

ENVIRONMENTAL FACTORS CONTROLLING FLORAL ZONATION AND  
THE DISTRIBUTION OF BURROWING AND TUBE-DWELLING ORGANISMS  
ON FRASER DELTA TIDAL FLATS, BRITISH COLUMBIA

by

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## ABSTRACT

The distribution of various burrowing and tube-dwelling organisms, their biogenic sedimentary structures, and the rates at which they turn over sediment are investigated on three different tidal flat environments of the Fraser Delta. The organisms studied include Callianassa californiensis and Upogebia pugettensis, both thalassinidean burrowing shrimps, the burrowing polychaete Abarenicola sp., the tube-dwelling polychaetes, Praxillela sp. and Spio sp., the bivalve Mya arenaria and the gastropods Batillaria attramentaria and Nassarius mendicus. Thalassinidean shrimps are of most interest because they are widespread over the Delta, in particular Callianassa, and because their distinctive burrows are well known in the geological record.

The 'marine' tidal flats of Boundary Bay on the inactive southern flank of the Fraser Delta, are mantled with fine to very fine, well to very well sorted sands. The intertidal region has five floral/sedimentological zones delimited primarily by elevation and exposure and characterized by distinctive macrofaunal assemblages. These are from the shoreline seawards, the saltmarsh, algal mat, upper sand wave, eelgrass and lower sand wave zones. Topography of both small and large scale of biogenic or physical origin creates lateral heterogeneity within the biofacies of each zone.

An estimated  $4.25 \times 10^8$  Abarenicola on Boundary Bay tidal flats annually rework about  $10^6 \text{ m}^3$  of sand. The bioturbation of this worm may be a factor limiting the extent of the algal mat zone. By irrigating its burrow, Abarenicola can separate a sand/clay mixture by floating the clay out in the head shaft irrigation current.

Thalassinidean burrowing shrimps are most abundant on the 'marine' tidal flats of southeastern Roberts Bank on the active Delta-front. These tidal flats

can be divided into four floral/sedimentological zones: the saltmarsh, algal mat, sandflat and eelgrass zones. Thalassinidean burrowing shrimps dominate the sandflat zone. Upogebia densities are positively correlated to mud content of the sediment. Callianassa show no clear grain size preference and are abundant in sediments ranging from 5 to 50% in mud content and from 2.6 to 4.0  $\phi$  in median grain size. At their peak density (446 burrow openings  $m^{-2}$ ) Callianassa rework the substrate they live in to a depth of 50 cm in about five months.

On central Roberts Bank a major transition from a 'marine' to a brackish environment occurs. A brackish marsh zone extending to much lower intertidal levels than the saltmarsh laterally replaces the algal mat zone and the upper half of the sandflat zone. A sandflat/mudflat zone cross-cut by channels displaces the eelgrass zone and lower half of the sandflat zone. The peak in Callianassa distribution moves to lower intertidal levels because of the presence of low salinity water at higher tidal levels and because of the absence of eelgrass in lower intertidal regions. Upogebia although physiologically better adapted to cope with reduced salinity demonstrates lower tolerance of brackish water in its distribution than Callianassa, probably because the function of its mud-lined burrow as a conduit for suspension feeding and respiration exposes Upogebia to low salinity surface waters, while Callianassa, in its unlined burrow used for deposit feeding, is protected from surface waters by high salinity interstitial waters. The distinction between these two types of burrow is considered to be very significant for paleoenvironmental reconstructions.

A new system of subdividing the intertidal region into exposure zones (the atmozone, amphizone and aquazone), based on critical tidal levels at which the maximum duration of continuous exposure or submergence 'jumps,' is advocated. It allows cross correlation between different tidal regions



experiencing different types of astronomically controlled tides and much of the intertidal zonation of Fraser Delta tidal flats may be causally related to these exposure zones. 83

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## INTRODUCTION

Geologists are becoming increasingly aware of the potential of trace fossils as paleoenvironmental indicators. Study of biogenic sedimentary structures and animal-sediment relationships in present day environments is an expanding field of research, which is attracting the attention of sedimentologists, paleontologists and marine biologists. In the past research by geologists in modern environments has tended to be largely descriptive. Investigation of the factors controlling the distribution of organisms was the domain of the marine biologist. However this situation is changing and geologists are becoming involved in increasing numbers in ecologically orientated studies of animal-sediment relationships. A wealth of ecological data already exists in the biological literature, but often its relevance to sedimentology and paleoenvironmental studies is not immediately apparent. For example much of the classic work on intertidal zonation by marine biologists has been carried out on rocky intertidal shorelines, which in themselves are of no particular interest to sedimentologists. However, many of the principles and findings on rocky intertidal shorelines can be applied to tidal flats, which are, of course, of great interest to sedimentologists. If trace fossils are to attain their full potential as paleoenvironmental indicators further information on the effects of pertinent environmental factors on the distribution of trace making organisms must be obtained. It was with this in mind that the following study was carried out. This study of the Fraser Delta is of necessity inter-disciplinary in nature involving the disciplines of sedimentology, biology, oceanography and even some astronomy! The buzz word inter-disciplinary may be new, but the approach is as old as science itself.

This thesis analyzes the distribution of various trace making organisms

on the tidal flats of the Fraser Delta. The organisms investigated include the thalassinidean burrowing shrimps Callianassa californiensis and Upogebia pugettensis, the burrowing polychaete Abarenicola pacifica and the tube-dwelling polychaetes Praxillela affinis pacifica and Spio sp., the gastropods Batillaria attramentaria and Nassarius mendicus and the bivalve Mya arenaria. As an integral part of this research the distribution of various floral zones in the intertidal region (e.g., saltmarsh, algal mats, eelgrass) is also analyzed. The burrowing shrimp Callianassa californiensis is the organism of most interest because it is ubiquitous to all Fraser Delta tidal flats, tolerating wide ranges in substrate type and salinity regime. Of almost equal interest is Upogebia pugettensis, but this shrimp is more restricted in occurrence. Thalassinidean shrimp burrows are well known in the trace fossil record (Thalassinoides and Ophiomorpha) extending at least as far back as the Cretaceous (Borradaile, 1903). The questions which this thesis sets out to answer are: (1) What is the distribution of these organisms on the tidal flats of the Fraser Delta and how do various environmental factors influence their distribution? (2) What is the nature of the biogenic sedimentary structures the organisms produce? (3) At what rate do they rework the substrate by burrowing into and/or ingesting sediment? The environmental factors which have been considered include: a) Elevation; which determines the duration of exposure and submergence b) Grain size of the substrate c) Environmental energy d) Salinity regime e) Bio-interactions. Bio-interactions include the influence of floral cover (e.g., saltmarsh, eelgrass or algal mats) on faunal distribution and vice versa, and also any inter-faunal interactions -- e.g., trophic group ammensalism (Rhoads and Young, 1970).

The study area lies on the coast of British Columbia in temperate latitudes and experiences a west coast maritime climate, characterized by summers

which are cool, sunny and not very humid and by winters which are cloudy, mild and wet. The Fraser River is the dominant source of terrigenous sediment to the Strait of Georgia (Pharo and Barnes, 1976). The Strait of Georgia lies on the western margin of the North American plate. The basin which it occupies began its formation about 150 million years ago as part of the extensive Georgia Depression. Mountain building ceased about two million years ago and the Strait took its present form about a million years later. Since then, glacial scouring, downwarping and erosion have continued to modify it. Present evidence indicates that the Fraser Delta began to fan out from a gap in the Pleistocene uplands at New Westminster, where the present Fraser River bifurcates into North Arm and Main Channel (Fig. 1), about 8,000 years ago. Since then an estimated 120-210 m of deltaic sediments have been deposited (Mathews and Shephard, 1962). The present delta meets the sea along a perimeter about 35 km long. Of this, a front approximately 20 km long faces west into the Strait of Georgia, while a now inactive front about 15 km long faces south onto Boundary Bay. Between these two fronts lies a former island, now the Point Roberts Peninsula. Intertidal marshes and tidal flats 4 to 8 km wide slope gently seaward from the edge of the cultivated lands of the delta, before the delta surface dips more steeply into the Strait of Georgia. The mean tidal range is about 3 m with extreme spring tidal ranges of 5 m and neap tidal ranges of 1.5 m. Tides are of mixed semi-diurnal type i.e., there are two high waters and two low waters each day but successive high and successive low waters are of different height. The Fraser River reaches its peak discharge during late spring and early summer. The less dense river water spreads over the saline waters of the Strait of Georgia as a visible plume of muddy fresh to brackish water. Central Strait of Georgia waters are thus stratified into a brackish surface layer and an underlying salt wedge (Waldichuk, 1957). The salt wedge intrudes

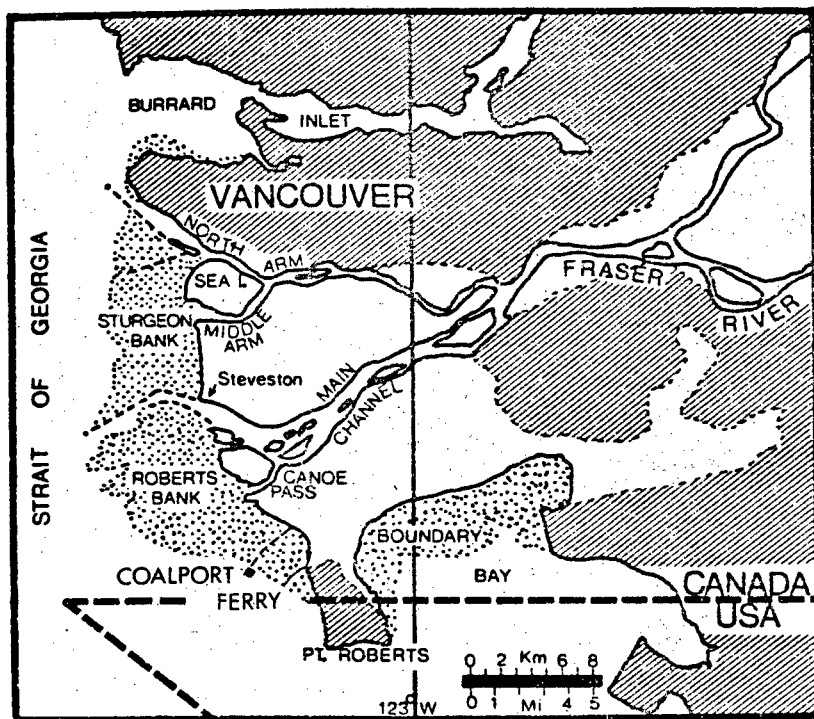


Figure 1. General location of Fraser Delta. Tidal flats are stippled, land area of Recent alluvium is blank, and older deposits cross-hatched (adapted from Luternauer and Murray, 1973).

the Fraser River on flood tides extending as far as 20 km upstream of the inner tidal flats during winter, but no further than the inner edge of the flats during the freshet (Ages and Woollard, 1976).

The format of this thesis is a series of papers -- Parts 1 to 4. Part 4 is split into two sections Part 4A and B. It is intended that shortened versions of each Part will be published in the near future. Each Part must therefore be able to stand on its own. Inevitably, as they all deal with the same study area, there is some repetition of facts and ideas between Parts but as far as possible this has been kept to a minimum. Cross references are usually made as Swinbanks (1979), unless it is not obvious the Part referred to in which case Part number is included, e.g., Swinbanks (1979, Part 3).

Part 1 provides a basis for describing location in the intertidal region which is applied in the tidal flat studies that follow. It is a new scheme for subdividing the intertidal region based on critical tidal levels at which the maximum duration of continuous exposure or submergence increases abruptly in a step-like manner. This scheme is advocated because (1) it allows meaningful cross correlation between intertidal regions experiencing different types of astronomically controlled tides, e.g., between a region experiencing mixed tides with one experiencing semi-diurnal (2) the critical tidal levels on which the scheme is based may be causally related to intertidal zonation. None of the schemes currently in use, based on mean tidal levels or mean exposure levels, fulfills either of these roles. A mean tidal level carries with it no information on the duration of continuous exposure or continuous submergence at that level, nor does a mean exposure value, as in the computation of mean exposure no distinction is drawn between continuous and discontinuous exposure or submergence. One might expect that organisms should respond to predictable recurrent extremes in exposure or



submergence, but one can hardly expect them to have a concept of abstract averages.

Part 2 is a study of the zonation of flora, fauna and their biogenic sedimentary structures on the tidal flats of Boundary Bay on the inactive southern flank of the Delta. These tidal flats are unusual in that the grain size of the substrate over much of the Bay varies little, consisting predominantly of fine to very fine well to very well sorted sands. The influence of the Fraser River on this Bay is slight and the Bay waters are 'normal marine' for the southern Strait of Georgia. As a result a distinct floral/faunal zonation exists, delimited primarily by elevation, which is comparable in many respects to the precise elevational delimitation of zonation found on rocky intertidal shorelines experiencing stable salinity regimes. The scheme of intertidal subdivision outlined in Part 1 is applied and developed for the specific case of Boundary Bay tides, and it is demonstrated that much of the zonation of Boundary Bay tidal flats may be causally related to critical tidal levels.

Part 3 supplements Part 2. It is a study of the sediment reworking and size sorting capabilities of Abarenicola pacifica a polychaete which is abundant on the Boundary Bay tidal flats. By constantly turning over the surface sediments this organism may well influence zonation on the tidal flat, and in particular the bioturbation of this worm may be a factor limiting the extent of the algal mat zone, one of the five major floral/sedimentological zones of Boundary Bay tidal flats.

Part 4 moves onto the active tidal flats of the Fraser Delta. It is a study of the distribution of the thalassinidean burrowing shrimps, Callinassa californiensis and Upogebia pugettensis on Roberts Bank. Roberts Bank divides naturally and abruptly into a 'marine' environment to the southeast and a brackish environment to the northwest. The transition occurs between the

Coalport causeway and Canoe Pass (Fig. 1). It was therefore felt appropriate to split Part 4 into two sections, Part 4A dealing with an exclusively 'marine' environment between the two man-made causeways on southeastern Roberts Bank and Part 4B dealing with the marine to brackish transition on northern and central Roberts Bank. The inter-causeway tidal flat studied in Part 4A lies between the Tsawwassen ferry terminal causeway and the Coalport causeway (Fig. 1). It has many of the characteristics of Boundary Bay and a similar floral/faunal zonation is developed, but there are differences which probably result from differences in the style of tidal channel drainage in the two areas, which in turn is a function of grain size. There is much greater variability in the grain size of the substrate on this tidal flat than in Boundary Bay. Mud contents of the sediment are an order of magnitude higher and grain size plays an important role in controlling the distribution of thalassinidean shrimps.

Thalassinidean shrimps attain their highest densities on the inter-causeway tidal flat and the effects of grain size on shrimp distribution and interactions between the two species of shrimp can readily be analyzed in an environment where salinity can be considered non-variable. Armed with the information from this tidal flat in Part 4B the complexities of the environment of northern and central Roberts Bank are tackled where salinity becomes an added variable among the factors influencing shrimp distribution. On passing from the 'marine' to brackish environment on central Roberts Bank the floral/sedimentological zones of the tidal flats are completely restructured and shrimp distribution responds to the changes. Some discoveries are made regarding the apparent salinity tolerance of these two species of shrimp which have important paleoenvironmental implications.

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Part 1

INTERTIDAL EXPOSURE ZONES: A NEW SCHEME  
FOR SUBDIVIDING THE INTERTIDAL REGION

## ABSTRACT

There are at least four orders of critical tidal level within the intertidal region, at which the duration of continuous exposure or submergence 'jumps' - daily (1st order), monthly (2nd order), annual (3rd order) and 18.6 year (4th order) critical tidal levels. Daily critical tidal levels delimit three exposure zones which experience markedly different extremes in exposure and submergence duration - the atmozone, the amphizone and the aquazone. Monthly critical tidal levels divide the atmozone and aquazone into upper and lower subzones. Subdivision of the amphizone is only possible for mixed tides. This scheme allows cross correlation between intertidal regions experiencing different astronomically controlled tides, and may be causally related to intertidal zonation.

## Introduction

The study of intertidal zonation has attracted the attention of marine biologists since the beginning of nineteenth century and a vast literature exists on the topic (Ricketts and Calvin, 1968). Geologists have been studying the distribution of organisms, both floral and faunal, on carbonate tidal flats for several decades, and more recently the expanding study of animal-sediment relationships has included study of organism distribution on clastic tidal flats. A record of the presence and distribution of intertidal organisms is preserved in ancient sediments in the form of biogenic sedimentary structures. Despite this extensive research over many years no universally accepted scheme for subdividing the intertidal region exists. Geologists have discussed the problem of defining intertidal location little, with the exception of Ginsburg et al. (1970) who advocate the use of 'exposure index' (mean percent exposure). Among biologists the extent of the role which tides play in intertidal zonation has been a matter of much controversy (Carefoot, 1977). At one extreme there are those who believe that tides are not causally related to zonation (Stephenson and Stephenson, 1949) and they advocate a scheme of intertidal subdivision based purely on biological grounds (e.g., the upper limit of barnacles or laminarians, etc.). At the other extreme are those who believe that specific tidal levels can be causally related to zone boundaries (Doty, 1957). The current consensus of opinion among biologists appears to be that the intertidal zone should be subdivided on the basis of biology, while only loosely correlating this subdivision to mean tidal levels or mean exposure levels (Ricketts and Calvin, 1968; Chapman, 1974). While adhering to this viewpoint Chapman and Chapman believe that "when more is known about the causal relationships between tidal phenomena and the major belt organisms it would probably be more desirable to use tidal data" (1973, p. 353). But

there is no reason to expect causal relationships between mean tidal levels or mean exposure levels and zone boundaries, and the continued use of mean tidal values to describe location in the intertidal region inhibits further understanding of causal relationships between tidal phenomena and zonation. Further, schemes based on mean tidal levels cannot justifiably be used to cross correlate areas experiencing mixed tides with those experiencing semi-diurnal, because there is no reason to think that a semi-diurnal mean tidal level (e.g., mean high water) is correlative with the 'equivalent' mixed mean tidal level (mean higher high water) either in respect to the frequency or duration of continuous exposure or submergence. Nor can mean exposure schemes be used, because in the calculation of mean exposure no distinction is made between continuous and discontinuous exposure or submergence.

#### Critical Tidal Levels

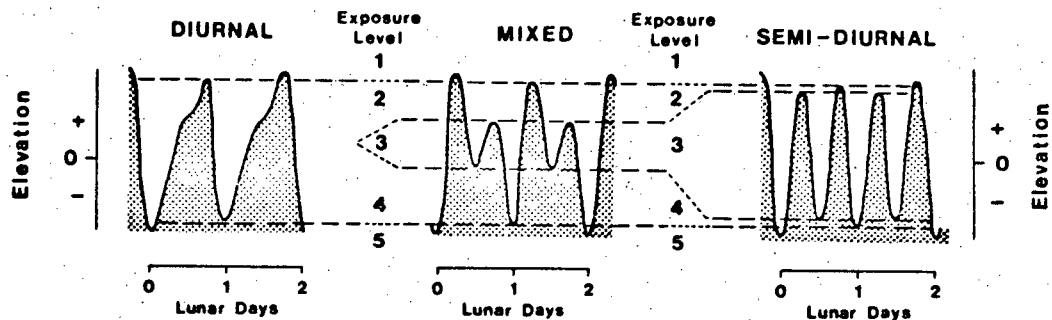
The concept on which the scheme presented here is based - critical tidal levels - was first described over thirty years ago by Doty (1946), and biologists were aware of the concept long before then (Doty, 1957). Doty, however, does not advocate the use of critical tidal levels in subdivision of the intertidal region, because he considers such a system 'too complex to be satisfactory' (1957, p. 542). Critical tidal levels are defined here as levels at which the duration of continuous exposure or submergence changes abruptly in a step-like manner at the height of a crest or trough in a daily, monthly, annual or longer term tidal cycle. This definition should not be confused with the 'critical tidal levels' discussed by Underwood (1978) and other workers in Britain (Colman, 1933; Evans, 1947a, b, 1957; Lewis, 1964), which are defined by breaks in slope of mean exposure curves and/or by the clumping of the upper and lower limits of organisms at particular tidal levels.

It has not, until now, been pointed out that there are several orders of critical tidal levels which can be recognized, depending on the duration of the lunar, solar or earthly cycle responsible (Fig. 1). Daily (1st order) critical tidal levels are a result of the earth's rotation on its axis combined with the declination of the moon. Of the three principal types of daily tidal cycle - semi-diurnal, diurnal and mixed - the mixed tide can be considered to be the general case and semi-diurnal and diurnal tides to be special forms. For mixed tides there are two high waters and two low waters for each lunar day of 24 hours and 50 minutes, but successive high and low waters differ in height due to the effects of the moon's declination. On any particular day an intertidal region experiencing mixed tides can be subdivided into five 'exposure levels,' which are defined by the heights of high and low waters (Fig. 1a). The duration of continuous exposure or submergence is at least halved or doubled on passing from one exposure level to the next. Figure 1a is somewhat over-simplified, as mixed tides have both a height asymmetry and a time asymmetry, and the times between successive high tides and successive low tides are not equal due to lag effects which are dependent on tidal range. For example, the time between higher high water and lower high water is less than the time between lower high water and the next higher high water. As a result, the maximum duration of continuous exposure or submergence is not exactly halved or doubled on leaving Exposure Level 3. Nevertheless, there is an abrupt step in exposure or submergence duration of the order of magnitude indicated. In areas experiencing semi-diurnal tides the moon's declination has little influence on the tides and thus they lack a pronounced diurnal inequality in tidal heights. As a result, Exposure Levels 2 and 4 are suppressed, spanning only a very narrow elevation range. In regions experiencing diurnal tides the moon's declination has such a pronounced influence on the tide that the lower

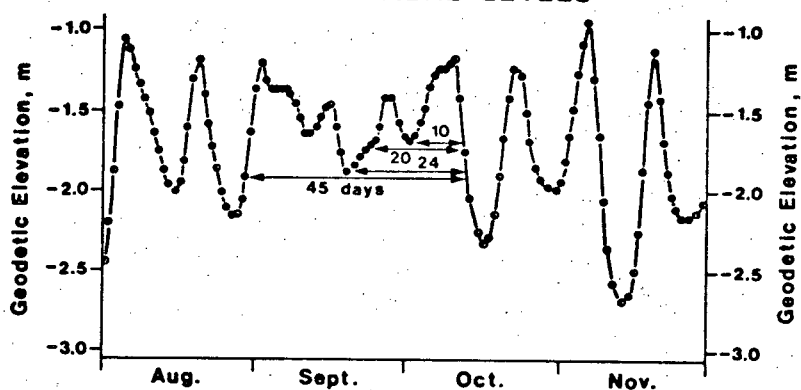


- Figure 1. (a) Schematic daily tidal curves for the three main types of tide. Shading indicates submergence. For mixed tides there are four critical tidal levels (dashed lines) at which the duration of exposure or submergence 'jumps' and which define five exposure levels within which exposure and submergence changes continuously with respect to elevation. Higher high water defines the boundary between Exposure Levels 1 and 2, and is a critical tidal level above which the duration of exposure doubles from less than one lunar day to at least nearly two. Lower high water defines the boundary between Exposure Levels 2 and 3 and is a level above which the duration of exposure doubles from less than half a lunar day to just under one lunar day. Equivalent critical tidal levels lie at the heights of higher low water and lower low water but involve steps in submergence duration. They define Exposure Levels 4 and 5. The same critical tidal levels and exposure levels can be recognized for semi-diurnal tides. Exposure Level 3 cannot be defined for diurnal tides because they lack lower high water and higher low water stages.
- (b) The predicted daily heights of lower low water at Point Atkinson, B.C. between August and November, 1977 are plotted as dots. The low waters are modulated into two neap tides and two spring tides per month. Successive spring tides are of different ranges. The spring tide of lesser range defines a critical tidal level at which duration of continuous submergence jumps from about 10 to 20 days, and that of greater range a jump from about 24 to 45 days.
- (c) Annual critical levels are defined by the spring higher high waters of June and December for predicted tides in 1977/78 at Point Atkinson, B.C. Dots indicate heights of spring and neap tides. The spring high tides of June, 1978 and December, 1978 are so similar in height that these two critical tidal levels merge into one, involving a jump from about six months to at least nearly two years of continuous exposure. The spring high tide of December, 1977 was higher and defines a critical tidal level above which the duration of exposure is at least nearly three years.
- (d) The level of the lowest low water (i.e., extreme spring lower low water) for each year from 1967 to 1987 at Tsawwassen, B.C. is graphed. This level has risen gradually from about -3.1 m Geodetic Datum in 1968 to about -2.6 m Geodetic Datum in 1978 based on observed tidal records. Mean spring lower low water (i.e., the mean of twelve monthly spring lower low waters for each year) helps define the trend. The predicted trends over the next nine years are dashed in. The level of the lowest extreme spring lower low water in December, 1968 defines a critical tidal level below which the duration of continuous submergence jumps from about 18 years to at least nearly 36 years.

