 14) for August, which may be largely attributed to sampling error, the other values are similar to those obtained during the regular sampling sessions (Table 14). The changes in mean rhizome diameter are difficult to interpret because of the relatively short period in which measurements were taken. During excavation the rhizomes were often cut with the shovel

Table 15. Leaf and rhizome measurements for samples collected at 0.8 meters (in relation to Chart Datum), August 1976 to January 1977. Number of observations in brackets

		Aug. 76	Oct. 76	Nov. 76	Jan. 77
Leaf Length (cm)	Mean	30.80 (87)	55.48 (27)	48.74 (22)	26.89 (43)
	SE	1.08	4.76	4.39	1.43
Leaf Width (cm)	Mean	0.45 (87)	0.54 (27)	0.56 (22)	0.47 (43)
	SE	0.01	0.02	0.03	0.01
Rhizome Diameter (cm)	Mean	0.37 (87)	0.41 (92)	0.47 (61)	0.40 (96)
	SE	0.02	0.01	0.01	0.01

blade. As diameters were measured on individual rhizome segments, each rhizome may have been represented several times in each sample.

4.7. Discussion

The influence of factors associated with tidal elevation on eelgrass leaf dimensions, vegetative and reproductive turion densities and standing stocks have been investigated in several other Pacific Coast eelgrass studies (see section 1.2.). Leaf measurements taken during this study indicate that the eelgrass of southern Roberts Bank corresponds to the short, narrow-leafed form (*Z. marina* var. *typica*) of Scagel (1961). The larger form *Z. marina* var. *latifolia* was not encountered during the study. Leaf dimensions of Roberts Bank eelgrass are similar to those of Puget Sound eelgrass (Phillips 1972). The relationships of increased leaf length with greater depth described for other Pacific Coast eelgrass populations (Phillips 1972, Keller and Harris 1966) and other seagrasses (Strawn 1961) is further supported by this study.

On Roberts Bank, turion densities were highest at the three middle elevations studied, intermediate near the upper limit of eelgrass growth and the lowest near the lower limit of eelgrass distribution. Keller and Harris (1966) found the same relationship of depth and turion density in northern California. In Puget Sound, Washington Phillips (1972) found that intertidal turion density was five times as great as subtidal turion density in the clear waters surrounding Bush Point and only twice as great in the turbid waters off Alki Point. Both Puget Sound study sites also exhibited a decrease in turion density with increasing depth. Eelgrass density on Roberts Bank is low compared to other Pacific Coast eelgrass populations (Phillips 1972, Keller 1963, Stout 1976) and a lack of comparable habitat information (e.g. water clarity) from these other areas limits speculation as to the reasons for these regional differences in population characteristics.

The findings of this study reveal that the mean leaf standing crops of the highest and lowest elevations were significantly lower than the mean leaf standing crops of the three middle elevations, which, in turn, were not significantly different from each other. This relationship of reduced standing crop near the upper and lower limits of growth is similar to that reported by Keller and Harris (1966) in California. The standing crop values of eelgrass on Roberts Bank closely resemble the values obtained by Phillips (1972) at his Alki Point, Washington study site. The standing crops of eelgrass at Alki Point, where the water was turbid, were much lower than at his Bush Point study site, where the water was clearer. Similarly, total biomass at Alki Point was much lower than at Bush Point. Both standing crop and biomass appear to be strongly influenced by water clarity. Sampling difficulties did not allow me to collect information on subtidal biomass. Intertidal biomass of eelgrass on southern Roberts Bank is comparable to the biomass of one of the intertidal stations at Alki Point, Washington (Phillips 1972).

Seasonal changes in vegetative and reproductive turion densities, leaf standing crop, biomass and, to a limited extent, leaf measurements have been studied in Puget Sound, Washington by Phillips (1972). The information collected during this study indicates that southern Roberts Bank eelgrass undergoes seasonal cycles similar to Puget Sound eelgrass. For both locations, leaf standing crop and turion density reach minimum values in January and maximum values from May to July. However, Phillips did not record the great losses in leaf standing crop and turion densities in the late summer which were observed in this study. Previous studies on eelgrass productivity and leaf dynamics have not considered the loss of whole turions as being a significant factor in the determination of net production and for this reason may have grossly underestimated actual net production. Phillips did not report seasonal changes in mean leaf dimensions but did find that reproductive turions first appeared in April in Puget Sound. On southern Roberts Bank, reproductive eelgrass turions were first observed in mid-May and had disappeared by mid-August. The reasons for the shortened reproductive season observed during this study were not investigated; however, Backman and Barilotti (1976) found that flowering is affected by reduced irradiance. The turbid estuarine waters of Roberts Bank reduce the amount of light available to eelgrass and a similar inhibition in flowering may be the result of reduced irradiance in this area.