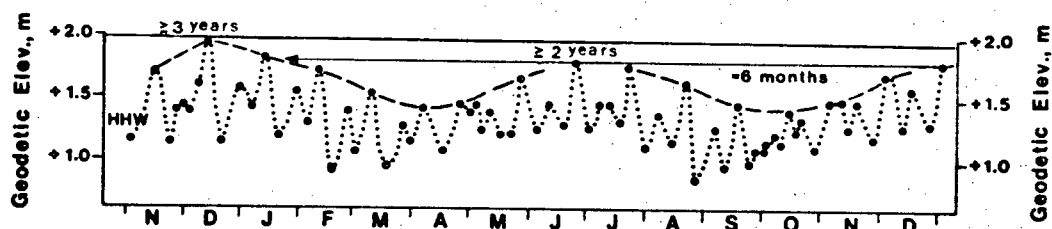
### A. DAILY CRITICAL TIDAL LEVELS



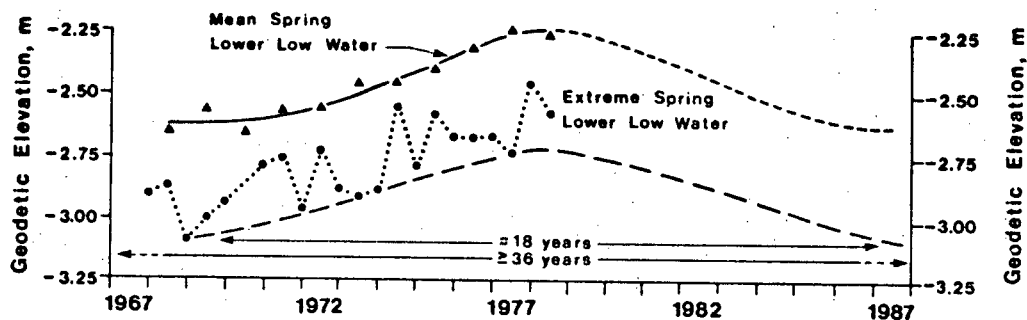
### B. MONTHLY CRITICAL TIDAL LEVELS



### C. ANNUAL CRITICAL TIDAL LEVELS



### D. FOURTH ORDER CRITICAL TIDAL LEVEL



high water and higher low water stages are eliminated due to extreme diurnal inequality in the tides. As a result Exposure Level 3 is absent. Despite these differences between tidal types the three types have two important features in common. The step in exposure duration in going from Exposure Level 2 to Exposure Level 1, involving a jump from less than one lunar day of continuous exposure to at least nearly two lunar days, is common to all three tidal types, as is the jump in submergence duration in passing from Exposure Level 4 to Exposure Level 5, which similarly involves a jump from less than one lunar day of continuous submergence to at least nearly two lunar days of continuous submergence. These two critical tidal levels defined by the fundamental cycle of the lunar day form the basis of the scheme of inter-tidal subdivision to be outlined here.

First order critical tidal levels are modulated into monthly cycles of spring and neap tidal periods which define 2nd order (monthly) critical tidal levels (Fig. 1b). Depending on the tidal region the monthly cycle can be caused by the phases of the moon (period 29.5 days), the declinational cycle of the moon (period 27.2 days), or the apogee/perigee cycle in earth-moon separation (period 27.5 days). These cycles are all of very similar duration as they are all governed by the period of the moon's orbit around the earth. There are two neap and two spring tidal periods each month but successive spring tidal periods are of different range. Each spring tidal period defines a 2nd order critical tidal level for both high and low waters. Figure 1b illustrates these critical tidal levels for lower low water at Pt. Atkinson, B.C. The first critical tidal level is defined by the spring tide of lesser range and involves a jump from about 10 to 20 days of continuous submergence, while the second critical tidal level is defined by the spring tide of greater range and involves a step from about 24 to 45 days of continuous submergence. The situation is the same for higher high

water (or high water) except that it involves steps in exposure rather than submergence.

Second order critical tidal levels are in turn modulated into annual cycles which define 3rd order (annual) critical tidal levels (Fig. 1c). Tidal ranges are maximized in June and December at the time of the solstices when the sun is over the tropics, and minimized at the equinoxes in March and September when the sun is over the equator. Tidal ranges are greater in December than in June because the earth is near perihelion (nearest the sun) in December while it is near aphelion in June. For Pt. Atkinson tides, 3rd order critical tidal levels are defined by the spring high tides of June and December (Fig. 1c). That of June involves a jump in the duration of continuous exposure from about six months to almost one year, while that in December involves a jump from about one year to at least nearly two years. (In Figure 1c these two steps are too close to resolve. There are equivalent critical tidal levels for lower low water (or low water).

Third order critical tidal levels are in turn modulated by an 18.6 year soli-lunar cycle defining 4th order critical tidal levels (Fig. 1d). Every 18.6 years, when the maximum declination of the moon coincides with the maximum declination of the sun, tidal ranges are maximized. This effect is only detectable for spring lower low waters for tides in the southern Strait of Georgia (Fig. 1d). The lowest level of lower low water reached around 1968/69 defines a critical tidal level at which the maximum duration of submergence probably jumps from about 18 to 36 years, although insufficient records are available to confirm this.

There are, no doubt, higher order critical tidal levels beyond 4th order defined by very long term astronomical cycles, but records are not available to analyze them. All of the critical tidal levels defined above can be recognized for all astronomically controlled tides the world over, with the

exception of the 1st order (daily) critical tidal levels defining Exposure Level 3, which cannot be defined for diurnal tides. Thus, critical tidal levels offer a means of cross correlation between different tidal regions regardless of the tidal types involved. Figure 2a illustrates such a cross correlation. Here the declinational mixed tides of the southern Strait of Georgia on the Pacific coast of Canada (Tsawwassen, B.C.) are cross correlated with the anomalistic semi-diurnal tides of the Bay of Fundy on the Atlantic coast of Canada (St. John's, New Brunswick) using extreme critical tidal levels at which the maximum duration of continuous exposure or submergence jumps. Despite the very different types of tide in the two areas, 24 extreme critical tidal levels at Tsawwassen can be cross correlated with 18 at St. John's. In several instances one critical tidal level at St. John's is split into two or three closely spaced steps at Tsawwassen, and occasionally vice versa.

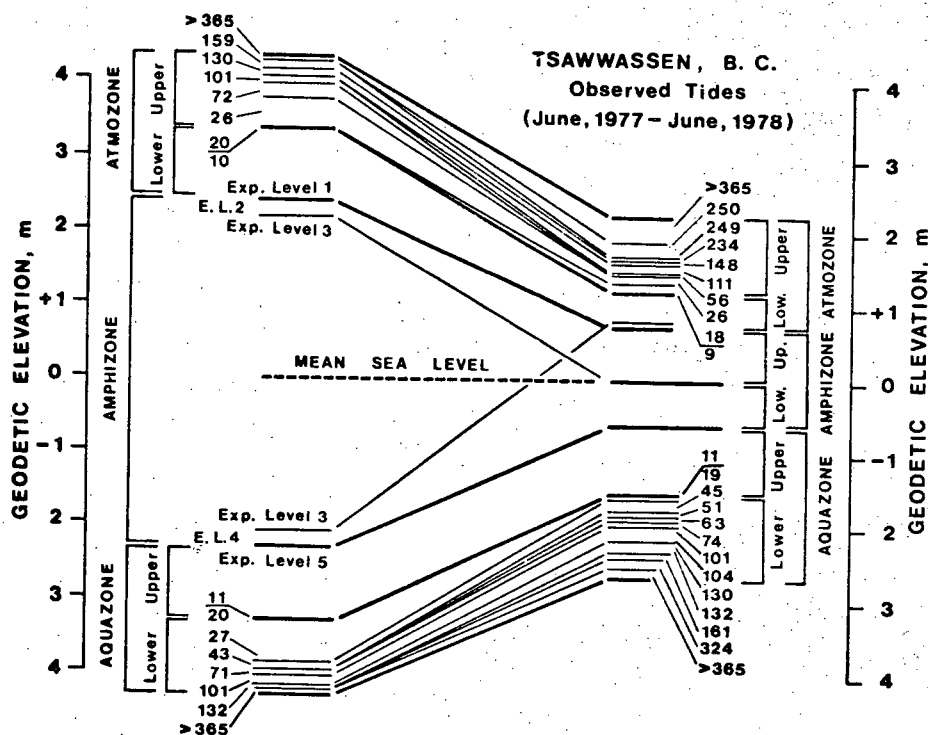
### Exposure Zones

The fundamental, 1st order critical tidal levels caused by the earth's rotation about its axis can be used to subdivide both intertidal regions in Figure 2a into three exposure zones. The critical tidal levels used are those between Exposure Levels 1 and 2 where the duration of exposure drops from at least nearly two lunar days to less than one lunar day, and between Exposure Levels 4 and 5 where the duration of submergence jumps from less than one to at least nearly two lunar days. The former critical tidal level reaches its lowest level, and the latter its highest level, in March and September at the time of the equinoxes, and these extreme levels are illustrated in Figure 2a. The intertidal 'amphizone' lies between these two extreme critical tidal levels and thus forms the core to the intertidal

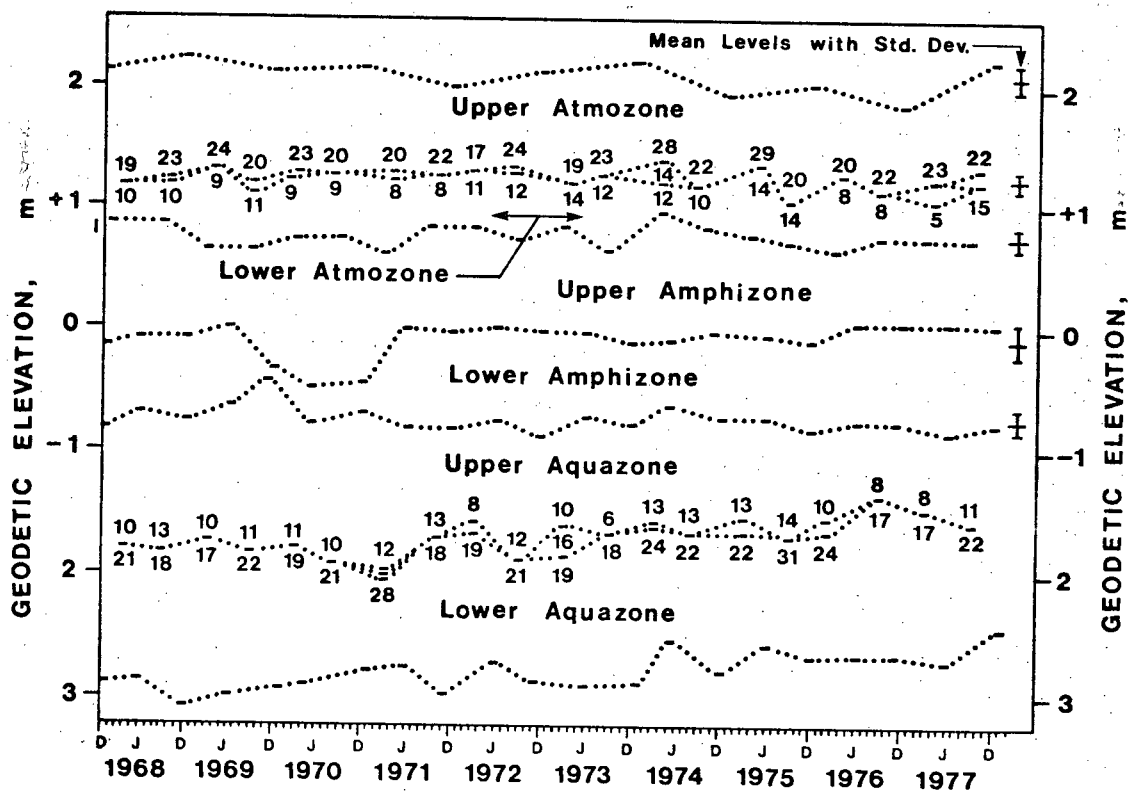
Figure 2.

- (a) Cross correlation of extreme critical tidal levels between the inter-tidal regions of St. John's, New Brunswick and Tsawwassen, B.C. Based on predicted tides for 1978 for St. John's and observed tides between June, 1977 and June, 1978 at Tsawwassen. The numbers above and below critical tidal levels indicate the maximum duration of continuous exposure in days in the case of atmozonal critical tidal levels, and the maximum duration of continuous submergence in days in the case of aquazonal critical tidal levels. For example at the upper limit of the lower atmozone at St. John's, the jump is from 10 to 20 days and the next critical tidal level up involves a jump from 26 to 72 days. In the case of atmozonal critical tidal levels only the lowest level attained by a particular critical tidal level is indicated. In the case of aquazonal critical tidal levels only the highest level attained by a particular critical tidal level is indicated, i.e., only extreme critical tidal levels are indicated.
- (b) Levels of exposure zone boundaries over the past ten years at Tsawwassen, B.C. based on observed tidal records. In the case of the boundary between the lower atmozone and the upper atmozone the numbers above and below critical tidal levels indicate the maximum duration of exposure in days. In the case of the boundary between the upper aquazone and the lower aquazone the numbers above and below critical tidal levels indicate the maximum duration of submergence in days. On the extreme right hand side of the diagram horizontal bars indicate the mean levels of exposure zone boundaries while the vertical bars indicate the standard deviation from the mean. Mean levels are not indicated in the case of the boundaries of the lower aquazone because they undergo significant modulation by the effects of an 18.6 year soli-lunar declinational cycle.

ST. JOHN, NEW BRUNSWICK  
Predicted Tides  
(1978)



(a)



(b)

region, experiencing both exposure and submergence every lunar day (hence amphizone from the Greek 'amphi' meaning both). Above the amphizone lies the 'atmozone' where the maximum duration of exposure exceeds nearly two lunar days. The atmozone can be subdivided at the level of the lowest 2nd order critical tidal level which involves a jump in exposure duration from about 10 to 20 days. Above this level are a whole series of closely spaced 2nd and 3rd order critical tidal levels. The upper limit of the atmozone lies at the level of the highest high tide of the year. Below the 'amphizone' lies the 'aquazone' within which the maximum duration of submergence exceeds nearly two lunar days. As in the case of the atmozone the 'aquazone' can be subdivided into an upper and lower part at the level of the highest 2nd order critical tidal level. The lower limit of the aquazone lies at the level of the lowest tide of the year. For mixed tides the amphizone can be subdivided at the lowest level of the critical tidal level between Exposure Levels 2 and 3 (Fig. 2a). For semi-diurnal tides the amphizone cannot be subdivided because critical tidal levels only occur within its upper and lower fringes. The intertidal region should be considered 'open-ended' in the sense that critical tidal levels of infinite order and infinite exposure or submergence duration define its upper and lower limits. But for most practical purposes this can probably be taken to lie at the levels of the highest and lowest 4th order critical tidal levels occurring within an 18 year period. Under this system there would be no such thing as the supratidal zone. For those geologists who define supratidal as lying above mean high water, supratidal is roughly equivalent to upper atmozonal.

For this scheme to be feasible the levels of the exposure zone and subzone boundaries based on observed tidal records must lie close to the same level each year, or, if not, must follow a predictable trend. Figure 2b illustrates the level of exposure zone and subzone boundaries over the past



ten years at Tsawwassen, B.C. based on observed tidal records. With the exception of the limits of the lower aquazone all boundaries stay close to the same level and the standard deviations from mean levels are 14 cm or less (range 8-14 cm) in a tidal range of 5 m. Occasionally, boundaries show erratic deviations (e.g., the limits of the lower amphizone in 1970, Fig. 2b) but this is only to be expected as exposure zone boundaries are defined by extreme tidal levels and these may occasionally be the result of unusual, unpredictable meteorological conditions rather than predictable astronomical events. Thus, this system probably could not be applied to areas where meteorological effects dominate over astronomical unless the meteorological effects are predictable (e.g., seasonal). The upper and lower limits of the lower aquazone at Tsawwassen are significantly modulated by the 18.6 year solilunar cycle mentioned above and the upper limit of the lower aquazone has risen about 30 cm over the past nine years from a level of -1.8 m Geodetic Datum in 1968/70 to -1.5 m Geodetic Datum in 1976/78. It should return to its 1968/70 level by the mid to late 1980's.

#### Intertidal Zonation

Quite apart from their use in cross correlation between different tidal regions there is justification for thinking that the exposure zones and critical tidal levels described above may be causally related to the intertidal zonation of flora and fauna. Doty (1946), and Widdowson (1965) have attempted to test the tide factor hypothesis by comparing floral and faunal zone limits with critical tidal levels, but, in the case of mixed tides the tide factor hypothesis will never be proven or disproven using this approach, because, for areas experiencing mixed tides, any point within the intertidal region will at some time in the year lie within a few centimeters of a 1st

order critical tidal level, since high and low water stages span the whole intertidal region. In addition, within the upper atmozone and lower aquazone there is a very high probability that one or more 2nd or 3rd order critical tidal levels will coincide with a zone boundary at any elevation one chooses to select. The question should not be "does the zone boundary coincide with a critical tidal level?," but "which critical tidal level(s) does the zone boundary coincide with and is there any justification for thinking they are causally related?." Swinbanks (1979) has demonstrated that Callianassa californiensis, a thalassinidean burrowing shrimp, extends up to lower atmozonal elevations on the Fraser Delta tidal flats, but does not extend beyond an elevation at which the maximum duration of continuous exposure rises abruptly from 4 to 9 days, because physiological studies (Thompson and Pritchard, 1969) indicate that (above) this point anoxia due to exposure would be lethal to Callianassa. Upogebia pugettensis, another thalassinidean burrowing shrimp extends up to but not beyond the lower limit of the upper amphizone. Within the upper amphizone the duration of anoxia during periods of Exposure Level 2 is probably lethal to postmolt Upogebia (Swinbanks, 1979). The saltmarshes of the Fraser Delta are restricted to upper atmozonal elevations. This may be because saltmarsh plant seedlings require the periods of exposure in excess of 10 days which occur in the upper atmozone in the spring, in order to germinate and root successfully (Swinbanks, 1979). In contrast to mixed tides, for semi-diurnal tides critical tidal levels do not occur within the amphizone except near its limits (Fig. 2a). Significantly biologists have found that for semi-diurnal tides the mid-intertidal (or mid-littoral) regions are devoid of floral or faunal zone boundaries (Stephenson and Stephenson, 1949), whereas for mixed tidal regions a major zone boundary occurs close to mean sea level (Ricketts and Calvin, 1968). If exposure zones and critical tidal levels are causal in intertidal zonation, this observation

might be anticipated a priori.

#### ACKNOWLEDGEMENTS

I thank the Regional Tidal Superintendent, W.J. Rapatz, and F. Stevenson of the Canadian Hydrographic Service, Institute of Ocean Sciences, Sidney, B.C. for providing tidal records for Tsawwassen, B.C. and St. John, New Brunswick. Dr. J.W. Murray, Dr. W.C. Barnes, Dr. C.D. Levings and Dr. L.F. Giovando critically read the manuscript.

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Part 2

BIOSEDIMENTOLOGICAL ZONATION OF BOUNDARY BAY TIDAL FLATS,  
FRASER RIVER DELTA, BRITISH COLUMBIA

## ABSTRACT

Boundary Bay tidal flats lie on the inactive southern flank of the Fraser Delta. The Bay waters are clear, and have salinities which are 'normal marine' for the Strait of Georgia. The grain size of the surface sediments varies little, consisting almost entirely of very fine to fine, well to very well sorted sands, which show a gradual fining shorewards trend. There are five floral/sedimentological zones on the tidal flats, which are, from the shoreline seawards, the saltmarsh zone, the algal mat zone, the upper sand wave zone, the eelgrass zone and the lower sand wave zone. The zones seaward of the saltmarsh have distinctive macrofaunal communities, producing assemblages of biogenic sedimentary structures diagnostic of each zone.

The lower limit of the saltmarsh lies at the lower limit of the upper atmozone, a level above which the maximum duration of exposure rises abruptly from about 12 to 40 days. The lower limit of the algal mat zone lies at the lower limit of the lower atmozone, a level above which the maximum duration of exposure jumps from less than one to nearly two lunar days. The upper limit of the eelgrass zone lies at the upper limit of the lower amphizone, a level above which the maximum duration of exposure jumps from about 0.5 to 0.7 lunar days. These correlations are believed to be causal.

Topography of small and large scale creates lateral heterogeneity within the biofacies of each zone. The algal mat zone and the eelgrass zone are flat, on the large scale. However, in both zones microtopography of biogenic origin, only a few centimeters high, profoundly influences faunal distribution patterns on the local scale. The upper sand wave zone is characterized by symmetrical sand waves with wavelengths of the order of 30 m and very low amplitudes ( $<0.1$  m), which probably form in response

to sea waves during severe winter storm activity and remain dormant for most of the time. Faunal densities maximize in the shallow water-filled troughs of these sand waves. The sand waves of the lower sand wave zone are of higher amplitude (up to 0.5 m), have longer wavelengths (60 m), are often lunate in outline and probably form in response to tidal currents. Faunal densities in this zone are low, and physical sedimentary structures dominate over biogenic.

In winter the floral zones retreat. The environmental energy of the Bay and surface sediment transport increase due to winter storm activity.

The densities of eight macrofaunal organisms which produce distinctive biogenic sedimentary structures were determined on two surveyed transects. The organisms investigated were Callianassa californiensis and Upogebia pugettensis, both thalassinidean burrowing shrimps, three polychaete worms, Abarenicola sp., Spio sp. and Praxillela sp., the bivalve Mya arenaria and the gastropods Batillaria attramentaria and Nassarius mendicus. The distribution patterns of each organism and the nature of the biogenic sedimentary structures they produce are described. Callianassa burrows are interpreted as being temporary feeding structures whereas Upogebia burrows, which are mud-lined, are suggested to be permanent dwelling burrows.



## INTRODUCTION

The topic of animal-sediment relationships has been receiving increasing attention in sedimentological literature, both in recent and fossil sediments. In recent sediments interest has focused on intertidal environments, because of their ease of access, although several studies have been carried out in subtidal areas (Rhoads and Young, 1970; Aller and Dodge, 1974). Work on clastic tidal flats has centred on the eastern seaboard of the U.S.A., in particular at Sapelo Island, Georgia (Frey and Howard, 1969; Howard and Dörjes, 1972; Howard and Frey, 1973), and studies are also being carried out on the eastern seaboard of Canada at Minas Basin, Bay of Fundy (Risk and Moffat, 1977; Featherstone and Risk, 1977; Risk et al., 1976). Biogenic sedimentary structures have been studied by European workers, in particular the German and Dutch, for many years (Van Straaten, 1952; Reineck, 1958; Seilacher, 1964; Dörjes, 1970; Schäfer, 1972).

This study, centred on Boundary Bay tidal flats on the inactive southern flank of the Fraser Delta, is one in a series of studies being carried out on the tidal flats of the Fraser Delta on the west coast of Canada (Swinbanks, 1979).

Boundary Bay tidal flats are unique, in that variations in grain size of the surface sediments over most of the flats are slight, and a distinct floral/faunal zonation exists, which is primarily controlled by elevation and exposure (Swinbanks and Murray, 1977). This is unlike most other tidal flats described in the literature, where variations in grain size of the substrate can play an important role in determining floral/faunal zonation, such as Minas Basin, Bay of Fundy (Risk and Moffat, 1977) and the active tidal flats of the Fraser Delta (Levings and Coustalin, 1975).

Boundary Bay lies on the southern flank of the Fraser Delta (Fig. 1). The Bay is protected from the sediment plume of the Fraser River by the Pleistocene peninsula of Point Roberts. As a result rates of sedimentation are low (0.42 mm/year, Kellerhals and Murray, 1969), and the Bay waters are clear and have salinities which are 'normal marine' (24-29 ‰) for the southern Strait of Georgia. Sediment is transported into the Bay by longshore drift along the western and eastern margins of the Bay, as evidenced by the accretion spits at Beach Grove and Crescent Beach, and by the relict beaches just south of Beach Grove, all of which indicate longshore drift towards the north (Figs. 2 & 3). The unconsolidated Pleistocene cliffs at Point Roberts are an important present day source of sediment to the Bay (Kellerhals and Murray, 1969). Two small rivers discharge minor amounts of sediment into the eastern end of the Bay (Fig. 1). In the western part of the Bay the saltmarsh is prograding, whereas to the east it has receded at least 1.2 km since 4,350 yrs. B.P. (Kellerhals and Murray, 1969).

Kellerhals and Murray (1969) divided the flats into four zones each having distinctive sedimentological and faunal/floral characteristics. The four zones described by Kellerhals and Murray (1969) are the saltmarsh, the high tidal flats, the intermediate tidal flats and the low tidal flats. The fauna and flora of Boundary Bay have been described by O'Connell (1975). In this paper the zonation described by Kellerhals and Murray (1969) is revised and mapped using aerial photographs and data collected from surveyed transects. Distribution of fauna on the tidal flats is given in quantitative terms and the biogenic sedimentary structures they produce are described.

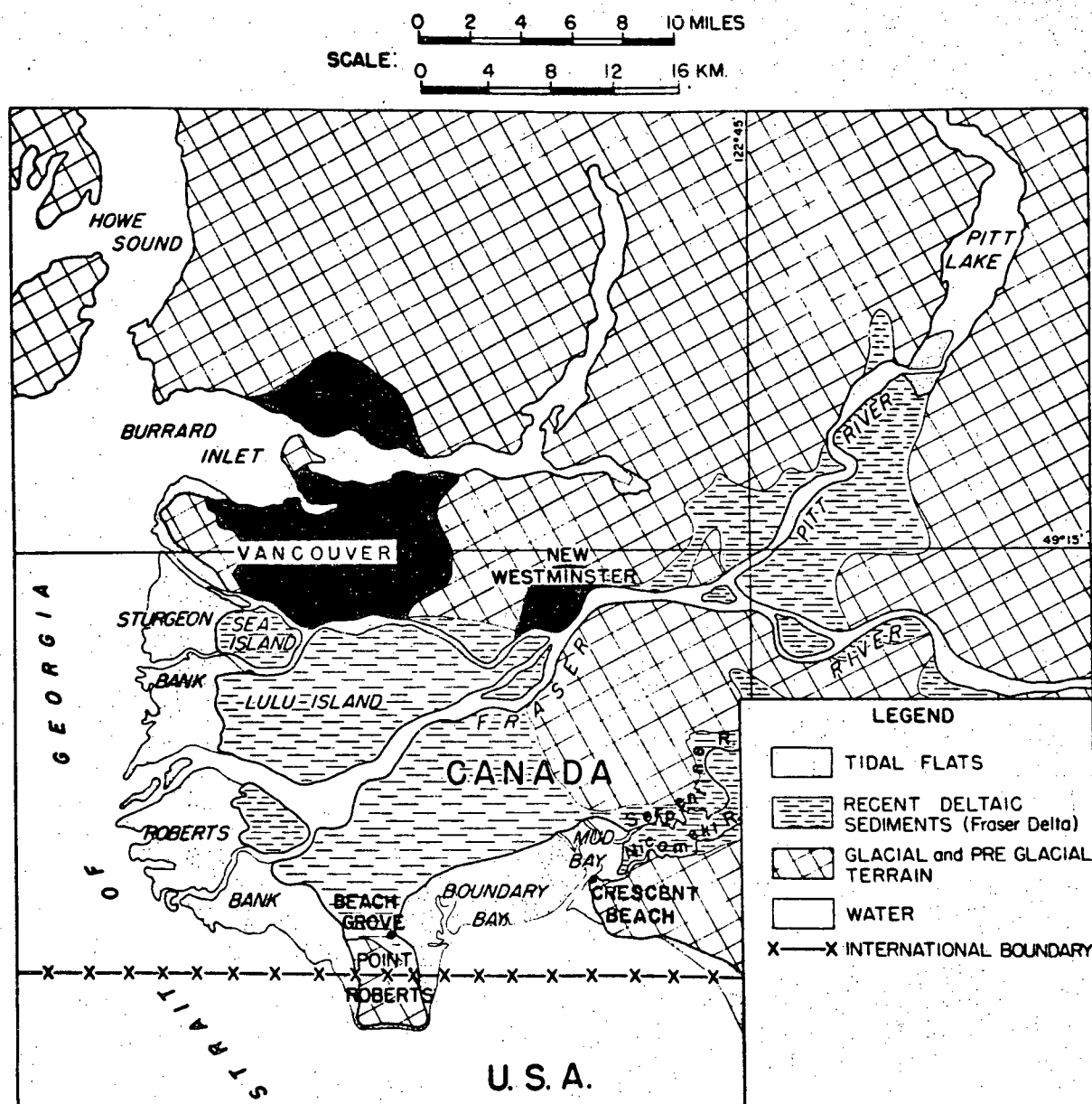


Figure 1. Map of the Fraser Delta area, showing the location of Boundary Bay tidal flats (reproduced from Kellerhals and Murray, 1969).

## METHODS

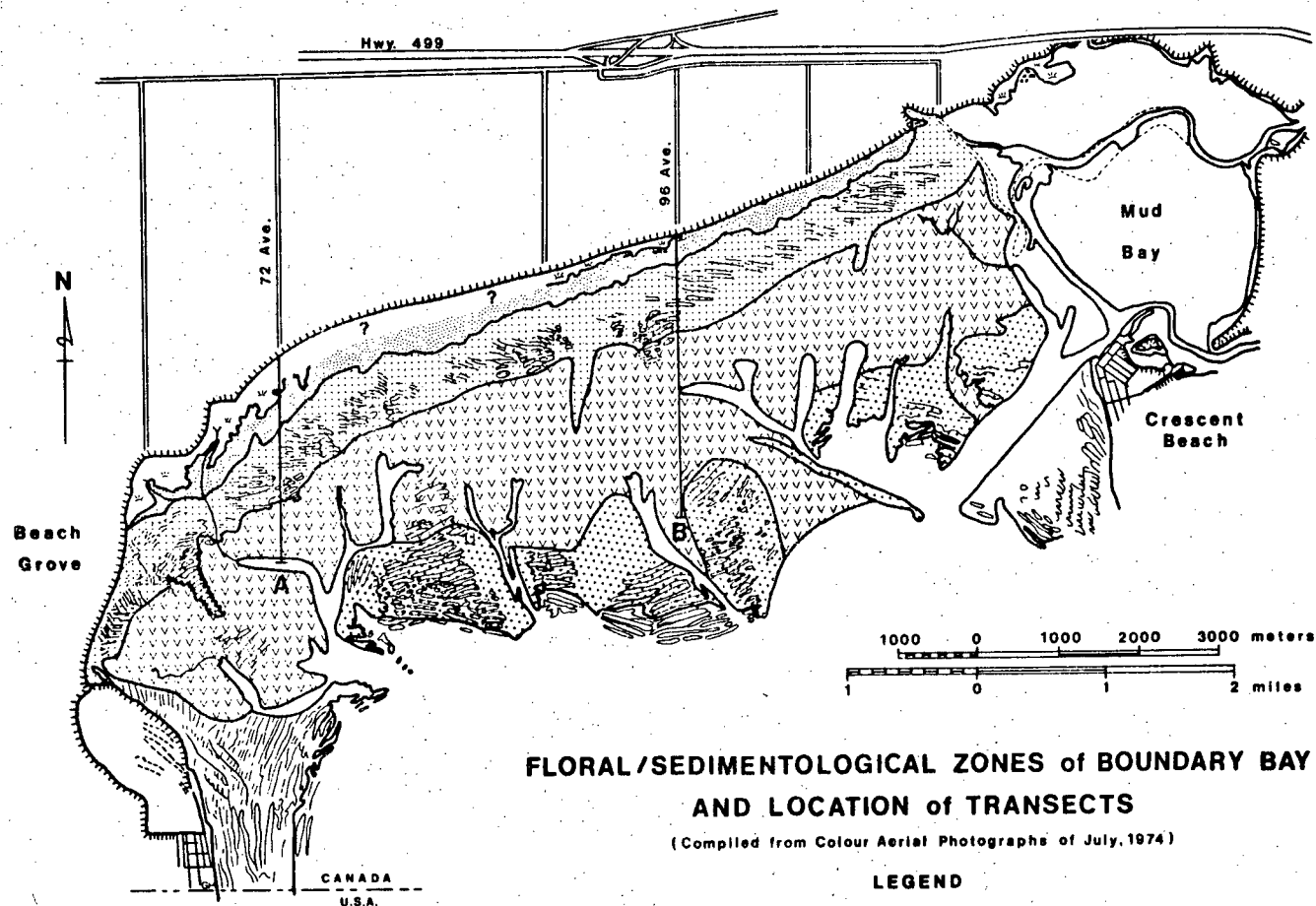
Two transects were established traversing the Boundary Bay tidal flats (Fig. 2). Transect A, which contained 22 stations, was set up and analysed during June and early July, 1976. Transect B, which contained 38 stations, was established and analysed in July and August, 1976. Further observations were made on the transects in November, 1976, and at various times of the year in 1977 and 1978 (Table I).

The two transects, A and B, were surveyed from bench marks with the use of a transit and an alidade. The transects run north/south from the edge of the saltmarsh to low water mark with stations taped at 91.4 m (300 ft) intervals and marked by wooden stakes. The change in elevation between successive stations was determined to an accuracy of about  $\pm 5$  mm. High accuracy was required because errors are cumulative along the transect.

Some burrowing organisms produce visible evidence of their density at the sediment surface, either directly by their presence in the case of epifauna, or indirectly in the form of burrow exits or fecal mounds in the case of infauna. Using this surface evidence it was possible to determine the density of the following organisms by quadrat sampling: Callianassa californiensis and Upogebia pugettensis, both thalassinidean burrowing shrimps, three polychaete worms, Abarenicola sp., Spio sp. and Praxillela sp., the bivalve Mya arenaria and the gastropods Batillaria attramentaria and Nassarius mendicus. Direct counts of organisms were made in the cases of Batillaria, Nassarius, Spio, Praxillela and Mya, whereas indirect counts of fecal mounds or burrow openings were made in the cases of Abarenicola, Upogebia and Callianassa.

Quadrats of four different sizes were used --  $1 \text{ m}^2$ ,  $0.25 \text{ m}^2$ ,  $100 \text{ cm}^2$ , and  $4 \text{ cm}^2$ . The quadrat size selected depended on the size and density of

Figure 2. Floral/sedimentological zonation of Boundary Bay with the locations of transects A and B indicated. Between the tidal channels the waterline approximates to the -2.4 m (-8.0 ft) contour (Geodetic Datum). The waterline in the tidal channels does not follow a specific contour since these depressions remain water-filled during low tide, despite the fact that they are well above sea level.



Source: Integrated Resources  
Photography, Flight  
No. 142, July, 1974.

# FLORAL/SEDIMENTOLOGICAL ZONES of BOUNDARY BAY AND LOCATION of TRANSECTS

(Compiled from Colour Aerial Photographs of July, 1974)

## LEGEND











- |   |                      |   |  |
|---|----------------------|---|--|
|  | Salt Marsh Zone      | ??  | Area Not Covered by<br>Aerial Photo Mosaic |
|  | Algal Mat Zone       |  | Relict Features                            |
|  | Upper Sand Wave Zone |  | Transect Line                              |
|  | Eelgrass Zone        |  | Dyke                                       |
|  | Lower Sand Wave Zone |  | Sand Wave Troughs                          |
|   |                      |  | Sand Wave Fixed by<br>Eelgrass             |

TABLE I

Dates and Locations of Field Observations

June 5-16, 1976	Transect A established and surveyed.
June 17-July 5, 1976	Sampling on transect A.
July 6-16, 1976	Transect B established and surveyed.
Aug. 2-22, 1976	Sampling on transect B.
Nov. 8, 1976	Salinity measurements at stations A5-A12.
Feb. 10, 1977	Observations of floral zone limits on transect A.
April 5-7, 1977	Observations of eelgrass and juvenile <u>Abarenicola</u> on transect A.
Sept. 21, 1977	Salinity measurements at stations A1-A22 and B1-B17.
Sept. 27, 1977	Salinity measurements at stations A6-A13.
March 25-26, 1978	Observations of juvenile <u>Abarenicola</u> at stations A1-A6, and eelgrass at stations A13-A17 and B12-B30.
April 8-9, 1978	Observations of juvenile <u>Abarenicola</u> at stations A1-A6.
* May 14, 18-21, 26, July 17, 1978	Quantitative observations of juvenile <u>Abarenicola</u> at stations A1-A6.

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\* Quantitative results to be published elsewhere (Swinbanks, in preparation).

the organism being investigated. The quadrat was thrown down randomly within 5 m of the station, and organisms or burrow numbers within the quadrat counted. When the origin of a burrow was in doubt, the burrow was excavated with a spade or trowel to determine the organism responsible. Sample specimens of each organism studied were collected and preserved in 10% formaldehyde for later identification. Light's Manual (Smith and Carlton, 1975) and the descriptions of Boundary Bay fauna by O'Connell (1975) were used in organism identifications.

Several of the organisms studied are sensitive to desiccation in the upper layers of sediment. To distinguish 'wet' sampling sites from 'dry,' a depression about 1 cm deep was made in the sand with a finger after ten hours of exposure. If the depression formed immediately filled with water, then the sediment was considered 'wet.' This procedure simply establishes whether or not the water table lies within 1 cm of the surface.

For all transects the densities of Abarenicola, Batillaria, Nassarius, Upogebia, Callianassa and Mya were determined by sampling a 2 m<sup>2</sup> area at each station with either a 1 m<sup>2</sup> or 0.25 m<sup>2</sup> quadrat (8 x 0.25 m<sup>2</sup> for stations A1-A22 and B1-B12, 2 x 1 m<sup>2</sup> for stations B12-B38). Praxillela densities were similarly determined, except where densities became excessive ( $>100 \text{ m}^{-2}$ ), in which case densities were determined by taking eight readings with a 100 cm<sup>2</sup> quadrat. The density of Spio, a small tube-dwelling polychaete worm, was determined by taking four readings at each station with a 4 cm<sup>2</sup> quadrat.

To determine the relationship between burrow density and organism density, in the case of Callianassa, all the sediment within a 0.25 m<sup>2</sup> open ended metal box was excavated to a depth of 50 cm, and the sediment examined for shrimps with the aid of a coarse sieve (2 mm mesh). Six results were obtained by sampling twice at stations A12, A13 and A14.



For Abarenicola the relationship between fecal cast density and worm density was determined using a box core constructed from a two gallon can, which gives a core of rectangular cross section (15 x 20 cm), 30 cm deep. Thirty cores were taken. Only two casts were enclosed within each core to ensure that the worms responsible for the casts were enclosed within the core.

Burrow morphologies were examined using two box cores, one giving a core 30 cm deep and the other 1 m. The burrow morphologies of the shrimps Callinassa and Upogebia were investigated by taking resin casts using the method developed by Shinn (1968). In several casts shrimps were visible, entombed in the resin cast. This gave a means of checking the shrimp to burrow ratio determined as described above.

Grain size samples of the surface sediment were collected at all stations using a 2 cm deep rectangular can. The salinity of surface waters at low tide were recorded at stations with a refractometer. In the lab, grain size samples were washed free of salt, treated with 30% H<sub>2</sub>O<sub>2</sub>, wet sieved through a 63  $\mu$ m sieve for extraction of the silt/clay fraction, and then dry sieved at 0.5  $\phi$  intervals. Between 10 and 30 g of sample was used.

Colour aerial photographs of Boundary Bay taken in July, 1974 (Integrated Resources Photography, Flight No. 142) were used to map the distinctive floral/sedimentological zones of the exposed tidal flats. A topographic base map with a 0.3 m contour interval (Kellerhals and Murray, 1969), was used to determine the elevation of zone boundaries between the surveyed transects.

## FLORAL/SEDIMENTOLOGICAL ZONATION OF THE TIDAL FLATS

Description

Aerial photographs taken in July, 1974 of Boundary Bay reveal five floral/sedimentological zones on the exposed tidal flats (Fig. 2), which can be recognized on the basis of their distinctive floral cover or by the presence of large scale bedforms. The zones visible in the photographs are, from the shoreline seawards, the saltmarsh zone, the algal mat zone, the upper sand wave zone, the eelgrass zone and the lower sand wave zone. Dense eelgrass growth also occurs in the tidal channels and extends down the channels into the subtidal zone below the lower sand wave zone.

The five zones are present throughout the Bay, except at the eastern and western extremities immediately south of Beach Grove and Crescent Beach (Fig. 2), where sand waves cover the entire intertidal zone, and no eelgrass beds, algal mats or saltmarsh have developed, because of the coarseness and probable instability of the sands in both these areas. In these two areas the entire intertidal zone has the characteristics of the lower sand wave zone. The five-fold zonation is also absent in the finer grained sediments of Mud Bay.

Table II tabulates the elevations of the various zone boundaries with respect to Canadian Geodetic Datum, on both transects, as determined by surveying in summer. The boundary between the algal mat zone and the upper sand wave zone is defined to be at the lower limit of continuous algal mat growth. Isolated algal mat hummocks are present below this level on both transects. All boundaries are elevation delimited except that between the eelgrass and lower sand wave zones, which in places extends down to low water line (- 2.4 m Geodetic Datum, Fig. 2).

In winter the floral zones retreat. The algal mats die back and

TABLE II

## Elevations of Zone Boundaries

Boundary	Transect A		Transect B	
	Station	Elevation (m)	Station	Elevation (m)
Lower Limit of Saltmarsh Zone	T6	+ 1.15 $\pm$ 0.05	2	+ 1.10 $\pm$ 0.01
Upper Limit of Algal Mat Zone	A1	+ 0.98 $\pm$ 0.06	B1	+ 1.04 $\pm$ 0.01
*Algal Mat Zone/Upper Sand Wave Zone	A5/A6	+ 0.75 $\pm$ 0.08	B4/B5	+ 0.76 $\pm$ 0.07
Upper Sand Wave Zone/Eelgrass Zone	A13	+ 0.10 $\pm$ 0.12	B12	0.00 $\pm$ 0.05
Eelgrass Zone/Lower Sand Wave Zone	--	Approximately - 1.2 m		

N.B. All elevations with respect to Canadian Geodetic Datum (to convert to 1978 Chart Datum at Tsawwassen, add 2.95 m).

\* This boundary is defined to be at the lower limit of continuous algal mat growth.

only a few isolated hummocks remain. The eelgrass retreats seawards.

Observations in mid-February on transect A revealed that the eelgrass had retreated 350 m seawards from its summer position, to an elevation of - 0.5 m (Geodetic Datum). On transect B only isolated patches of eelgrass remain during winter.