During the study, two problem areas arose which warrant further comment in regard to future investigations of seagrasses. One of the criteria used in the selection of the study site was the apparent homogeneity of the eelgrass bed. No areas of bare substrate or sparse eelgrass growth were observed at the study site; however, the data collected indicate that considerable patchiness existed within the eelgrass meadow. Highly significant differences between locations within study elevations and sampling sessions were found for both turion density (Table 6) and leaf standing crop (Table 5). The patchy distribution of eelgrass plants within an eelgrass meadow should be incorporated into sampling schemes of future investigations. The problems encountered in trying to assess total plant biomass originate in the difficulties of sampling the root and rhizome components of eelgrass. Consistent results were not obtained for root to rhizome to shoot ratios or for the organic dry weight determinations of these components during the study, even after laborious hand sorting and cleaning of the roots and rhizomes. A much greater degree of sophistication in approach and technique will be required to obtain consistent and useful results.

5. SUMMARY AND CONCLUSIONS

The results of the study have been discussed in each section. The purpose of this portion of the study is to synthesize the previous discussions and findings in view of the stated objectives of the study.

The discussion of eelgrass habitat factors on southern Roberts Bank showed that the restricted depth range encountered there was the result of desiccation and reduced light. In addition, the discussion of turion densities, leaf standing crops and leaf dimensions showed that significant differences existed for some of these parameters at the different study elevations. How do the environmental factors of the study site relate to the differences in morphological, biomass and population characteristics of eelgrass at the study site? What are the adaptive strategies which eelgrass has evolved to deal with the depth dependent factors controlling its upper and lower distributional limits?

The information presented in this study indicates that the eelgrass of southern Roberts Bank can be grouped, on the basis of leaf standing crop, turion density and leaf measurements, into three distinct categories which correspond to three tidal zones. Near the upper limit of eelgrass growth, comparatively low standing crops and intermediate turion densities are observed. Mean leaf length is less than at lower elevations, as is organic dry weight per turion. In other areas, the upward extension of eelgrass depends greatly on the degree of "desiccation" (den Hartog 1970); reduced blade length appears to be the adaptive mechanism employed by eelgrass in response to increase desiccation on Roberts Bank. The three middle elevations studied exhibited high turion densities and large leaf standing crops. Mean leaf length and mean organic dry weight per turion were greater than at the highest elevation. It appears that optimal conditions for eelgrass growth and development are found at the intermediate portions of the depth range of eelgrass. The lowest elevation (-1.2 m) had the lowest mean turion density of all and yet maintained an intermediate leaf standing crop. Leaf length and organic dry weight per turion were the same as those of the middle elevations. Near the lower distributional limit, eelgrass responds to decreased light intensity by reducing turion density. Where light is limiting self-shading may become an important consideration and a mechanism which will reduce turion density, and thus shading will be advantageous to the plant.

The major conclusions of the study are:

1. The salinity, temperature and water motion conditions of southern Roberts Bank are close to the world-wide optima for eelgrass growth.
2. The restricted depth distribution of eelgrass on southern Roberts Bank is due to the light environment and substrate characteristics of the area.
3. Reduced light availability in the turbid estuarine waters of southern Roberts Bank is responsible for the elevated

lower distributional limit of eelgrass found there.

4. The sandy nature of the sediments of the study area controls the upper distributional limit of eelgrass on southern Roberts Bank.
5. Sediments within an eelgrass bed experience pronounced seasonal changes in surface levels.
6. Fine sediment fractions and particulate organic matter are concentrated near the edges of eelgrass meadows.
7. Eelgrass undergoes pronounced seasonal changes in leaf standing crop and turion density; a large decline in both takes place in late summer.
8. Flowering of eelgrass on southern Roberts Bank occurs from mid-May to mid-August; this relatively short reproductive season observed may be the result of reduced light availability.
9. Leaf standing crops are lower near the upper and lower limits of eelgrass beds. Leaf standing crop is greatest at intermediate elevations.
10. Turion density is highest at intermediate elevations, lower near the upper edge of the eelgrass bed and lowest near the subtidal distributional limit of eelgrass growth.
11. Organic dry weight per turion near the upper edge of eelgrass growth is approximately one-half of the value of lower elevation turions.
12. During the summer the mean leaf length near the upper edge of the eelgrass bed is approximately one-half of the mean length of leaves from lower elevations; in winter mean

leaf length is the same for all elevations.

13. The ratio of above substrate to below substrate standing crops is 2:1; during winter the ratio is 1:1.
14. Reduced leaf length appears to be a response to desiccation in eelgrass.
15. Reduced turion density appears to be a response to reduced light availability in eelgrass.

GLOSSARY

Biomass. The weight of all parts of all the plants on a unit area at a given time.

Carbonate carbon. Carbonate carbon was used as an indirect measure of benthic bivalve populations in this study. The source of carbonate in marine sediments is generally shell fragments.

Chart Datum (CD). In Canada, Chart Datum represents the plane of lowest normal tides. In the text positive and negative elevations refer to elevations above and below the specified reference plane (MLLW or CD).

Dry weight. The weight of plant material after heating in an oven at 105°C to constant weight.

Fines. For the purpose of this study the sediments which passed through the finest (0.1 mm) sieve available constituted the fine fraction.

Fresh weight. The true weight of the living plant.

Organic carbon. The organic content of a sediment reflects the amount of particulate plant and animal residues present and thus provides a rough estimate of the food available for filter feeding infauna for the purposes of this study.

Organic dry weight. The loss in weight of plant matter after ignition at 550°C. Also known as ash-free dry weight.

Prostrate. Horizontal, trailing along the ground.

Quadrat. A square or rectangular area used to quantitatively sample vegetation. A 0.25 m^2 (0.5 x 0.5 m) quadrat was used in this study.

Reproductive turion. An erect stem bearing inflorescences.

Rhizome. Horizontal, elongated, subterranean stem.

Secchi disc. A round white disc which is lowered into the water column to provide an estimate of the transmission of visible light in water and hence, water clarity.

Standing crop. The weight of plant material that can be sampled or harvested by normal methods, at any one time, from a given area. Does not necessarily include all parts of plants or all plants.

Sympodial Branching. Occurs when the terminal bud loses its capacity for active growth and all subsequent growth occurs at the auxillary shoots.

Total turion density. Total number of turions (vegetative and reproductive) per unit area.

Turion. A cluster of foliage leaves arising from a vegetative axis. Common usage does not adhere to the correct botanical definition which describes a turion as a winter bud on some water plants that becomes detached, overwinters, and under favorable conditions develops a new plant.

Vegetative turion. A non-reproductive turion (i.e., not bearing inflorescences).

Wet weight. Experimental value obtained after removing adherent water from plant material.

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APPENDICES

APPENDIX 1: SECCHI DEPTH AND SURFACE AND SUBSURFACE (1.5 m) SALINITY AND TEMPERATURE MEASUREMENTS MARCH 1976 TO JANUARY 1977

Date	Secchi Depth (meters)	Salinity (parts per thousand)		Temperature (°C)	
		Surface	1.5 m	Surface	1.5 m
31.3.76	5.25				
2.4.76	6.75				
3.4.76	5.40				
5.4.76	5.25	26.0	10.5	28.5	8.0
6.4.76	3.25				
19.4.76	3.30	27.2	9.0	27.6	9.0
3.5.76	1.80				
14.5.76	1.60	28.0	11.0	28.0	10.5
31.5.76	2.30	26.3	11.6	27.0	10.8
13.6.76	2.00	24.0	11.8	24.3	11.9
28.6.76	2.30	22.7	15.5	23.7	14.3
10.7.76	2.30	22.5	15.0	23.5	14.0
28.7.76	2.90	22.8	17.5	24.0	16.0
10.8.76	2.60	19.9	17.0	21.2	15.0
24.8.76	1.80	13.8	16.0	18.2	14.8
4.10.76	1.60	20.1	11.2	26.2	10.8
20.10.76	2.90	22.9	10.3	23.8	10.4
23.11.76	4.10	21.4	8.0	30.0	7.8
22.12.76	4.10	22.5	8.2	27.6	8.6
18.1.77	5.40	26.5	8.0	26.0	8.0

APPENDIX 2: DIURNAL SURFACE AND SUBSURFACE (1.5 m) SALINITY (PARTS PER THOUSAND) MEASUREMENTS. MAY 2, JULY 28 AND OCTOBER 4, 1976. JANUARY 18, 1977.