The eelgrass which dies back in winter consists largely of the smaller species Zostera americana, while a permanent growth is maintained by the larger species Zostera marina. Zostera americana reappears from seedlings in the spring. Considerable quantities of both species of eelgrass are uprooted by winter storms and rafted into the edge of the saltmarsh zone, forming an organic rich mat on which saltmarsh plant seedlings sprout in the spring.

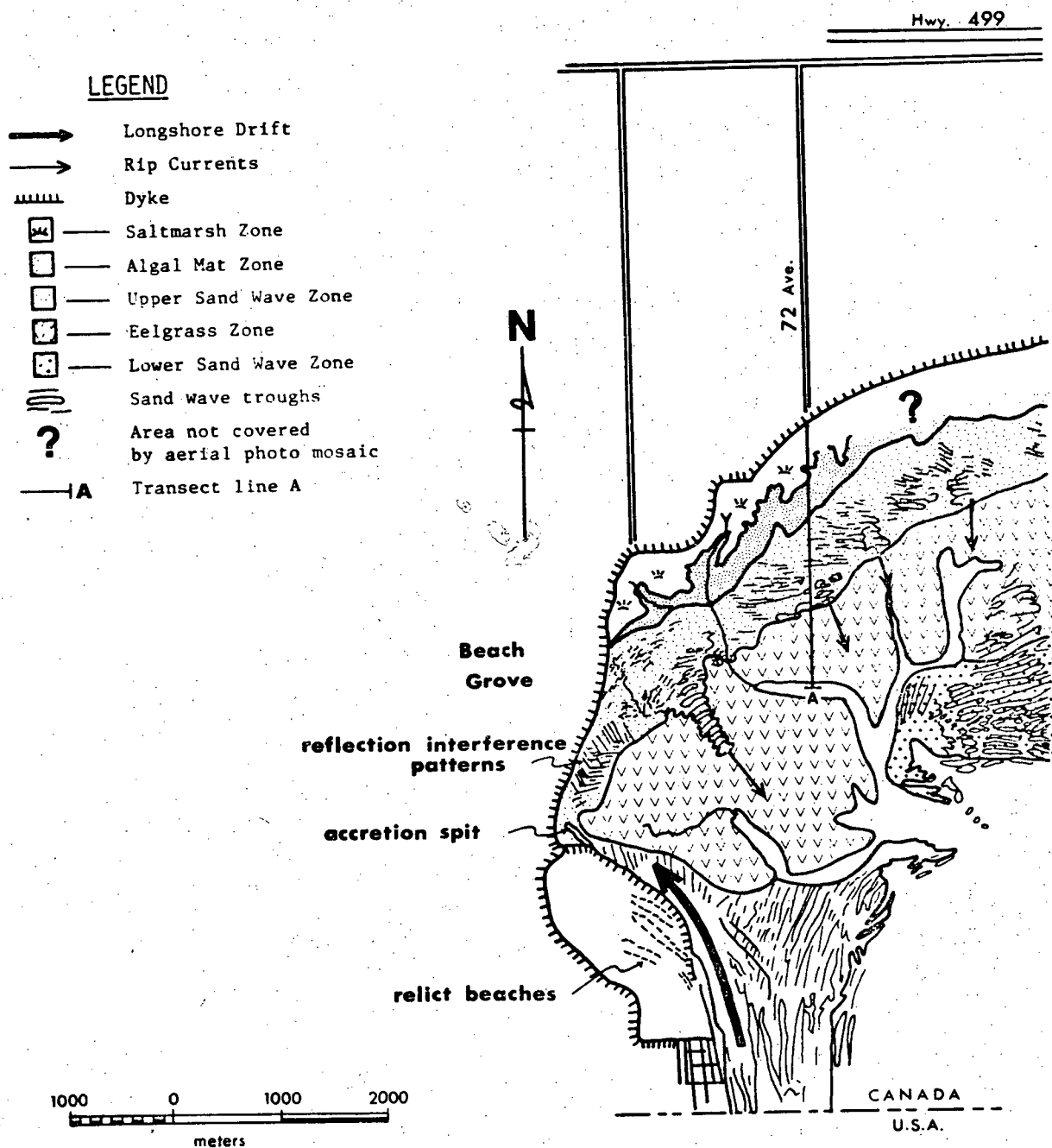
Figure 2 depicts sand wave troughs in position as traced from aerial photographs. The sand waves of the upper sand wave zone are distinctly different from those of the lower sand wave zone. Those of the upper sand wave zone have wavelengths averaging 30 m (range 20-70 m) and amplitudes of <0.1 m, giving a wavelength:amplitude ratio greater than 300:1. From qualitative observations the waves appear to be symmetrical in profile. The sand waves of the lower sand wave zone have wavelengths averaging 60 m (range 40-80 m), and, according to Kellerhals and Murray (1969), amplitudes from 0.3 m to 0.5 m. In plan view these sand waves have both straight-crested and lunate outlines. The lunate forms are predominantly concave seawards. At fairly regular intervals along the lower limit of the upper sand wave zone, sand waves similar to those of the lower sand wave zone occur. They are lunate in outline and concave seawards (Fig. 2 & 3).

The algal mat zone is devoid of sand waves. This may in part be due to the sediment binding effects of the algal mats. A few sand waves occur in the eelgrass zone. Some are completely overgrown by eelgrass during summer (Fig. 2).

### Discussion of Sand Waves

The justification for calling the large scale bedforms of the upper sand wave zone 'sand waves' lies in the fact that they meet the loose specifications of sand waves given by Harms et al. (1975) -- viz. spacing between 5-100 m, straight to sinuous crested and having a relatively small height/spacing ratio -- and they exhibit a characteristic property of waves, namely interference patterns. The bedforms are thought to be produced in response to surface sea waves. The wave properties of these bedforms and their response to surface sea wave activity is best illustrated in the western part of the Bay next to Beach Grove, where reflection interference patterns are visible (Fig. 3). A concrete breakwater is present along the waterfront of Beach Grove, and the beach profile in this area of the Bay is steeper than elsewhere. Surface sea waves are reflected by the concrete breakwater, whereas in the rest of the Bay wave energy is dissipated in the saltmarsh zone without reflection. The sand waves mirror the reflection interference patterns of the surface sea waves. The lunate sand waves near the lower edge of the upper sand wave zone could perhaps be produced by rip currents set up in response to wave action (Fig. 3).

Between the period of June, 1976, to July, 1978, the sand waves of the upper sand wave zone on transect A have not moved or changed shape noticeably with respect to the positions of stakes placed along the transect. The sand waves of the upper sand wave zone are probably only active during winter storms, and when active may be in a state of dynamic equilibrium. The sand waves indicate storm wave propagation from the south. Twenty-two percent of winds in excess of 48 km/hour (30 m.p.h.) during winter (October - March) are from the south, and on average occur for 5.5 hours per month (Swan Wooster, 1968). Southerly winds have a greater fetch than any others, and should produce the most severe storm waves.



Source: Integrated Resources  
Photography, Flight  
No. 142, July, 1974

Figure 3. Reflection interference patterns in the upper sand wave zone in the area of Beach Grove. Also indicated are the probable directions of wave induced currents.

The orientation of tidal channels in the lower sand wave and eelgrass zones give a good indication of tidal current directions, in particular of ebb currents (Kellerhals and Murray, 1969; Weir, 1963). In the lower sand wave zone it can be seen that sand waves are aligned approximately perpendicular to the axis of the tidal channels, indicating that the sand waves may be produced by tidal current action. Weir (1963), during the summer of 1959, recorded maximum flood and ebb tidal currents, during spring and mean tides, ranging from  $24 \text{ cm sec}^{-1}$  to  $49 \text{ cm sec}^{-1}$  (average of several readings through water column) in the four major tidal channels west of the "Great Channel" (beside Crescent Beach). Several of the readings for both flood and ebb currents exceeded  $35 \text{ cm sec}^{-1}$ . The water depths in the lower sand wave zone at the time of these measurements ranged between 0.0 m and 1.7 m. Current velocities in excess of about  $35 \text{ cm sec}^{-1}$  in these water depths are capable of forming sand waves (Harms et al., 1975). However, to determine conclusively whether the sand waves are of tidal origin, current velocity data would have to be collected from the lower sand wave zone itself, rather than extrapolating from data collected in the adjacent tidal channels. The sand waves could be the result of currents induced by the combined action of tides and storm waves.

#### ENVIRONMENTAL FACTORS AND ZONATION

There are three factors in the physical environment which have the potential of being primary agents in causing floral/faunal zonation on tidal flats. These are the grain size characteristics of the substrate, the properties of the covering waters at high and low tides, in particular their salinity and turbidity levels, and the duration of exposure, which is a function of tides, elevation and topography.

### Grain Size of Surface Sediments

Figures 4 and 5 present the grain size characteristics of surface sediments on transects A and B. In addition to these results, one surface sample (upper 2 cm) from the saltmarsh zone, collected on transect A 100 m landward from the seaward perimeter of the marsh, was analysed. It proved to be a moderately well sorted very fine sand (Graphic Mean 3.6  $\phi$ ), containing 25% silt and clay, and 8% organic matter half of which consisted of fibrous peat.

On both transects A and B the surface sediments gradually coarsen seawards from very fine sands to fine sands in going from the saltmarsh zone to the lower eelgrass zone, giving a very limited mean grain size range of less than 1  $\phi$  (Figs. 4 & 5). This coarsening in mean grain size is best illustrated on transect B (Fig. 5). Towards the lower end of transect A there is a slight reversal in the trend, but this is due to an increase in the mud content of the sediment rather than being due to a fining in the grain size of the sand fraction. The sands on transects A and B are predominantly well to very well sorted (Incl. Graphic Std. Dev. <0.5  $\phi$ ). Fluctuations in the sorting values are largely a function of mud content, as indicated by the fact that sorting and mud content values fluctuate in harmony (Figs. 4 & 5). With the exception of the saltmarsh zone, mud contents are low, amounting to only a few percent. Box cores from both transects reveal monotonous sequences of sand with little variability in grain size with depth.

A fining in grain size shorewards is typical of tidal flats (Klein, 1971), but the variation is usually much more extreme, ranging from mud in the upper intertidal zone to sand in the lower intertidal zone (Linke, 1939; Evans, 1965; Klein, 1971; Larssonneur, 1975; Risk and Moffat, 1977). The processes responsible for this textural trend have been extensively



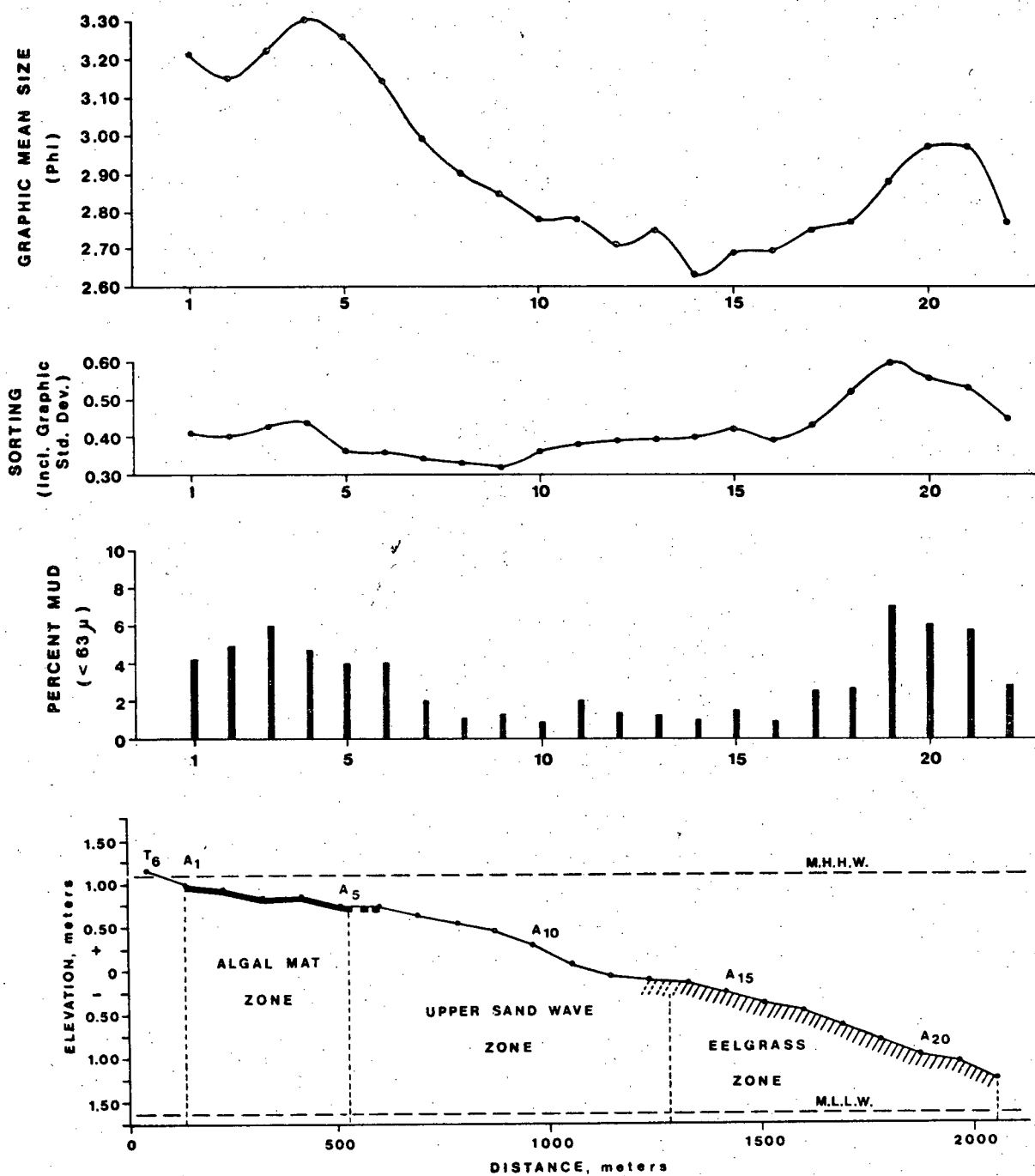


Figure 4. Variations in mean grain size, sorting and mud content on transect A.

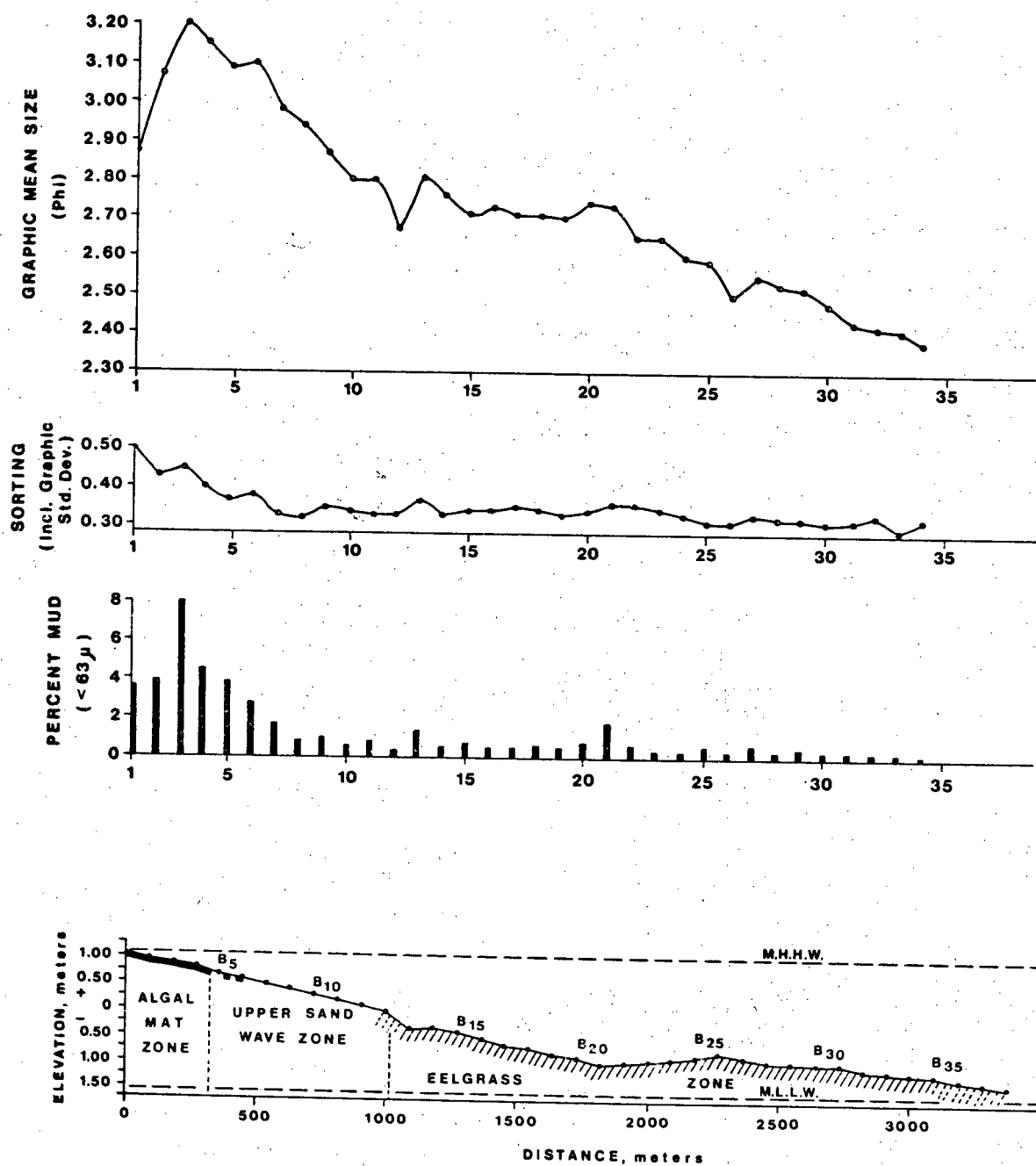


Figure 5. Variations in mean grain size, sorting and mud content on transect B.

discussed in the literature. They include "scour lag" (Van Straaten and Kuenen, 1958) and "settling lag" (Postma, 1961), combined with a net transport of sediment shorewards due to tidal velocity asymmetry (Postma, 1961; Groen, 1967), under the influence of a decreasing wave and current energy regime (Reineck, 1967). To this list the authors would add that the initial sheet flow of water onto the dry tidal flat on flood tide is a potent sediment transporting agent, which may play an important role in producing the fining shorewards trend. On the initial influx of flood waters any protruding sediment mounds (e.g. fecal casts) are swept flat by the advancing waterline. This sediment gradually settles back onto the substrate. The finer grains travel further inshore because their settling velocities are lower. Dry sediment also has an ability to float. buoyed up by surface tension and foam, particularly finer sediment because of its larger surface area to volume ratio. The film of foam and sediment carried by the advancing waterline is deposited along with organic debris at high water mark. This flood tide process is not reciprocated by the late stages of ebb tide, because, on ebb, subsurface water continually seeps off the waterlogged tidal flat, no foam or pronounced waterline forms, and strong current action due to late stage runoff is localised in channels.

The lack of mud and high degree of sorting in the sands of Boundary Bay tidal flats is probably due in part to reworking by winter storm waves, although it is also due to the lack of a significant source of suspended mud size sediment in the Bay. On the active tidal flats of the Fraser Delta, which experience tides and wave action similar to Boundary Bay, mud contents of the surface sediments are an order of magnitude higher, due to the influx of mud from the Fraser River (Swinbanks, 1979).

Superimposed on the gradation in mean grain size, which is controlled by physical processes, is a biologically controlled fluctuation in the percentage of silt and clay (material  $<63 \mu\text{m}$ ), due to the ability of vegetation to entrap fine grained material, much as described by Ginsburg and Lowenstam (1958). Mud contents decrease in a steplike fashion from about 25% to 5% to 1%, in passing from the saltmarsh zone through the algal mat zone to the upper sand wave zone, as the extent of floral cover decreases abruptly. In the lower eelgrass zone on transect A (Stations A17-A22, Fig. 4), where a continuous and extensive mat of eelgrass is present throughout the year, the percentage of mud rises abruptly to between 2.5 and 7%.

In conclusion, because variations in the grain size of the substrate are slight and gradual, grain size of the sediments is not considered to play a primary role in determining floral/faunal zonation in Boundary Bay. The steplike variation in mud contents of the sediments, rather than being a cause of zonation, is considered to be an effect of floral zonation.

#### Salinity and Turbidity

The plume of turbid, brackish water from the Fraser River seldom if ever enters Boundary Bay. The plume is only directed south-eastwards towards the Boundary Bay area when north-westerly winds blow in conjunction with an ebbing tide (Giovando and Tabata, 1970). North-westerly winds only occur about 13% of the time (Luternauer and Murray, 1973). Even on these occasions the Point Roberts peninsula prevents the plume from entering the Bay, and on the subsequent flood the plume is not flushed into the Bay, because initial flood currents at the entrance to the Bay are from the south-east (Weir, 1963). Analysis of satellite imagery and aerial photographs reveals that the plume of the Fraser does not enter the Bay and the Bay waters are clear (Table III). A number of salinity

TABLE III

Aerial photographs and satellite imagery illustrating the low turbidity levels of Boundary Bay waters

<u>Film Roll No.</u>	<u>Frame No.</u>	<u>Emulsion</u>	<u>Flight Altitude</u> (m)	<u>Date</u>	<u>Remarks</u>
*A 37597	132	nat. colour	10976	June 20, 1978	Contrast frame 132 with the muddy plumes in frame 146. Taken at low tide.
A 37170	38 & 39	nat. colour	9451	June 11, 1975	Frame 38 shows clear demarcation between muddy Fraser plume and blue Bay waters in vicinity of Point Roberts. Taken at low tide.
**IRP 142	19 - 27	nat. colour	3810	July, 1974	Taken at low tide.
A 30339	113, 114 & 116	nat. colour	12195	July 16, 1971	Contrast frames 113 & 114 with frame 116. Taken at mid-tide.
ERTS EMG-1283-A	mosaic	infrared	satellite	1973 - 1974	Mosaic with Fraser plume clearly visible.
ERTS-1	--	infrared	satellite	11:36 a.m. July 30, 1972	Taken at mid-tide on ebb, three hours after lower high water.

\* Film rolls prefixed (A) are federal government photographs, available through the National Air Photo Library, Ottawa, Ontario, Canada.

\*\* The roll prefixed IRP is available through Integrated Resources Photography Ltd., Vancouver, B.C., Canada.