Time (PDST)	May 2		July 28		October 4		January 18	
	Surface	1.5 m	Surface	1.5 m	Surface	1.5 m	Surface	1.5 m
0000	26.3	26.3	21.8	23.2	15.7	19.3		
01.00								
02.00	26.3	26.3			15.5	22.0		
03.00								
04.00					18.0	19.2		
05.00							24.2	24.3
06.00	24.2	24.2	23.8	25.1	19.5	22.5		
07.00								
08.00	24.0	25.0	22.9	26.0	24.0	25.8		
09.00								
10.00	23.7	24.2	20.8	25.2	20.1	26.2		
11.00							27.2	27.2
12.00	24.0	24.7	24.0	24.7	20.4	22.5		
13.00							26.5	26.0
14.00	24.7	25.0	22.8	24.0	21.2	22.3		
15.00							27.2	27.2
16.00	23.6	23.5	20.8	22.2	21.8	24.7		
17.00							27.0	27.3
18.00	23.5	24.6	22.2	23.8	21.75	23.8		
19.00							27.2	27.5
20.00	24.0	26.0	24.2	27.2	20.5	21.9		
21.00							27.2	27.3
22.00	24.0		21.5	23.0	21.3	20.4		
23.00							26.8	26.8
24.00	24.0		23.8	26.5	21.0	20.2		

APPENDIX 3: DIURNAL AIR, SURFACE AND SUBSURFACE (1.5 m) TEMPERATURE (^{o}C) MEASUREMENTS MAY 2, JULY 28 AND OCTOBER 4, 1976. JANUARY 18, 1977.

Time (PDST)	May 2		July 28			October 4			January 18		
	Surface	1.5 m	Surface	1.5 m	Air	Surface	1.5 m	Air	Surface	1.5 m	Air
0000	12.5	12.5	14.5	13.8	16.3	10.4	10.8	9.5			
01.00									7.5	7.5	14.0
02.00	12.5	12.5				10.0	11.5	10.4			
03.00											
04.00						10.0	10.8	9.0			
05.00									8.0	8.0	12.0
06.00	11.0	11.0	13.4	12.8	14.2	10.1	11.0	9.2			
07.00											
08.00	11.0	11.5	14.75	12.25	20.5	10.8	11.0	9.8			
09.00											
10.00	11.33	11.5	17.0	14.0	26.25	11.2	10.8	10.8			
11.00									7.6	7.6	7.5
12.00	11.5	11.75	16.0	14.0	23.0	11.8	10.3	14.1			
13.00									8.0	8.0	9.6
14.00	11.6	12.0	17.5	16.0	20.0	12.6	11.8	14.5			
15.00									8.2	8.1	12.9
16.00	11.75	12.0	15.3	14.8	18.2	12.5	11.2	14.8			
17.00									8.2	8.0	10.6
18.00	11.5	11.25	14.8	13.8	17.2	12.1	11.5	12.5			
19.00									8.0	7.9	8.2
20.00	11.0	10.5	14.8	12.6	15.8	12.5	12.1	11.8			
21.00									7.8	7.8	8.2
22.00	11.5		15.0	14.8	16.0	11.8	12.2	12.9			
23.00									7.8	7.8	8.0
24.00	12.0		15.0	12.5	15.9	11.5	11.8	12.9			

APPENDIX 4: DIURNAL SECCHI DEPTH AND PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR) MEASUREMENTS MAY 2, JULY 28 AND OCTOBER 4, 1976. JANUARY 18, 1977.

Time (PDST)	Secchi Depth (meters)	PAR Quanta (microeinsteins per square meter per second)		
		10 cm Above Surface	Surface	1.5 m
May 2				
06.00	2.1		30	7
08.00	2.1		49	12
10.00	2.2		180	42
12.00	2.2		150	23.5
14.00	2.2		195	52.5
16.00	1.0		350	78
18.00	1.8		100	35
20.00	2.2		12	3
July 28				
06.00	3.1	170	45	19
08.00	3.9	1200	500	200
10.00	3.5	1900	1100	550
12.00	2.8	2200	1450	650
14.00	2.9	2500	1600	800
16.00	1.5	310	170	53
18.00	2.1	250	150	80
20.00	2.75	150	33	17
October 4				
08.00	2.2	114	64	27
10.00	1.6	500	220	44
12.00	1.8	2150	975	325
14.00	2.4	2100	1050	450
16.00	2.4	2000	850	275
18.00	2.5	500	90	29
January 18				
11.00	5.7			
13.00	5.4			
15.00	5.2			
17.00	5.2			