Note: All of these photographs except ERTS EMG-1283-A were taken in June or July when the Fraser River reaches its peak discharge.

measurements taken in tidal pools at low tide confirm that brackish water from the Fraser does not enter Boundary Bay, even in June when the Fraser is in freshet (Table IV). The salinities measured nearest to low tide line are probably most indicative of the salinities of water entering the Bay, since these are least affected by exposure or fresh water drainage from the marsh (Table IV, Stations A12, \*A9, A22, B17, & A13). They indicate that the Bay water salinities probably lie in the range of 24 to 29‰, which can be considered 'normal marine' for the southern Strait of Georgia as they are typical of the salinities of surface waters of the 'vertically mixed' water mass of the southern Strait of Georgia (Waldichuk, 1957), as opposed to the 'brackish stratified' water mass of the central Strait of Georgia (Waldichuk, 1957). The exceptionally high value of 39‰ recorded next to the saltmarsh (Station \*A1) by O'Connell (1975), was probably due to evaporation during prolonged exposure on a warm day (Air Temp. 20-24° C).

Salinity does not vary appreciably over the exposed tidal flats (Table IV) and thus does not influence zonation. This is in complete contrast to the tidal flats on the active Fraser Delta front, where surface water salinities at low tide range between 1 and 33‰, and markedly influence faunal and floral distribution patterns (Swinbanks, 1979).

#### Exposure Time

Exposure time on a tidal flat is an important parameter influencing floral/faunal zonation, although its effects can be masked or even overridden by other factors, such as variations in the grain size of the substrate and/or variations in salinity or turbidity levels of the covering waters. However, as already stated, these parameters do not vary appreciably over most of Boundary Bay tidal flats. As a result on these tidal flats exposure

TABLE IV

## Salinity of Water in Tidal Pools at Low Tide

Date	Station	Distance from saltmarsh (meters)	Salinity (‰)	Remarks
8/11/76	A5	366	26.0	Cool and Cloudy  (Air Temp. 4-11° C)
	A6	457	26.5	
	A7	549	26.0	
	A8	640	26.5	
	A9	732	27.0	
	A10	823	27.5	
	A11	915	28.5	
	A12	1006	29.0	
10/6/75	*A1	50	39.0	Warm  (Air Temp. 20-24° C)
	*A2	200	33.0	
	*A3	350	32.0	
	*A4	500	33.0	
	*A5	650	32.0	
	*A7	975	33.0	
	*A8	1275	30.0	
	*A9	1575	28.0	
21/9/77	A1	0	23.0	Cool and Cloudy
	A2	91	23.0	
	A3	183	25.5	
	A4	274	26.0	
	A5	366	26.5	
	A6	457	25.5	
	A7-A14	549-1189	24.5 (8 readings)	
	A15-A22	1280-1921	24.0 (8 readings)	
	B1	0	20.0	
	B2	91	21.0	
21/9/77	B3	183	22.0	
	B4	274	22.0	
	B5	366	23.0	
	B6-B17	457-1463	24.0 (12 readings)	
27/9/77	A6-A13	457-1098	28.0 (8 readings)	Cool and Cloudy

\* Station locations and data from O'Connell (1975)

can be seen to play a major role in determining floral/faunal zonation, and a detailed analysis of the relationship between exposure time and elevation is warranted.

At this point it should be stressed that it is the effects of exposure rather than exposure itself which probably most influence the distribution of flora and fauna. The effects include such things as dehydration, and instability of oxygen levels, pH, temperature and salinity, which may directly kill flora or faunal offspring or, alternatively, critically impair their ability to cope with competing, predatory or non-compatible organisms. It should be borne in mind that other parameters, in particular small and large scale topography and drainage, can drastically alter the effects of exposure, and that the interaction of tides and elevation do not alone determine exposure effects.

Ginsburg et al. (1970) suggested that for any tidal flat an exposure vs. elevation curve should be computed, and then at any given elevation on the tidal flat an 'exposure index' can be assigned, which is equal to the mean exposure expressed as a percentage. Such a curve, with some additions, is presented in Figure 6 for Boundary Bay. Ginsburg et al. (1970) attempted to relate the occurrence of mudcracks, algal stromatolites and other biogenic sedimentary structures to their 'exposure index.' However, the 'exposure index' curve has a number of deficiencies which severely limit its usefulness in interpreting the distribution of flora and fauna. The curve's major deficiency is that it is an average, and as such can provide no information regarding the range of possible exposures at any given elevation. From the point of view of flora and fauna the most extreme exposures are probably of more concern than the average. Even for some physical sedimentary structures, such as mudcracks, it is the longest periods of exposure which determine whether or not they form, not



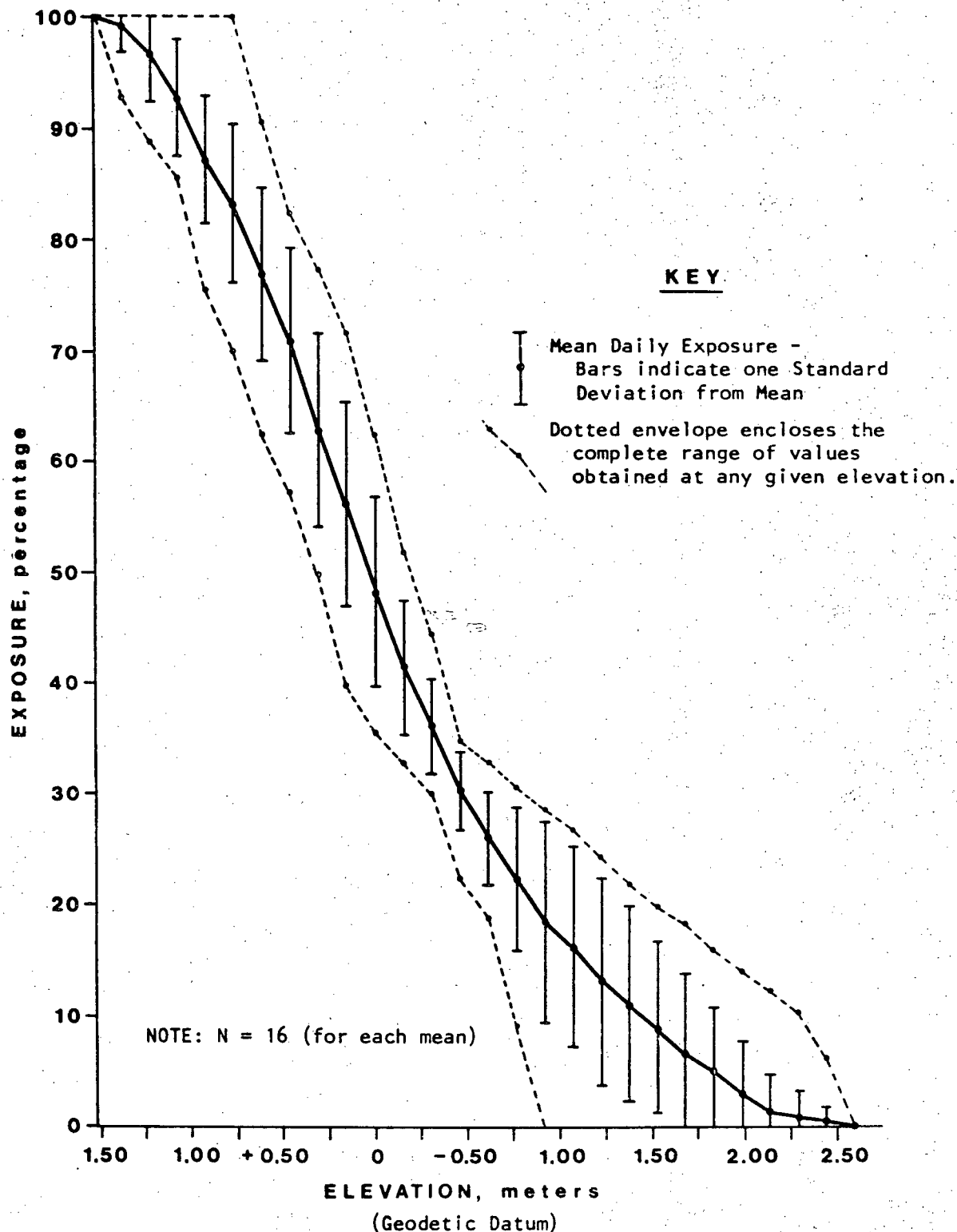


Figure 6. Mean daily exposure with respect to elevation for Boundary Bay tides. This was compiled from 16 representative daily tidal curves (eight mean tides, four spring tides and four neap tides) selected from 25 available in the data of Weir (1963) covering the period of June to September, 1959. Using more than 16 days of tidal records would probably reduce some of the standard deviations, but it would if anything increase the ranges of possible values.

the average.

In Figure 6 an attempt has been made to overcome these deficiencies by delimiting the range of daily exposure values which are possible at any elevation. A measure of the natural day-to-day variability in exposure is also given by including the standard deviation from each mean. It can be seen that at most levels, and in particular in the uppermost and lowermost intertidal regions, exposure varies tremendously from day to day and 'exposure index' is a misleading indication of exposure. Even with the addition of range and standard deviation Figure 6 can give no indication of the maximum duration of continuous exposure possible at any elevation, because in its computation no distinction is made between continuous and discontinuous exposure.

Swinbanks (1979) has recently elaborated on the concepts of critical tidal levels (Doty, 1946), and has advocated their use in the description of intertidal exposure and in the subdivision of the intertidal zone. A critical tidal level is a particular tidal elevation at which the duration of continuous exposure or continuous submergence changes abruptly in a step-like fashion. There are daily, monthly, annual and longer term critical tidal levels, which can be defined depending on the time scale considered (Swinbanks, 1979). As the concepts of critical tidal levels are probably unfamiliar to most geologists, they will be outlined below as they apply in the specific case of Boundary Bay tides, although much of what is said applies to all astronomically controlled tides.

The tides in Boundary Bay are of mixed-semi-diurnal type. This means that there are two high tides and two low tides a day, but that successive high tides and successive low tides are of different height (Fig. 7a). As a result on any given day there are five different levels of exposure which can be experienced, depending on the elevation considered. The duration of

continuous exposure or submergence jumps on passing from one level to the next. The five 'exposure levels' (Swinbanks, 1979) as indicated in Figure 7a are:

- Level 1. At an elevation above higher high water continuous exposure is at least nearly two lunar days.
- Level 2. At a level intermediate between higher high water and lower high water, exposure occurs once and is greater than half a lunar day, but less than one.
- Level 3. At a level between lower high water and higher low water, exposure is split into two periods by lower high water, each period of exposure or submergence being less than half a lunar day. The total daily exposure may or may not exceed half a lunar day, but the length of each period of continuous exposure does not.
- Level 4. Below higher low water exposure occurs once in the lunar day, and exposure is less than half a lunar day. Submergence is greater than half a lunar day, but less than one.
- Level 5. Below lower low water the tidal flat is continuously submerged for at least nearly two lunar days.

The above five statements are based on the assumption that the time between successive high or low tides is half a lunar day. This is not strictly true, because there is a time asymmetry to mixed tides caused by a lag between the position of the moon and the response of the tide, which is dependent on tidal range. However, examination of twenty-five tidal curves of all ranges reveals that despite this fact the five statements still always hold true, for Boundary Bay tides, except for Level 3 exposures for which continuous exposure can on occasion marginally exceed half a lunar day (Figs. 7b & 7c).

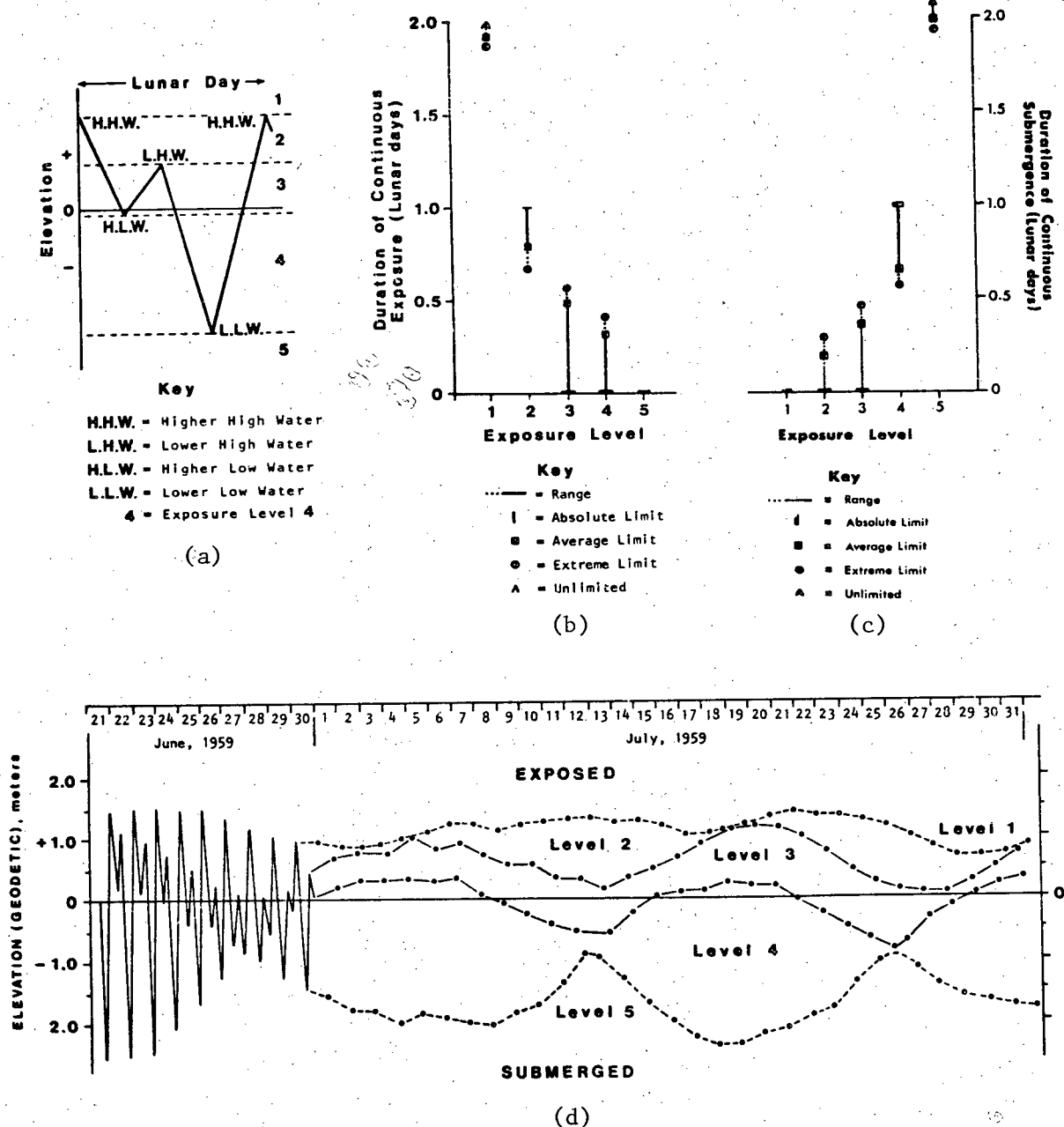


Figure 7. (a) The five 'exposure levels' possible for mixed semi-diurnal tides. (b) The ranges of duration of continuous exposure for each of the five exposure levels. (c) The ranges of duration of continuous submergence for each of the five exposure levels. (d) The monthly modulation of the five exposure levels for the period June 21-July 31, 1959. Tidal data from Weir (1963).

The four boundaries between exposure levels are 1st order (daily) critical ~~tidal~~ tidal levels, as they are defined by the daily tidal cycle. Higher order critical tidal levels, defined by monthly, annual and longer term tidal cycles, are common to all astronomically controlled tides (Swinbanks, 1979).

Over a period of months exposure at any elevation is a combination of the five exposure levels (Fig. 7d). Figure 8 graphs the frequency of each exposure level at 6.1 cm (0.2 ft) elevation intervals. The lowest elevation attained by Level 1 exposures defines the 'atmozone'; the intertidal exposure zone in which the maximum duration of continuous exposure exceeds at least nearly two lunar days (Swinbanks, 1979). Similarly the highest level attained by Level 5 exposures defines the upper limit of the 'aquazone' (Swinbanks, 1979) in which the maximum duration of continuous submergence exceeds at least nearly two lunar days. Between lies the core to the intertidal region, the 'amphizone' (Swinbanks, 1979), in which the maximum duration of continuous exposure or submergence is always less than one lunar day. The lowest level reached by Level 2 exposures defines the boundary between upper and lower amphizones. Monthly (2nd order) critical tidal levels, at which the maximum duration of continuous exposure or submergence begins to rise abruptly from about 10 to 20 days subdivide the atmozone and aquazone into upper and lower parts (Fig. 8).

Superimposed on Figure 8 are the floral/sedimentological zones previously described. Some correlations between these zones and the exposure zones are immediately apparent, but discussion of any causal relationships between exposure and zonation must await the presentation of faunal distribution data in the following section. Although Figure 8 provides an extremely useful framework for describing floral/faunal zonation with respect to tidal exposure it should be realized that computation of Figure 8 assumes a perfectly flat tidal flat which drains free of water at each low tide. This is not the case. Topographic depressions of small and large scale cause water cover

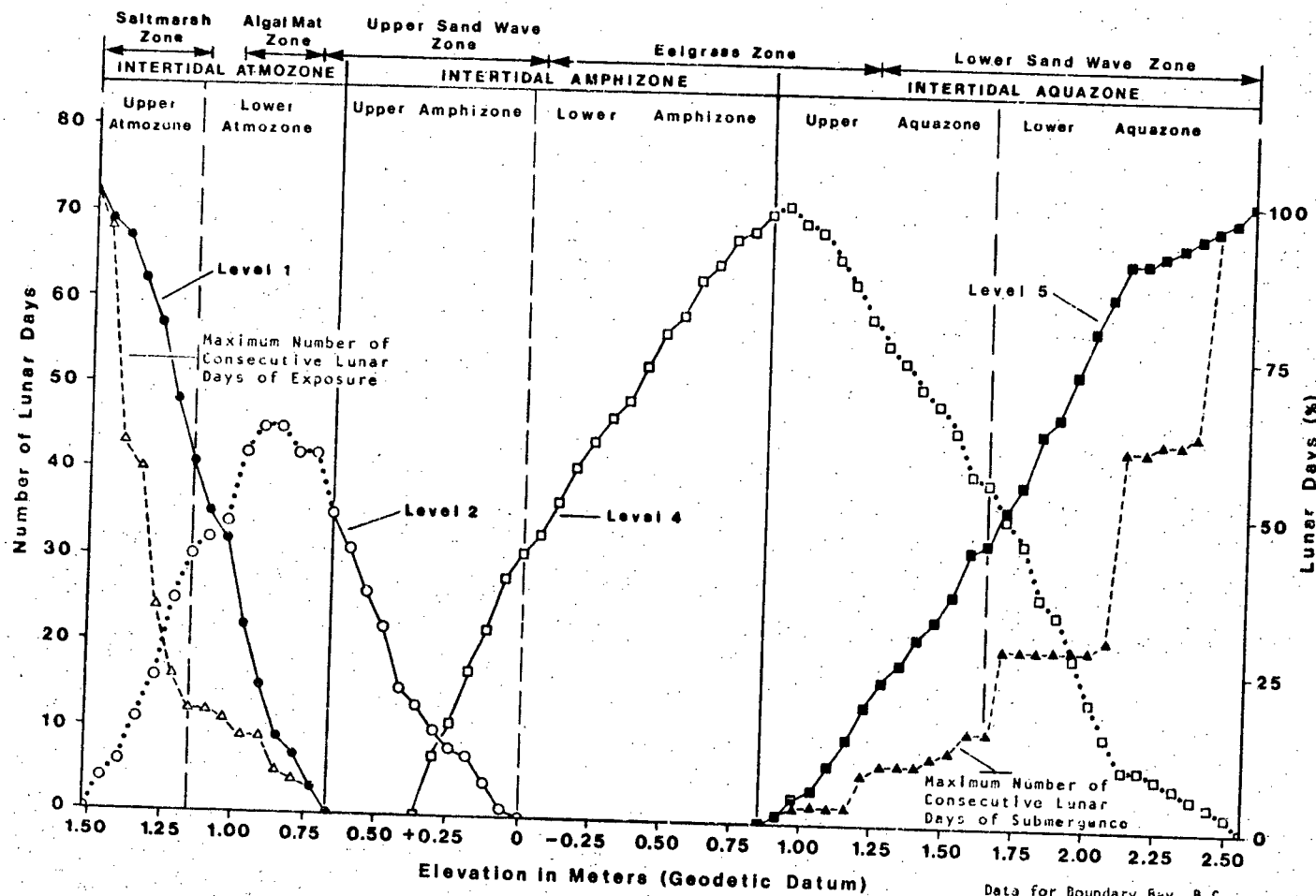


Figure 8. The frequency of four of the five exposure levels with respect to elevation for a period of 73 lunar days from June 21-September 4, 1959 (source: Weir, 1963). Left hand scale in percent. Also plotted is the maximum number of consecutive lunar days of exposure or submergence for those elevations where exposure or submergence can exceed one lunar day.

to be maintained during low tide in tidal pools within the depressions. This has a profound influence on the distribution of flora and fauna on the local scale, particularly of the smaller macrofauna. Eelgrass can be found growing in the water-filled troughs of sand waves in the upper sand wave zone, and isolated algal mats may be found growing on the sand wave crests, defying their respective zone limits..

## FLORA FAUNA AND THEIR BIOGENIC SEDIMENTARY STRUCTURES

### Saltmarsh Zone

The saltmarsh lies at an elevation which is upper atmozonal in exposure (Fig. 8). Atriplex patula, Grindelia integrifolia, Rumex crispus, Achillea millefolium, and Aster sp. dominate on the landward portion of the marsh, whereas on the seaward side halophytes that are more salt tolerant predominate, such as Salicornia sp., Triglochin maritima and Spergularia maritima, (Kellerhals and Murray, 1969; O'Connell, 1975; Parsons, 1975). Distichlis spicata is abundant at all levels. (Parsons, 1975).

The sediments accumulating in this region consist of irregularly stratified sand, peat, silt and clay. Sand and organic debris (eelgrass and driftwood) are transported onto the saltmarsh by winter storms, whereas peat and finer grained sediment accumulate during the summer. However, due to disruption of bedding by vigorous rootlet growth, seasonal stratification is fairly poorly developed. It is noteworthy that, even within this densely vegetated zone of the uppermost intertidal region, sand is still the dominant sediment component.

None of the organisms investigated in this study occur within the saltmarsh zone. The small shore crab Hemigrapsus oregonensis is abundant along the saltmarsh perimeter.

### Algal Mat Zone

The algal mat zone is lower atmazonal in exposure (Fig 8). It is characterised by an almost continuous growth of cyanophyte algal mats in summer. The algal mats consist predominantly of Microcoleus sp. and Phormidium sp. with minor amounts of the chlorophytes Enteromorpha sp. and Rhizoclonium sp. (Kellerhals and Murray, 1969). In winter, storms smother the algal mats with sand. Thus, an annual stratification of organic rich and sandy laminae is produced (Kellerhals and Murray, 1969). The following organisms and biogenic sedimentary structures are characteristic of the zone.