APPENDIX 5: NET OSCILLATIONS OF SEDIMENT SURFACE LEVELS - MEASUREMENTS AND STATISTICS. JUNE 1976 TO JANUARY 1977

Date	30.6.76	29.7.76	11.8.76	26.8.76	4.10.76	20.10.76	23.11.76	22.12.76	19.1.77
Number of Observations	20	12	14	9	15	19	17	12	12
Mean height (cm) of pegs above sediment surface	10.00	9.64	9.36	9.29	9.83	10.10	10.90	11.74	-11.87
Net change		+0.36	+0.64	+0.71	+0.17	-0.10	-0.90	-1.74	-1.87
Standard Deviation		2.04	1.21	0.65	1.38	1.41	1.71	1.76	1.92
Standard Error		0.59	0.32	0.22	0.36	0.32	0.42	0.51	0.55

APPENDIX 6: STATISTICS OF STANDING CROP INFORMATION (ORGANIC DRY WEIGHT PER QUADRAT) USED FOR OPTIMUM QUADRAT SIZE DETERMINATION

Quadrat Area	Number of Quadrats	Quadrat Dimensions	Mean (g)	SD (g)	SE (g)	Percentage SE	C.V.
1.0 m^2	4	1 m x 1 m	16.69	4.45	2.22	13.33	0.27
0.5	8	0.71 m x 0.71 m	12.21	4.08	1.44	11.82	0.33
0.25	12	0.5 m x 0.5 m	5.53	1.25	0.36	6.52	0.22
0.04	25	0.2 m x 0.2 m	0.81	0.46	0.09	11.22	0.56
0.01	50	0.1 m x 0.1 m	0.20	0.37	0.05	26.98	1.90

APPENDIX 7: ORGANIC DRY WEIGHTS IN GRAMS PER SQUARE METER FOR FIVE ELEVATIONS (CHART DATUM) APRIL 1976 to JANUARY 1977

0.8 m		0.3 m		-0.2 m		-0.7 m		-1.2 m	
Date	Mean SE	Date	Mean SE	Date	Mean SE	Date	Mean SE	Date	Mean SE
Apr. 6	9.91	Apr. 6	43.25	Apr. 6	43.37	Apr. 6	34.67		
	2.27		3.77		3.82		5.08		
Apr. 17	18.61		33.0	Apr. 19	36.78	Apr. 19	33.33	Apr. 19	30.30
	3.31		4.41		8.82		4.37		6.80
May 2	16.32	May 3	42.43	May 3	33.60	May 3	37.31	May 3	17.93
	2.63		5.43		3.84		1.77		9.82
May 14	22.02	May 14	49.98	May 14	50.29	May 15	53.41	May 15	12.43
	4.17		9.13		11.86		8.60		5.19
May 30	13.68	May 31	32.01	May 31	49.47	May 31	61.81	May 31	38.45
	1.90		4.83		9.32		11.44		7.38
June 12	18.67	June 12	57.26	June 12	38.61	June 13	55.67	June 13	22.35
	2.14		10.91		9.14		9.35		6.85
June 27	16.05	July 2	47.97	July 2	46.91	July 2	37.07	July 3	12.69
	3.05		15.16		5.63		2.17		4.43
July 10	16.30	July 10	47.44	July 10	88.40	July 10	59.38	July 10	38.42
	2.43		17.93		23.74		17.05		11.22
July 28	17.72	July 29	41.12	July 29	15.02	July 28	26.12	July 28	8.82
	3.58		4.22		7.43		11.15		2.90
Aug. 7	16.16	Aug. 10	41.22	Aug. 10	49.52	Aug. 10	53.23	Aug. 10	31.68
	1.40		4.36		4.01		8.09		4.79
Aug. 25	13.03	Aug. 25	20.22	Aug. 26	35.69	Aug. 25	43.44	Aug. 25	18.81
	2.14		3.66		6.88		8.77		9.51
Sept. 28	14.19	Oct. 4	11.35	Oct. 4	20.48	Oct. 4	32.23	Oct. 4	17.10
	2.07		3.31		3.23		2.90		1.64
Oct. 25	14.21	Oct. 20	16.84	Oct. 20	10.62	Oct. 20	17.46	Oct. 20	12.04
	1.74		3.88		5.26		3.41		5.12
Nov. 23	9.57	Nov. 23	11.23	Nov. 23	17.59	Nov. 23	14.97	Nov. 23	16.10
	1.80		0.87		3.38		2.99		3.32
Dec. 20	11.93	Dec. 20	14.14	Dec. 22	10.46	Dec. 22	11.65	Dec. 22	3.68
	2.46		2.12		1.90		2.29		1.25
Jan. 18	10.46	Jan. 18	12.23	Jan. 19	7.00	Jan. 19	20.52	Jan. 19	11.90
	1.51		1.54		1.72		3.24		3.73