#### Batillaria

Batillaria attramentaria (Sowerby) is a herbivorous, deposit-feeding gastropod (Fig. 10a). According to Whitlatch (1974), it feeds mainly on diatoms. Batillaria is found throughout most of the intertidal area in summer, but its numbers decrease to zero in the lower eelgrass zone (Figs. 9a & 9b). Batillaria densities maximize in shallow tidal pools (Fig. 9a). Batillaria's presence is most noticeable in the algal mat zone, where its traces are well preserved in the cohesive algal mats. Batillaria produces both resting traces and grazing traces.

Resting Traces--Batillaria produces a resting trace by burying itself head first in the sand using a corkscrew spiralling action. Often only the pointed tip of its shell remains protruding. This behaviour is probably a protective response against desiccation. Resting trace pits are preserved between tidal cycles, while the grazing traces leading to them (Fig. 10b), which are much shallower depressions, are usually removed by the incoming tide. Hence, extensive areas of dense pitting result with little evidence of the originator remaining (Fig. 10c). Pitting by Batillaria is most prevalent on the upraised algal mats.



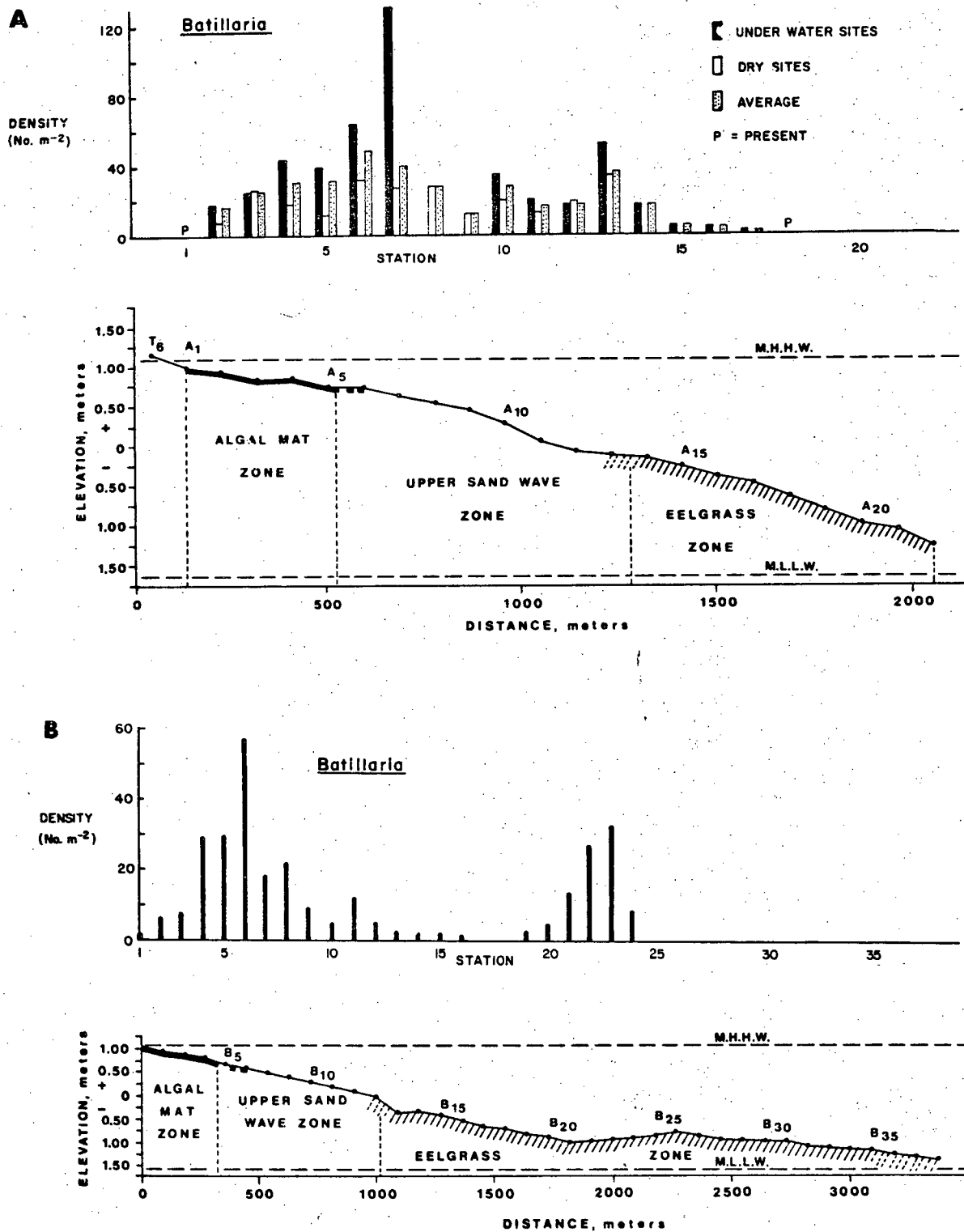
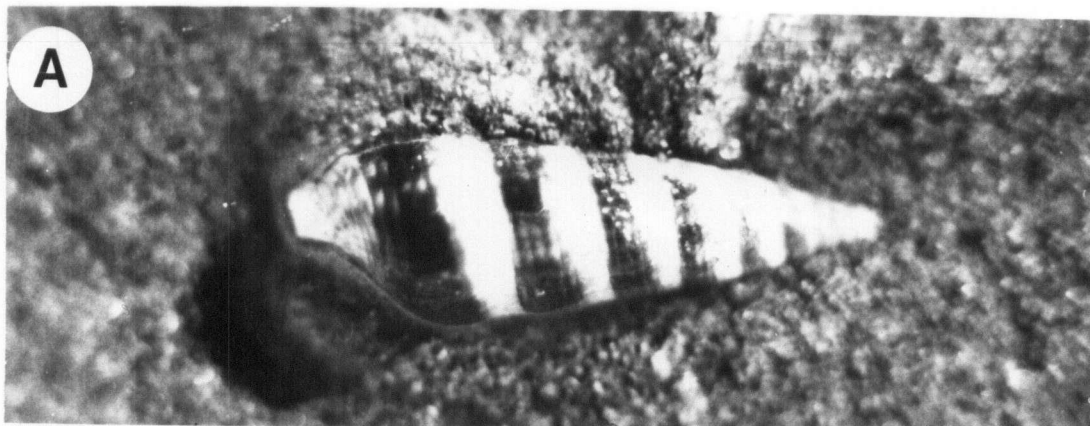


Figure 9. a) Densities of Batillaria sp. on transect A, differentiating between dry sites and under water sites (shallow tidal pools).  
b) Densities of Batillaria sp. on transect B.

- Figure 10 (a) Batillaria attramentaria producing a grazing trail. Its shell is about 3 cm long.
- (b) Batillaria grazing trails and resting traces (pits). Note the trails leading to pits. Trowel head is about 5 cm wide.
- (c) Resting trace pits produced by Batillaria sp. Four Batillaria sp. can be seen still occupying pits. Trowel head is about 5 cm wide.



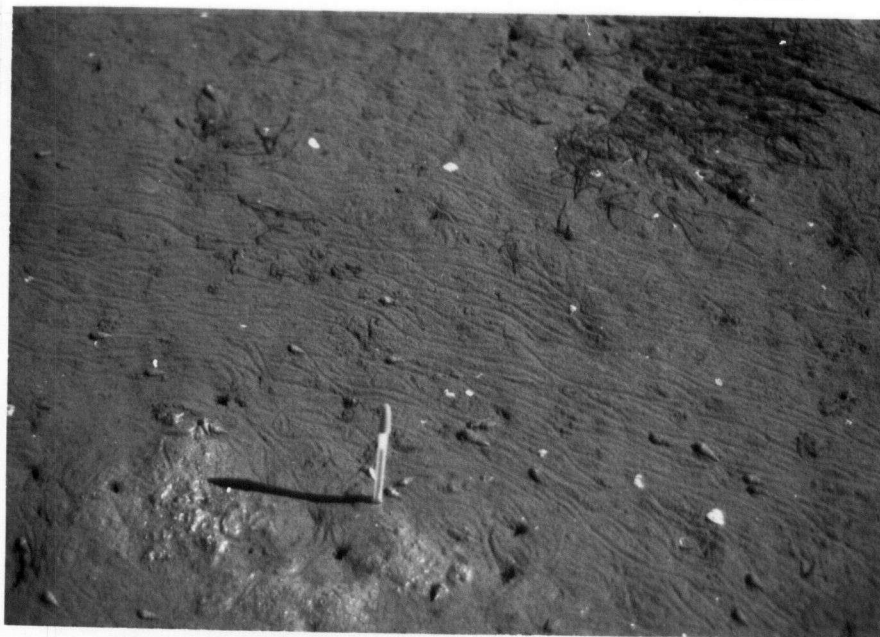
Grazing Traces--Batillaria, as it grazes on the sediment, produces a simple furrow with upraised edges (Figs. 10a, & 10b). Batillaria does not exhibit phototactic behaviour--avoidance of previously grazed sediment. In fact, on occasion Batillaria were observed to follow precisely grazing trails only minutes old, with as many as three Batillaria on one trail.

In the presence of weak currents, for example where water drains out of sand wave troughs, Batillaria heads upstream grazing on the sediment, leaving grazing trails paralleling the current direction (Fig. 11a). The abrupt termination of trails due to rolling of the gastropod by the current indicates current sense as well as direction (Fig. 11b). The currents in which this behaviour was observed were too weak to remove the trails. In stronger currents Batillaria dives head first into the sediment with its pointed tip pointing downcurrent, and ceases moving. Alignment of biogenic structures with a current has been described by Rhoads (1975) for bivalve siphon openings and polychaete dwelling tubes. It has also been described in the geological record by Seilacher (1964) for trilobite trails.

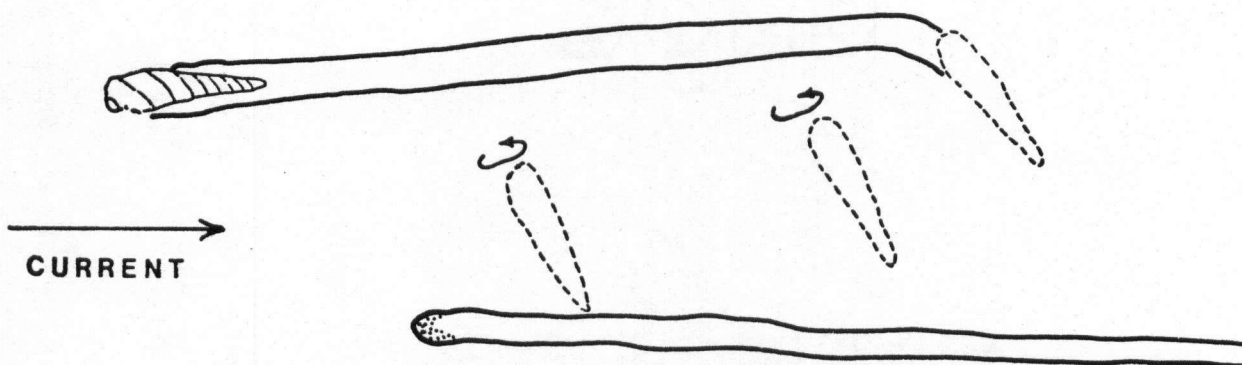
On the rare occasions in summer that strong winds blow from the south to southeast, waves are blown into Boundary Bay from the open Strait of Georgia, and fairly considerable movement of sediment by wave-formed ripples occurs. On these occasions Batillaria burrows itself out of sight about 1 cm below the surface to avoid being rolled over by wave induced currents. Such occurred on August 4, 1976, when on first sight the tidal flats appeared to be almost completely devoid of Batillaria, but on scraping the surface with a trowel Batillaria was revealed in its usual densities.

### Spio

Spio sp. is a small tube-dwelling polychaete worm (Figs. 12a, 12b & 12c). It constructs an agglutinated sand tube. It lives upright in the tube and draws food and sediment into its tube with its two tentacle-like palps



(a)

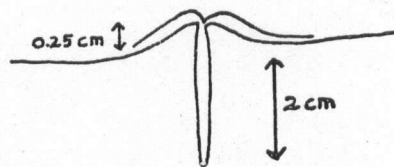


(b)

- Figure 11. a) *Batillaria* sp. heading upstream producing grazing trails paralleling the current direction (eelgrass at top of photo indicates current direction). Ballpoint pen is about 15 cm long.
- b) Behaviour of *Batillaria* sp. in weak currents: the gastropod heads upstream grazing, and produces a trail paralleling the current. Occasionally the current causes the gastropod to roll. Once stabilized again the gastropod turns in towards the current and reverts to grazing in an upstream direction.



(a)



(b)

- Figure 12. a) Mounds produced by the feeding activities of Spio sp. Pen is about 15 cm long.
- b) Plan view of Spio sp. Two tentacle-like palps draw food into its tube and are also used to void sandy pseudo-fecal strings in a radial pattern.
- c) Cross section of Spio sp. in its dwelling tube.

(Figs. 12b & 12c). Sediment, particularly larger sand grains, tends to catch on the tip of the tube as the worm draws in its food laden palps. As a result a mound up to 0.5 cm in height forms around the tube (Fig. 12a). The worm also voids fragile, elongate, sandy pseudo-fecal strings. These are extruded radially around the tube (Fig. 12b). The sediment mounds are flattened by the incoming tide.

Spio is abundant in the algal mat zone (Figs. 13a & 13b) attaining its maximum density of about  $10^4 \text{ m}^{-2}$  next to the saltmarsh (A1 & B1). However, Spio only occurs in tidal pools between the upraised algal mats. In the upper sand wave zone Spio decreases in density by an order of magnitude (Figs 13a & 13b). There are two possible reasons for the lower densities of Spio in the upper sand wave zone. Firstly, the sand wave crests, although of very low amplitude, make an inhospitable, dry environment for Spio during low tide and Spio is restricted to the water-filled troughs of the sand waves. Secondly, in winter, storm waves cause wave-formed ripples to disturb the upper 2-3 cm of sediment uprooting many Spio in the process. In the eelgrass zone Spio increases markedly in density attaining  $5 \times 10^4 \text{ m}^{-2}$ , but Spio does not colonize the conical mounds formed by Callianassa californiensis. Comparable densities of Spiophanes wigleyi, another spionid worm, have been reported by Featherstone and Risk (1977) in Minas Basin, Bay of Fundy.

Measurements of sediment turnover by Spio could not be made directly, however, an estimate can be made. During exposure at low tide (about 20 hours in the algal mat zone) Spio produces a mound of about  $0.02 \text{ cm}^3$  of sediment. At a density of  $10^4 \text{ m}^{-2}$  this turnover amounts to  $200 \text{ cm}^3$  per  $\text{m}^2$ . This is equivalent to reworking a monogranular surface layer of sand 100  $\mu\text{m}$  thick in that one square meter twice between tides.

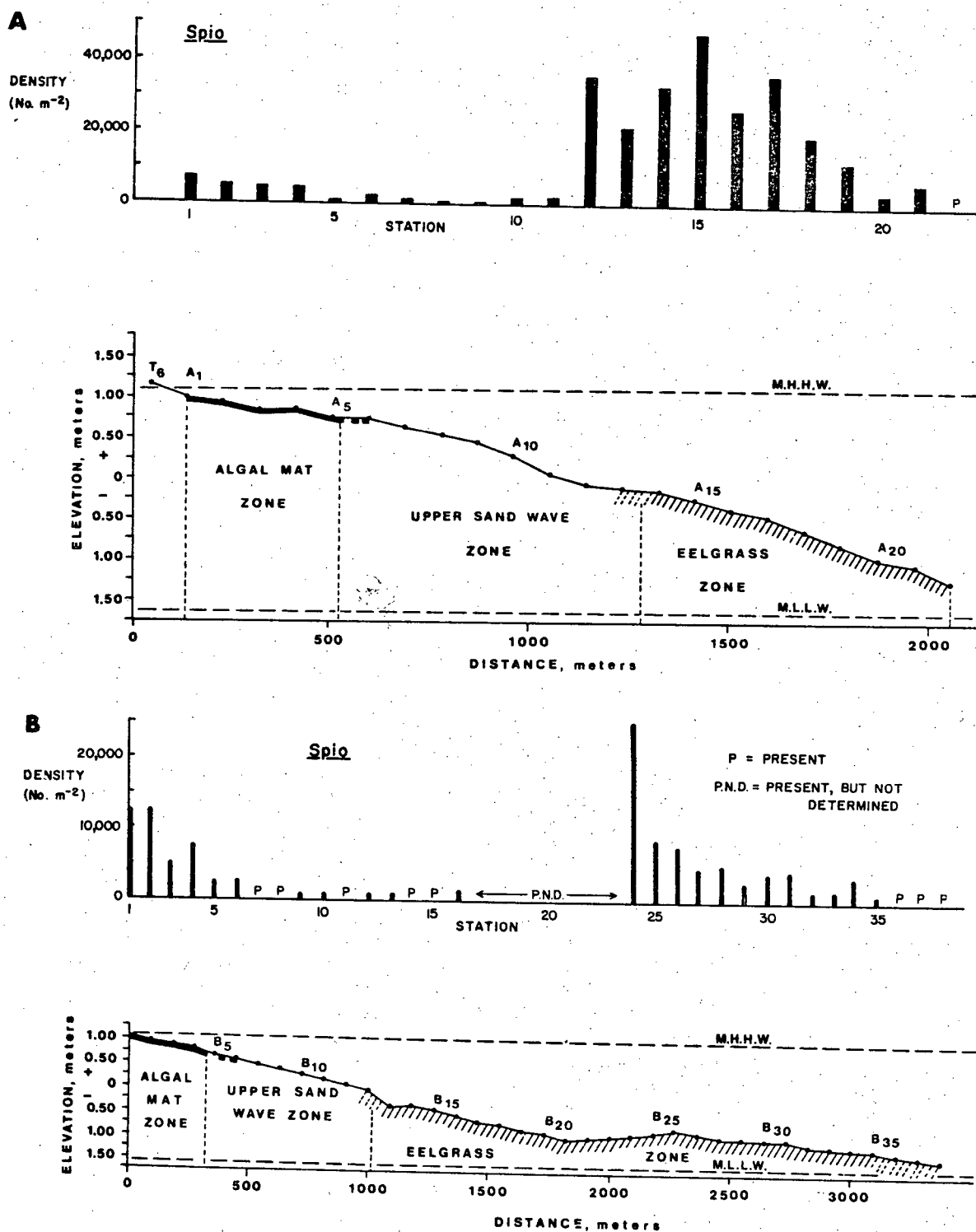


Figure 13. a) Densities of Spio sp. on transect A.

b) Densities of Spio sp. on transect B.



### Fly Larvae

In the upper half of the algal mat zone the raised algal mat platforms are riddled with small 'U' shaped burrows. The burrows are 1.5 to 10 cm deep and 0.25 to 1.0 mm in diameter. They only occur on the upraised algal mats and their densities are highly variable, ranging from 0 to  $10^5 \text{ m}^{-2}$  (extrapolating from measurements taken with a  $4 \text{ cm}^2$  quadrat), but in general of the order of  $10^4 \text{ m}^{-2}$ . Despite thorough searching through numerous box core samples the organism responsible for the burrows could not be found. The burrows are thought to be produced by fly larvae. The flies lay eggs in or on the algal mats. The larvae hatch, burrow downward feeding on the nutritious algal mat seams, then burrow out and fly off without a trace.

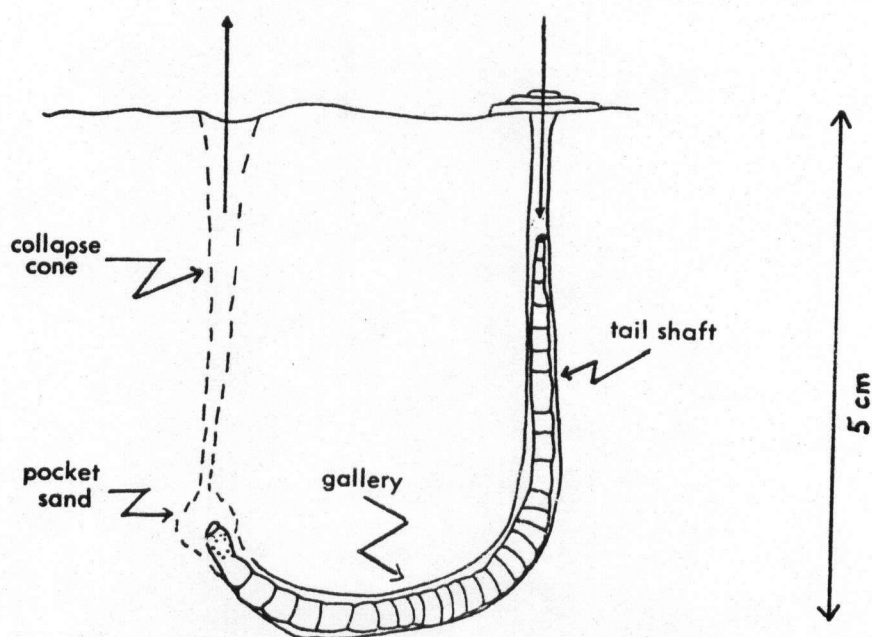
### Upper Sand Wave Zone

The upper sand wave zone is upper amphizonal in exposure (Fig. 8). It is characterized by very low amplitude sand waves, lacks any extensive floral mat, and is dominated by the following organisms and biogenic sedimentary structures.

### Abarenicola

Abarenicola pacifica Healy and Wells is a deposit-feeding polychaete worm (Hobson, 1967), which constructs a vertically orientated 'J' shaped burrow (Fig. 14a). The tail shaft reaches the surface and fecal casts are excreted here in the form of sand coils. The head shaft consists of a collapse cone produced by the feeding activities of the worm, and this is occasionally visible as a depression at the surface. Abarenicola pacifica circulates water through its burrow system (Hylleberg, 1975).

The ratio of fecal cast density to worm density was determined to be 1.07:1 by taking 30 box cores between Stations A6-A11. Sixty fecal casts (30 x 2) were found to be associated with 56 worms (26 x 2, 4 x 1).



(a)



(b)

Figure 14. (a) Morphology of an Abarenicola burrow (after Hylleberg, 1975). Arrows indicate direction of respiration current.  
 (b) Patchy distribution of Abarenicola fecal casts. The highest densities of casts occur in and around tidal pools. Trowel is about 25 cm high.

For all intents and purposes the ratio can be taken as 1:1. Abarenicola appears abruptly near the lower edge of the algal mat zone. Densities rise from zero to about  $20 \text{ m}^{-2}$  ( $A5 \bar{x} = 19 \text{ m}^{-2}$ ,  $\sigma = 12 \text{ m}^{-2}$ ;  $B5 \bar{x} = 20.5 \text{ m}^{-2}$ ,  $\sigma = 37 \text{ m}^{-2}$ ) in the distance of less than 100 m (Figs. 15a & 15b). Sixty-four quadrat readings between Stations A1-A4 and B1-B4, sampling in total  $16 \text{ m}^2$ , registered zero Abarenicola. The upper limit of the worms' occurrence on transect A lies between A4 at + 0.87 m elevation (Geodetic Datum) and A5 at + 0.75 m elevation, and on transect B between B4 (+ 0.83 m) and B5 (+ 0.70 m). There is no change in grain size over the 100 m interval in which the worms appear. Abundant juvenile Abarenicola have been observed well above this limit, up to the saltmarsh perimeter, in early spring. However, they disappear from this area by July, probably because desiccation during prolonged exposure on warm, sunny days at neap tidal periods results in high mortality amongst juvenile Abarenicola within the atmozone (Fig. 8), whereas mortality within the amphizone (Fig. 8) is reduced because the tidal flat is inundated with fresh sea water at least once everyday (Swinbanks, in preparation).

Abarenicola attains its maximum densities in the upper sand wave zone and extends into the eelgrass zone (Figs. 15a & 15b). Its densities are higher in wet sediments than dry (Fig. 15a). Abarenicola congregates in the troughs of sand waves and in tidal pools which are wet or under water (Fig. 14b). This is probably the result of differential mortality amongst juvenile Abarenicola.

In the upper sand wave zone Abarenicola excretes on average about  $1\text{--}5 \text{ wet ml worm}^{-1} \text{ day}^{-1}$  (1 wet ml  $\equiv$  1.5 g dry weight), but rates vary depending on the wetness of the sediment. In dry sediment average rates can be as low as  $0.02 \text{ ml worm}^{-1} \text{ day}^{-1}$  while in tidal pools average rates can be as high as  $8.4 \text{ ml worm}^{-1} \text{ day}^{-1}$ . In the eelgrass zone large Abarenicola

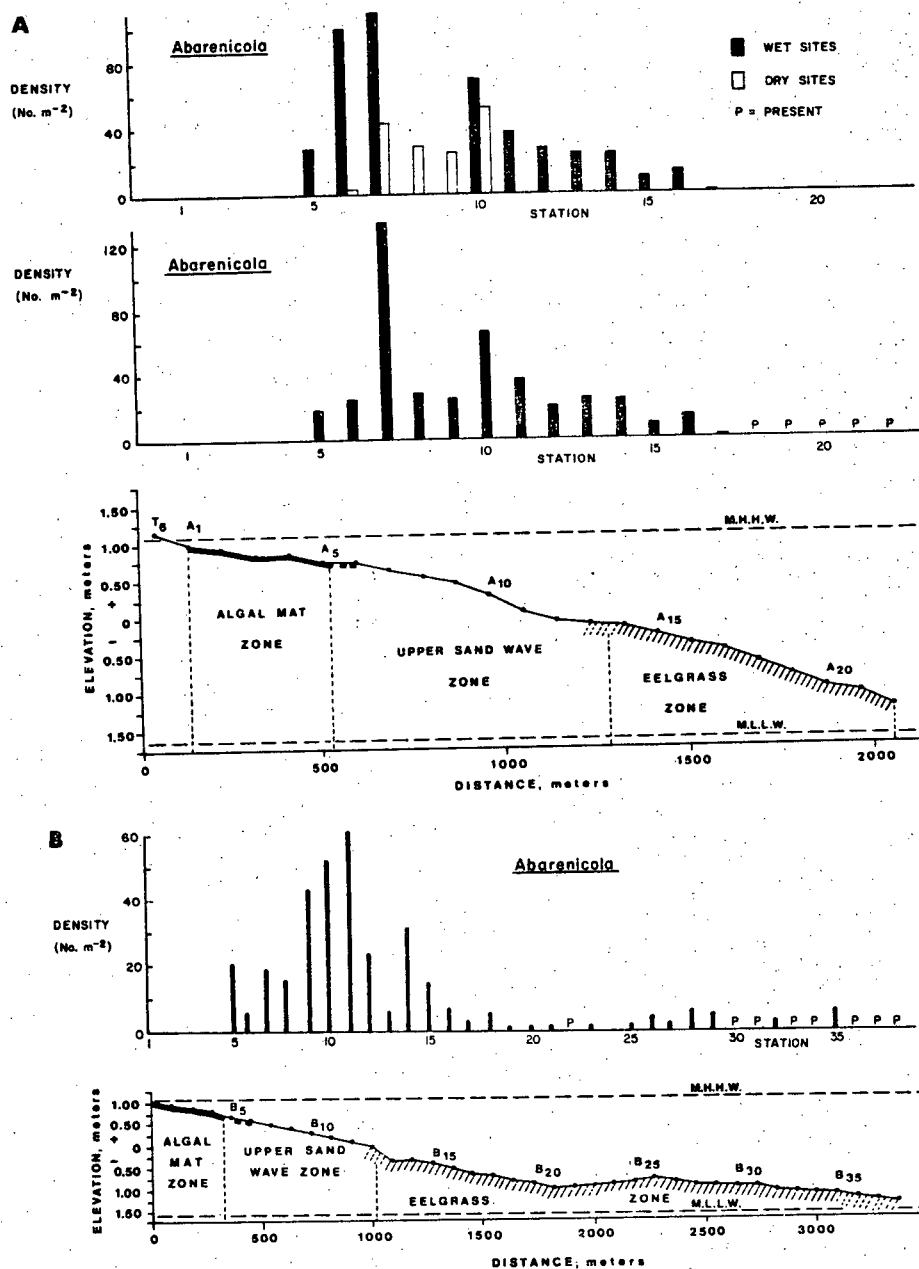


Figure 15. a) Densities of Abarenicola fecal casts on transect A. Upper histogram distinguishes between wet and dry sites, and is based on four wet site readings and four dry site readings at each station with a 0.25 m<sup>2</sup> quadrat. Stations A8 and A9 had no wet sites which could be sampled. Stations A11-A17 had no dry sites. Station A5 had dry sites, but Abarenicola was absent from them. Lower histogram presents the average densities, based on random quadrats.

b) Densities of Abarenicola fecal casts on transect B.

excrete on average 29 wet ml worm<sup>-1</sup> day<sup>-1</sup> (Swinbanks, 1979).

Abarenicola pacifica in the course of eating rejects coarse grains (Hylleberg, 1975) and through irrigation of its burrow can float clay towards the surface in the head shaft irrigation current (Swinbanks, 1979). This could result in biograded bedding as described by Rhoads and Stanley (1965). However, the fine grain size and low mud content of Boundary Bay sands renders these processes virtually undetectable.

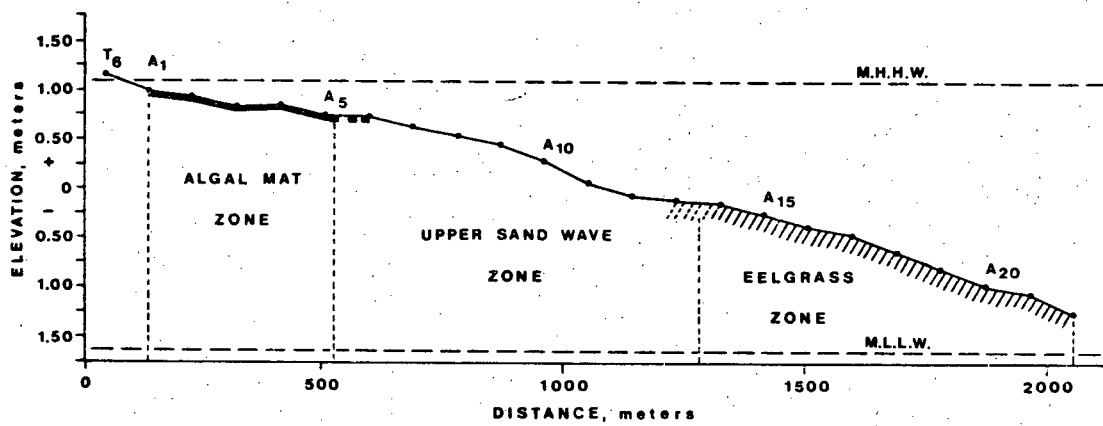
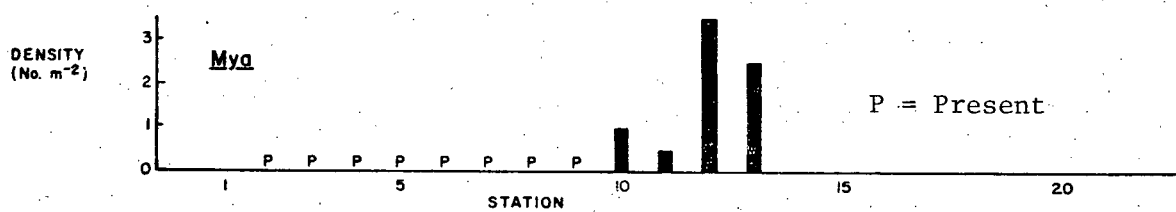
### Mya

Mya arenaria Linnaeus, a suspension feeding bivalve, occurs in the upper sand wave zone (Fig. 16a). A few individuals also occur in the tidal pools of the algal mat zone, but in densities less than 0.5 m<sup>-2</sup>. Mya was not observed in the eelgrass zone. The maximum density Mya attains is about 4 m<sup>-2</sup>. It occurs in the upper sand wave zone on transect B but in densities less than 0.5 m<sup>-2</sup>.

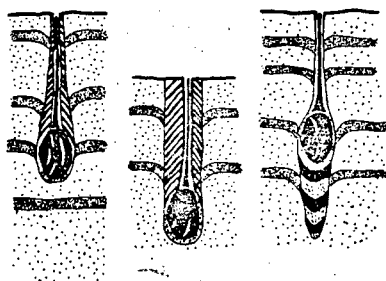
Mya constructs a simple vertical tube up to 15 cm in depth (Fig. 16b). Movement of Mya within its burrow causes downward warping of algal mat laminations (Fig. 16b). The vertical tube constructed by Mya accommodates the inhalent and exhalent siphons which are fused together. Fecal pellets are voided from the exhalent siphon. Because of its low densities Mya is not considered to contribute significantly to the sediments of Boundary Bay through defecation.

### Callianassa

Callianassa californiensis Dana is a burrowing thalassinidean shrimp. Figures 17a and 17b present the density distribution of Callianassa burrow openings on transects A and B. Isolated individual Callianassa burrows occur in the algal mat zone, but in very low densities. Eighty quadrat readings on transects A and B taken within the algal mat zone, sampling in total 20 m<sup>2</sup>, registered zero Callianassa burrow openings.



(a)



(b)

Figure 16. (a) Densities of Mya sp. on transect A.  
 (b) Spreite traces left by Mya sp., and downwarping of laminations caused by movement of the clam within its burrow due to its growth or changes in the level of the sediment water interface (after Reineck, 1958).

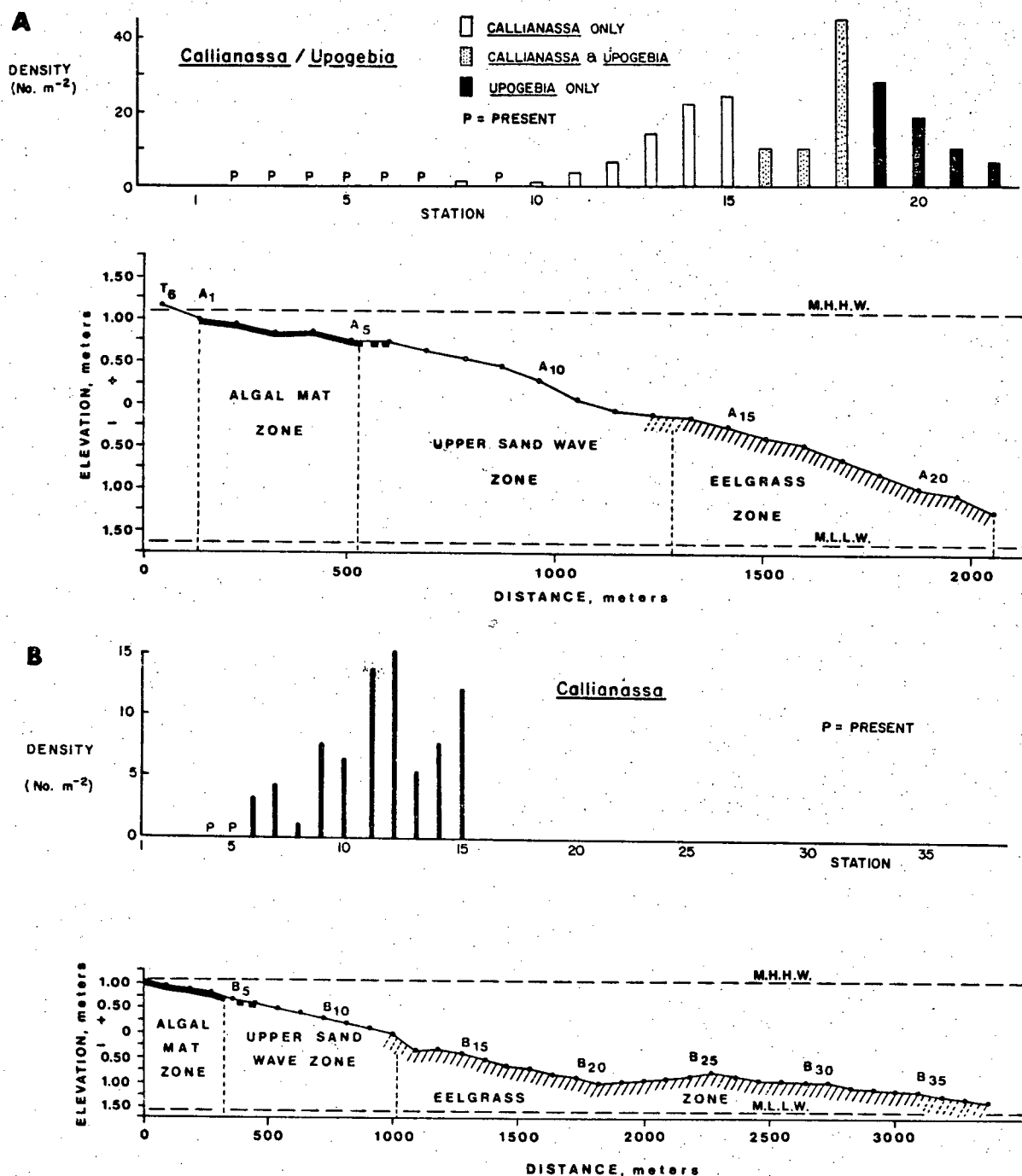


Figure 17. a) Densities of Callianassa and Upogebia burrow openings on transect A.

b) Densities of Callianassa burrow openings on transect B.

Walking seawards along the transect and scanning approximately 2 m on either side of the transect line the first Callianassa burrow encountered was at A2 ( $+ 0.94 \pm 0.07$  m, Geodetic Datum) on transect A, and at B4 ( $+ 0.83 \pm 0.02$  m, Geodetic Datum) on transect B (Figs. 17a & 17b). On exposure the dissolved oxygen content of Upogebia burrows, which are mud-lined, decreases rapidly and anoxic conditions can prevail within one hour (Thompson and Pritchard, 1969). Anoxic conditions are probably reached more rapidly in the burrows of Callianassa californiensis because the lack of a firm burrow lining exposes the burrows to hypoxic interstitial waters (Thompson and Pritchard, 1969). Callianassa californiensis can survive approximately 5.7 days of anoxia (range 3.2-7.8 days, N=35, Thompson and Pritchard, 1969). At  $+ 0.79$  m (Geodetic Datum) the maximum duration of continuous exposure is 4 lunar days, at  $+ 0.85$  m it is 5 lunar days while at  $+ 0.91$  m and  $+ 0.97$  m it is 9 lunar days (Fig. 8). In Boundary Bay the upper limit of Callianassa, lying at about  $\pm 0.9$  m (Geodetic Datum), is, therefore, almost certainly determined by exposure because above this level the maximum duration of anoxia due to exposure exceeds the lethal limit for Callianassa. Conceivably the occasional Callianassa individual could survive above this level, if a tidal pool with oxygenated water happened to overlie its burrow entrance, because Callianassa could then draw oxygenated surface water into its burrow by rapidly fanning its pleopods, as reported by Farley and Case (1968). Rare individual Callianassa burrows have been observed off transect in tidal pools next to the saltmarsh perimeter, and these may fall into the above category. However, the precise elevations of these pools are unknown.

In the upper sand wave zone Callianassa burrow openings appear in clusters covering areas of about one square meter. Burrow opening density within a cluster may be  $10 \text{ m}^{-2}$ , but clusters are separated by tens of



meters, and as a result average densities are less than  $0.5 \text{ m}^{-2}$ . Below about + 0.6 m elevation (Geodetic Datum) Callianassa's distribution is more uniform and greater than  $0.5 \text{ m}^{-2}$ . Callianassa probably requires the day-to-day reliability of tidal inundation found within the amphizone in order to thrive, unhindered by the stress of periods of excessively prolonged anoxia (Torres et al., 1977), as must occur in the atmozone. Average Callianassa burrow densities maximize at about  $20 \text{ m}^{-2}$  around the edge of the eelgrass zone. Callianassa densities are very low below - 0.6 m elevation. Seventy-eight quadrat readings taken on both transects below - 0.6 m elevation, sampling in total  $54 \text{ m}^2$ , registered zero Callianassa burrow openings. These low densities may be the result of the dense rootlets of Zostera marina inhibiting the mining activities of the shrimps, thereby limiting their population.

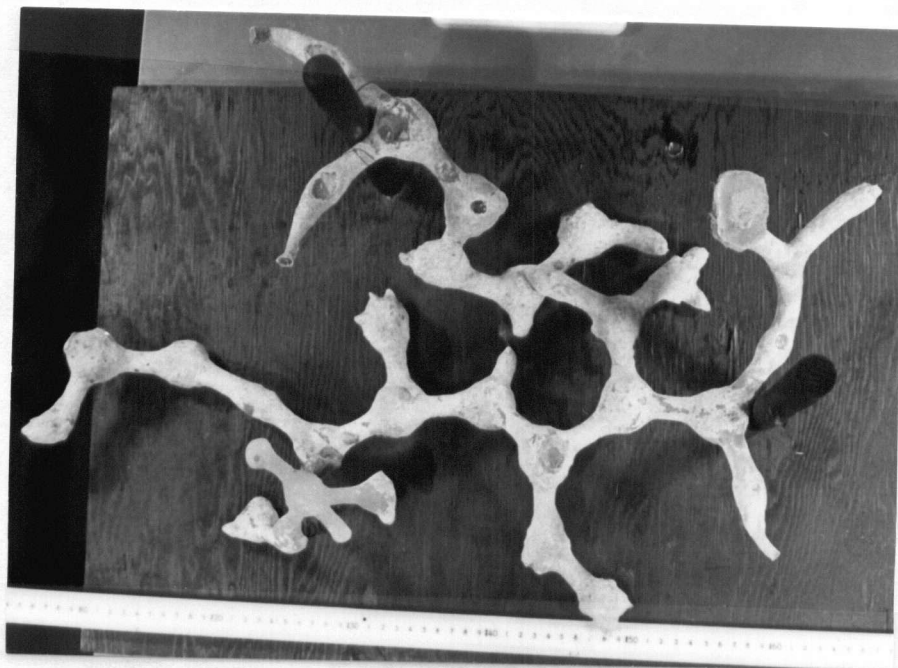
Using an open ended metal box the ratio of burrow openings to shrimp density was determined to be 2.5 (arithmetic mean deviation 0.8,  $N=6$ ) to 1. In several resin casts shrimps were visible entombed within the casts. Invariably each burrow system was occupied by one shrimp. There are usually two openings to each burrow system, although occasionally there may be three and rarely four openings. Hence, the average burrow opening to shrimp ratio is 2.5 to 1. This agrees with the findings of Ott et al. (1976) and Hertweck (1972) for other thalassinidean shrimps.

Burrow Morphology--Since the development of a resin casting technique by Shinn (1968), burrow morphology of thalassinidean shrimps has been studied quite extensively. Frey and Howard (1975) cite numerous references.

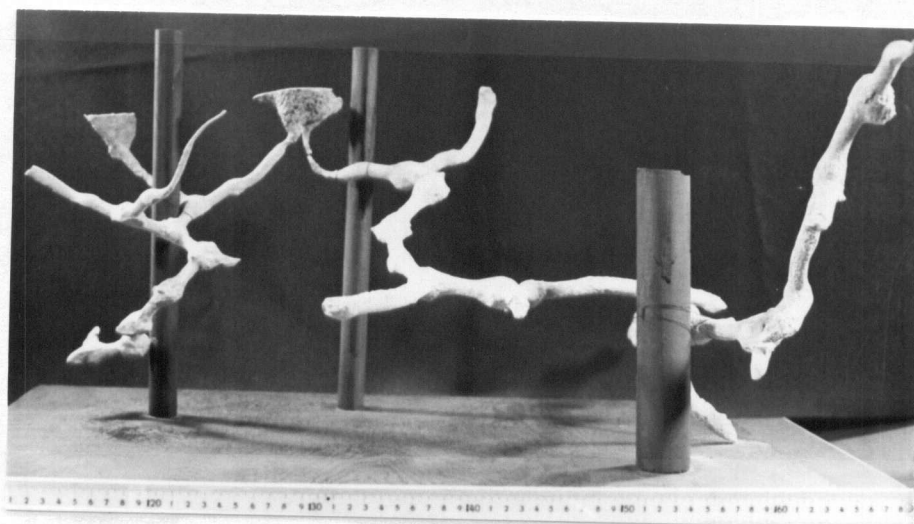
Figures 18a, 18b and 18c illustrate the morphology of these callianassid burrows. They extend 20-30 cm down into the sediment and then branch horizontally for distances of up to a meter. Each system usually has two exits which join as a bulbous chamber at from 5 cm to 10 cm depth. The

- Figure 18. a) Plan view of a Callianassa burrow cast, showing bulbous 'turnarounds.' Cast is about 60 cm in plan view length. Metric ruler (1m) with centimeter subdivisions provides scale.
- b) Side view of a Callianassa burrow cast showing horizontal mine-like nature of burrow system. Burrow extends to about 30 cm depth. Metric ruler (1 m) with centimeter subdivisions provides scale. Overflow of resin produced 'heads' on cast.
- c) Plan view of a large Callianassa burrow cast which is just over 1 m long. Metric ruler (1 m) provides scale.