APPENDIX 8: ANALYSIS OF VARIANCE SUMMARY TABLE FOR MEAN LEAF STANDING CROP (ORGANIC DRY WEIGHT IN GRAMS PER 0.25 SQUARE METER QUADRAT)

Source of Variation	SS	DF	MS	Calculated F	Critical F	Conclusion
Total	8,170.13	299				
Elevation (A)	1,465.82	4	366.45	16.55**	$F_{0.01(1),4,70} = 3.60$	Reject H_O
Time (B)	2,592.68	14	185.19	8.36**	$F_{0.01(1),14,70} = 2.34$	Reject H_O
Location (C)	1,415.65	56	22.14	3.21**	$F_{0.01(1),70,140} = 1.60$	Reject H_O
A x B	1,660.57	75	25.28	1.14_{ns}	$F_{0.01(1),50,70} = 1.83$	Accept H_O
Error	1,035.41	150	6.90			

APPENDIX 9: DENSITY IN TURIONS PER SQUARE METER FOR FIVE ELEVATIONS (CHART DATUM) APRIL 1976 TO JANUARY 1977

0.8 m			0.3 m			-0.2 m			-0.7 m			-1.2 m		
Date	Mean	SE	Date	Mean	SE	Date	Mean	SE	Date	Mean	SE	Date	Mean	SE
Apr. 6	43	9.84	Apr. 6	89	3.77	Apr. 6	86	0.86	Apr. 6	119	4.07			
			Apr. 9	66	1.56				Apr. 19	106	2.47	Apr. 19	64	2.80
May 2	36	2.05	May 3	95	3.30	May 3	83	2.56	May 3	81	3.09	May 3	43	5.72
May 14	63	3.74	May 14	106	5.39	May 14	123	5.35	May 15	123	2.87	May 15	36	3.49
May 30	53	1.54	May 31	71	3.35	May 31	105	5.94	May 31	134	4.52	May 31	77	3.38
June 12	61	1.85	June 12	107	3.64	June 13	86	2.10	June 13	110	2.26	June 13	44	2.35
June 27	67	2.51	July 2	82	0.96	July 2	66	1.04	July 2	67	1.38	July 3	35	3.40
July 10	66	2.80	July 10	70	4.74	July 10	133	6.05	July 10	93	7.19	July 10	55	3.64
July 28	79	2.06	July 29	86	3.57	July 29	29	1.44	July 28	49	1.44	July 28	27	2.25
Aug. 7	79	1.30	Aug. 10	87	2.28	Aug. 10	72	0.42	Aug. 10	94	3.28	Aug. 10	47	1.11
Aug. 25	51	2.14	Aug. 25	44	1.78	Aug. 26	73	3.28	Aug. 25	81	3.09	Aug. 25	33	3.68
Sept. 28	53	2.07	Oct. 4	39	2.56	Oct. 4	44	2.49	Oct. 4	62	1.19	Oct. 4	40	2.28
Oct. 25	51	1.71	Oct. 20	38	1.85	Oct. 26	27	3.30	Oct. 20	43	2.14	Oct. 20	33	2.75
Nov. 23	43	1.68	Nov. 23	37	1.03	Nov. 23	46	1.66	Nov. 23	48	1.36	Nov. 23	35	0.86
Dec. 20	42	1.58	Dec. 20	43	1.75	Dec. 22	34	0.65	Dec. 22	42	1.85	Dec. 22	14	1.19
Jan. 18	42	1.48	Jan. 18	58	3.86	Jan. 19	25	1.11	Jan. 19	58	1.76	Jan. 19	37	0.86

APPENDIX 10: ANALYSIS OF VARIANCE SUMMARY TABLE FOR MEAN TURION DENSITY (TURIONS PER 0.25 SQUARE METER QUADRAT)

Source of Variation	SS	DF	MS	Calculated F	Critical F	Conclusion
Total	21,287.43	279				
Elevation (A)	3,128.41	4	782.10	13.52**	$F_{0.01(1),4,70} = 3.60$	Reject H_O
Time (B)	6,462.38	13	497.11	8.59**	$F_{0.01(1),13,70} = 2.40$	Reject H_O
Location (C)	4,050.25	70	57.86	2.345**	$F_{0.01(1),70,140} = 1.60$	Reject H_O
A x B	4,191.89	52	80.61	1.393*ns*	$F_{0.01(1),50,70} = 1.83$	Accept H_O
Error	3,454.50	140	24.67			

APPENDIX 11: REPRODUCTIVE TURION DENSITY (PER SQUARE METER) FOR FIVE ELEVATIONS. JUNE TO AUGUST, 1976.

		Elevation (m)				
Date		0.8	0.3	-0.2	-0.7	-1.2
May 14, 15	Reproductive	0	3	0	0	0
	Total	71	106	123	123	36
	% Reproductive	0	2.83	0	0	0
May 30,31	Reproductive	1	0	2	1	0
	Total	51	71	105	134	77
	% Reproductive	1.96	0	1.90	0.75	0
June 12, 13	Reproductive	5	3	0	1	0
	Total	91	107	86	110	44
	% Reproductive	5.49	2.80	0	0.91	0
July 2, 3	Reproductive	0	2	4	0	3
	Total	100	82	66	67	35
	% Reproductive	0	2.44	6.06	0	8.57
July 10	Reproductive	0	2	3	0	0
	Total	70	70	133	93	55
	% Reproductive	0	2.86	2.26	0	0
July 28, 29	Reproductive	0	2	0	2	0
	Total	69	86	29	49	27
	% Reproductive	0	2.33	0	4.08	0
August 7	Reproductive	0	0	0	0	0
	Total	79	87	72	94	47
	% Reproductive	0	0	0	0	0

APPENDIX 12: ANALYSIS OF VARIANCE SUMMARY FOR SLOPES OF THE REGRESSIONS OF TURION NUMBERS ON ORGANIC DRY WEIGHT FOR FIVE ELEVATIONS (CHART DATUM)

Elevation (meters)	Number of Observations	Source of Variation	SS	DF	MS	Calculated F	$F_{0.01(1),1,n-2}$	Conclusion
0.8	88	Total	224.74	87				
		Linear Regression	127.76	1	127.76	113.30	6.96	Reject $H_0: \beta = 0$
		Residual	96.98	86	1.13			
0.3	64	Total	1643.43	63				
		Linear Regression	1056.68	1	1056.68	111.66	7.08	Reject $H_0: \beta = 0$
		Residual	586.75	62	9.46			
-0.2	62	Total	2481.98	61				
		Linear Regression	1992.71	1	1992.71	244.36	7.08	Reject $H_0: \beta = 0$
		Residual	489.28	60	8.15			
-0.7	64	Total	1636.33	63				
		Linear Regression	1111.82	1	1111.82	131.42	7.08	Reject $H_0: \beta = 0$
		Residual	524.51	62	8.46			
-1.2	60	Total	841.38	59				
		Linear Regression	658.55	1	658.55	208.92	7.08	Reject $H_0: \beta = 0$
		Residual	182.83	58	3.15			

APPENDIX 13: MEAN BIOMASS OF INTERTIDAL (0.8 m) EELGRASS IN GRAMS PER SQUARE METER (ORGANIC DRY WEIGHT). APRIL 1976 TO JANUARY 1977.

	Leaves		Roots		Rhizomes	
Date	Mean	SE	Mean	SE	Mean	SE
16.4.76	28.80	0.25	4.36	0.20	13.37	0.26
15.5.76	16.98	1.18	1.80	0.15	4.58	0.34
12.6.76	27.45	1.64	3.70	1.18	9.69	1.88
10.7.76	25.33	2.62	3.09	0.24	10.91	1.84
7.8.76	7.90	1.84	1.00	0.24	9.85	1.85
24.8.76	10.68	0.68	1.76	0.29	9.01	2.29
25.10.76	10.64	3.77	1.05	0.47	7.27	2.93
23.11.76	10.10	1.82	0.97	0.21	10.29	1.76
17.1.77	9.29	1.58	1.30	0.23	6.95	1.21