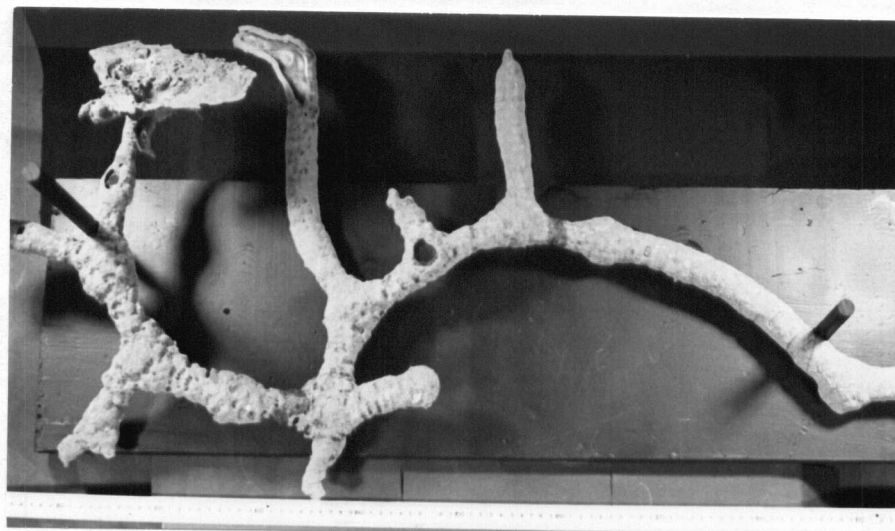
A



B



C



exits have constricted apertural necks. Branching is dichotomous. There are bulbous turnarounds within the systems and blind alleys. There is no distinct lining to the burrow walls except that the sediment is oxidized and lighter in colour.

The lack of a firm burrow lining and the horizontal, branching nature of the burrows suggest they are temporary feeding burrows rather than permanent dwelling burrows. Ott et al. (1976) came to a similar conclusion regarding the burrows of Callianassa stebbingi. The geometry of the burrows of Callianassa californiensis have all the characteristics of a mine used for deposit feeding. However, the presence of a bulbous chamber close to the surface does suggest that the shrimps may suspension feed while the tide is in.

All organisms to some extent alter their environment to the benefit of some and detriment of others. This is nowhere more apparent in Boundary Bay than in the case of Callianassa. For example Cryptomya californica, a small bivalve, uses the sediment-water interface of the Callianassa burrow as a surface for suspension feeding, clustering around the bulbous chamber 5-10 cm below the surface. On the other hand, on the surface, Spio cannot colonize the mounds heaped up by Callianassa because they dry out during low tide, and Callianassa's excavation activities probably choke surface suspension feeders like Mya arenaria.

#### Eelgrass Zone

The eelgrass zone is largely lower amphizonal to upper aquazonal in exposure (Fig. 8), and is, on the large scale, flat, except where the upper reaches of tidal channels cross the zone producing broad, shallow, water-filled depressions (e.g., between Stations B18 to B25 on transect B). The uppermost part of this zone is dominated by a summer growth of Zostera americana, while in the rest of the zone a perennial growth of Z. marina

is present. The following organisms and biogenic sedimentary structures are typical of the Z. marina subzone.

### Upogebia

Upogebia pugettensis (Dana), like Callianassa, is a thalassinidean burrowing shrimp. It has been studied in detail by Thompson (1972).

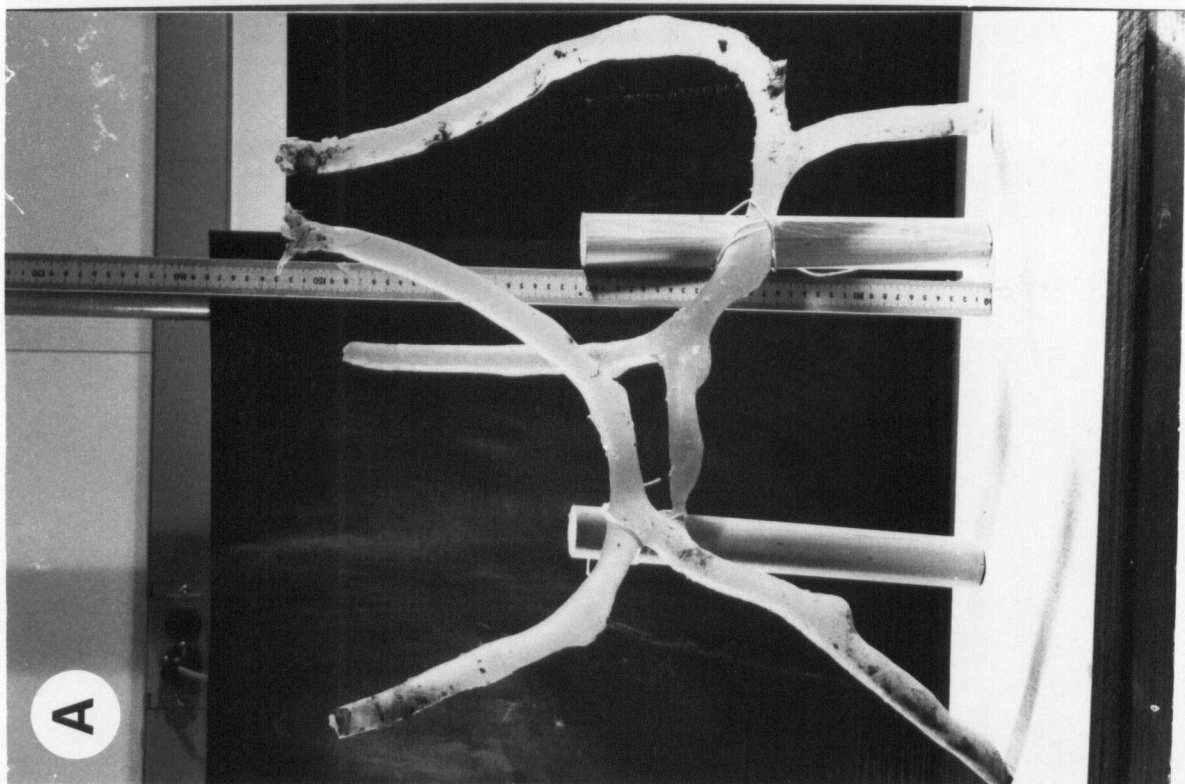
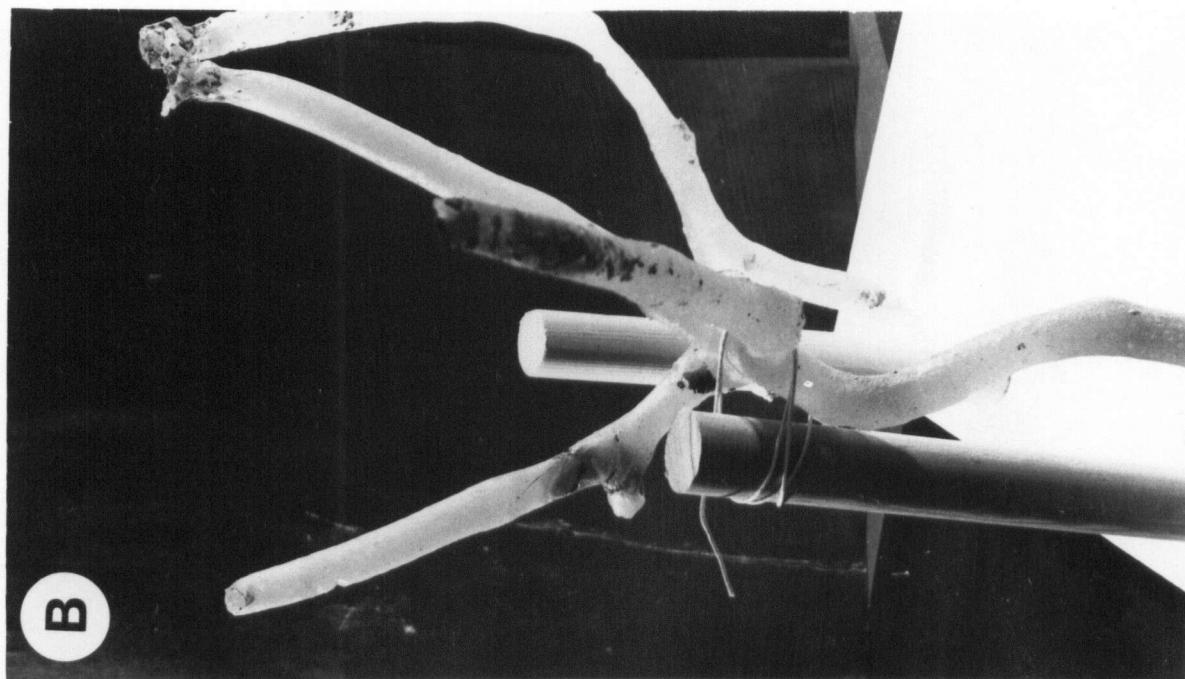
Upogebia only occurs on transect A, appearing abruptly at the edge of the Z. marina subzone at A16, and attaining a maximum burrow opening density of  $44 \text{ m}^{-2}$  (Fig. 17a). There is a region of overlap where Callianassa and Upogebia burrows occur side by side. Data collected from the tidal flats of the active Fraser Delta front indicates that Upogebia prefers muddy substrates (Swinbanks, 1979, Part 4A).

Upogebia is probably restricted to the Z. marina beds on transect A in Boundary Bay because of their higher mud content. Upogebia uses mud to line its burrow, and so it is not surprising that Upogebia's occurrence is restricted by the mud content of the sediment, particularly in an environment such as Boundary Bay where mud contents are only a few percent. Amongst the organisms studied Upogebia is an exception to the earlier contention that exposure time, rather than substrate, is the prime controlling agent of floral/faunal zonation in Boundary Bay.

Burrow Morphology--The Upogebia burrow is a 'Y' shaped (Fig. 19a). The two branches of the 'Y' system meet 20-30 cm below the surface, and the burrow stem continues down to depths of 50 to 60 cm. In contrast to Callianassa burrows, Upogebia burrows are predominantly vertically oriented, do not have constricted entrances, and lack bulbous turnarounds. The internal walls of the burrow are smooth and lined with mud. Upogebia burrows very seldom have sediment mounds outside their entrances, indicating that the burrows are probably not used for mining purposes. Upogebia burrows appear to be permanent dwelling burrows. Ott et al. (1976) reached

Figure 19. a) Cast of two Upogebia 'Y' shaped burrows joined by a constricted neck. Cast is just over 50 cm in depth. Metric ruler (1 m) with centimeter subdivisions provides scale.

b) Side view of cast in (a.) showing shrimp entombed within the cast.



a similar conclusion regarding the burrows of Upogebia litoralis. Adjacent 'Y' burrow systems are often interconnected by constricted apertual necks much like those described by Frey and Howard (1975) for Upogebia affinis (Fig. 19a).

The excavated casts are free of any sand coating, because of the mud lining to the burrows, and shrimps are clearly visible entombed within the casts (Fig. 19b). Five 'Y' tube casts were obtained and invariably each 'Y' tube contained one shrimp, giving a burrow opening to shrimp ratio of 2 to 1. The body width of the shrimp determines the internal diameter of the burrow.

#### Praxillela

Praxillela affinis pacifica Berkeley is a tube-dwelling maldanid polychaete worm, and is closely related to Clymenella torquata described by Rhoads and Stanley (1965) and Featherstone and Risk (1977). Praxillela constructs an agglutinated sand tube up to 15 cm in length and the worm lives upside down in the tube and excretes unconsolidated sandy feces onto the surface (Fig. 21). It occurs in the same area of the eelgrass zone as Upogebia, but is present on both transects. It attains densities of  $650 \text{ m}^{-2}$  (Figs. 20a & 20b), and extends into the lower sand wave zone.

No evidence of biograded bedding as described by Rhoads and Stanley (1965) for Clymenella was found in the case of Praxillela. However, this is not surprising, since the sands in which Praxillela lives on these tidal flats are fine grained and the worm need not be selective about the grain size of sediment it eats. The grain size distribution of the dwelling tubes of Praxillela were found to have an identical grain size distribution to that of the surrounding sediment, within the experimental errors of grain size analysis. This is contrary to the findings of Featherstone and Risk (1977) who found that the grain size distribution of Clymenella tubes was



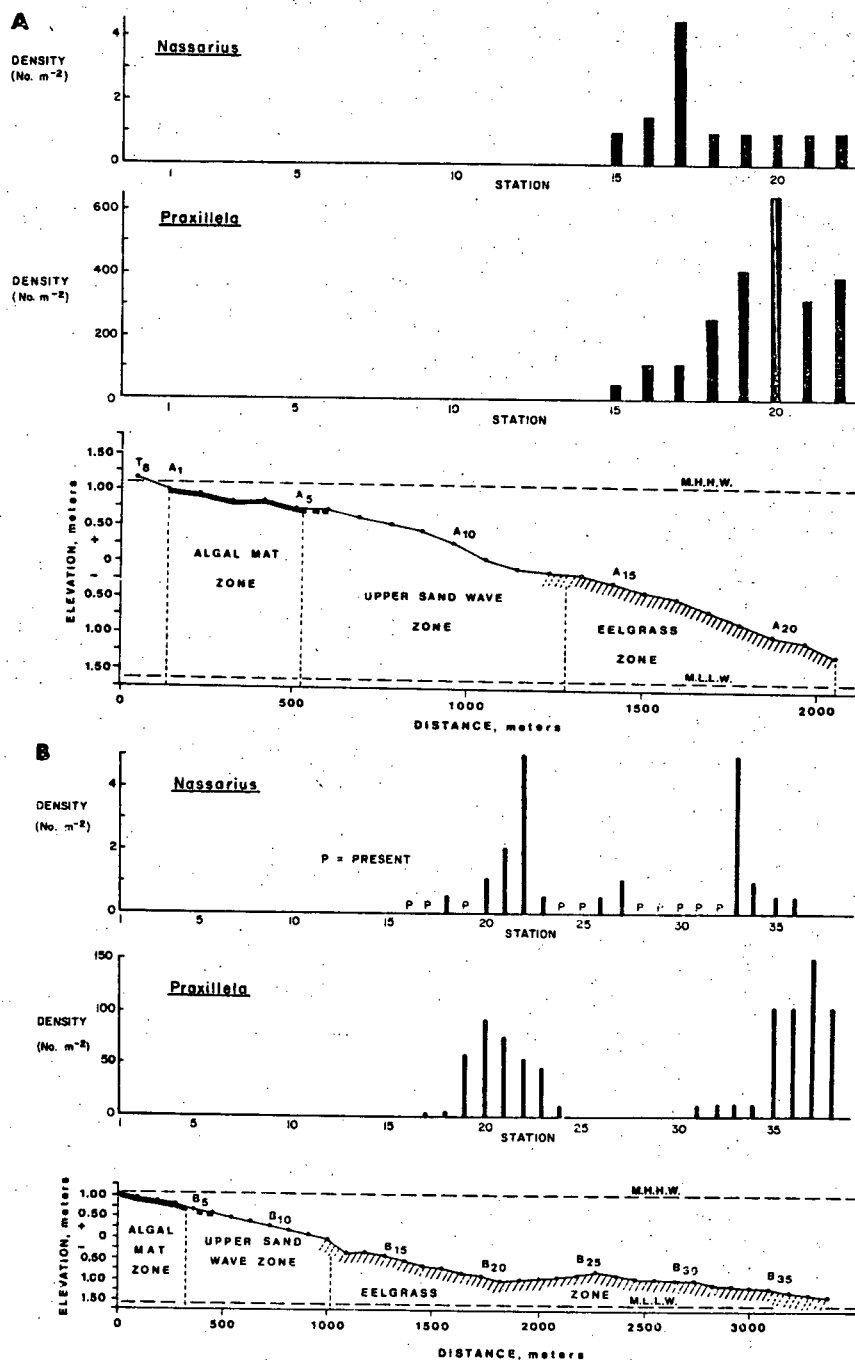


Figure 20. a) Densities of Praxillela sp. and Nassarius sp. on transect A.  
 b) Densities of Praxillela sp. and Nassarius sp. on transect B.

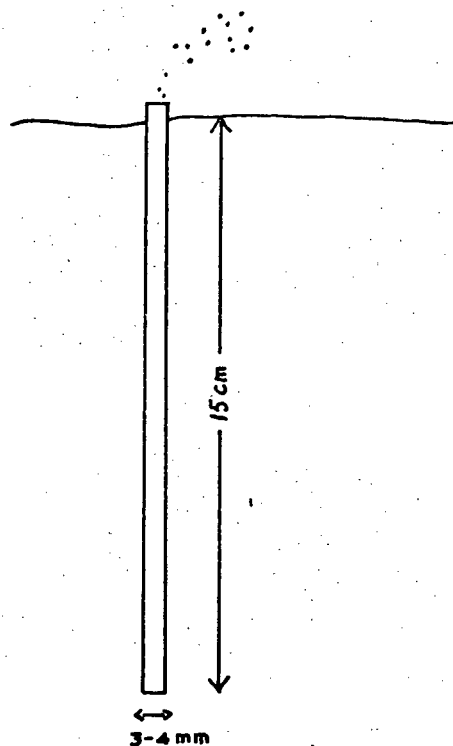
PRAXILLELA

Figure 21. Vertical agglutinated sand tube of Praxillela sp.

significantly coarser than that of the surrounding sediment. Perhaps the slightly coarser grain size of the sands in Minas Basin (median grain size about 2.2  $\phi$  as opposed to 2.7  $\phi$  in Boundary Bay) induces selection of coarser grains during tube building. The coarser grains possibly being derived from those rejected during feeding.

### Nassarius

Nassarius mendicus (Gould) is a gastropod which occurs alongside Upogebia and Praxillela (Figs. 20a & 20b). It is more active and faster moving than Batillaria but it does not produce any distinctive traces, apart from a very superficial grazing trail.

On transect B the distributions of Nassarius and Praxillela are bimodal (Fig. 20b). This is due to the presence of a topographic high at B25. Water drains off this elevated region from both sides and it rapidly dries out during low tide, whereas the depression centred on B20 remains water-filled, despite the fact that it lies above sea level, because water constantly drains into it. As a result the region near B25 has the characteristics of higher elevations on the tidal flat, whereas the depression around B20 has the characteristics of lower elevations. A bimodal distribution of Praxillela and Nassarius results, the modes being split by the topographic high. This emphasizes the fact that the method of subdividing the intertidal zone into exposure zones, presented earlier, only holds true if the slope of the tidal flat is relatively constant, with no topographic highs or lows producing abnormal exposure or prolonged submergence due to drainage effects.

### Lower Sand Wave Zone

The lower sand wave zone is aquazonal in exposure (Fig. 8) and is characterized by large sand waves, and by the lack of a floral cover.

Some qualitative observations of this zone have been made, particularly at the end of transect B which encroaches upon it (Fig. 2). Praxillela and

large Abarenicola are present in this zone, as are sand dollars (Kellerhals and Murray, 1969), but all other organisms considered in this study are absent or present in very low densities. The zone is dominated by physical sedimentary structures. Dunes line the sides of the tidal channels (Kellerhals and Murray, 1969). Ripples and sand waves are the characteristic bedforms of the rest of the zone. Kellerhals and Murray (1969) report coarse sands along the lower perimeter of this zone. The tidal channels which dissect this zone are lined with a dense growth of eelgrass (Z. marina), and shell lag deposits are also present (Kellerhals and Murray, 1969).

#### DISCUSSION OF ZONATION

The cause of intertidal zonation has been a topic of great debate amongst biologists for many years, and the extent of the role which tides play in zonation has been a matter of much controversy (Doty, 1957; Ricketts and Calvin, 1968; Chapman and Chapman, 1973; Chapman, 1974; Carefoot, 1977). In Boundary Bay the evidence suggests that tides, and in particular critical tidal levels, are a major cause of zonation.

There are three floral zone limits which surveying and topographic maps have revealed to be delimited by elevation. These are the lower limit of the saltmarsh zone, the lower limit of the algal mat zone and the upper limit of the eelgrass zone. Figure 8 can offer explanations for all three.

The lower limit of the saltmarsh lies at + 1.15 m (Geodetic Datum) on transect A and + 1.10 m on transect B (Table II). This is coincident, within the errors of surveying, with the lower limit of the upper atmozone (+ 1.16 m, Fig. 8), which is a level at which the maximum duration of continuous exposure begins to rise abruptly from 12 to 40 days. It is also the upper limit of Level 3 exposures and the elevation of the highest lower high water. As a result sea water only covers this area during the late afternoon, evening or

at night in summer. The saltmarsh apparently thrives under conditions of prolonged daylight exposure. The period that a plant is continuously flooded and the duration of continuous exposure are both limiting factors in their own right (Chapman, 1974). Continuous flooding limits plant growth by water-logging roots reducing respiration due to lack of oxygen, imposing salinity stress and by reducing light availability. A saline environment imposes physiological stress. Nutrient deficiency stress is caused by uptake of sodium ions in preference to potassium ions. Hormonal stress is induced by salt stressed roots being inhibited in transport of hormones to leaves, and osmotic pressure also increases root resistance thereby decreasing water delivery to leaves, all of which results in growth reduction (Levitt, 1972; Waisel, 1972). This may not apply to Salicornia sp., the pre-dominant halophyte in the lower saltmarsh zone (Parsons, 1975), as some consider Salicornia sp. to be an obligate halophyte (Chapman, 1974)--i.e. a halophyte which requires salt for optimum growth. However, the existence of obligate halophytes is questionable (Barbour, 1970; Ungar, 1966). Ungar, (1966) suggested that halophytes grow in saline soils simply because they cannot compete effectively with terrestrial plants in non-saline soils. Parsons (1975) found that Distichlis spicata, which is abundant throughout the saltmarsh zone in Boundary Bay, grows better in soil saturated with tap water than with dilute seawater or seawater. It is therefore reasonable to suggest that flooding frequency is a limiting factor in the Boundary Bay saltmarsh, at least in the case of Distichlis spicata, because flooding imposes physiological stress. Chapman (1974) stressed the importance of also considering the maximum duration of exposure, since saltmarsh plant seedlings require several days of continuous exposure without flooding in order to germinate and root successfully. Salicornia stricta requires two to three days while Aster tripolium requires five (Chapman, 1974). Continuous exposure

must coincide with germination. The critical tides which define the boundary between the upper and lower atmozones occur at the spring and autumn equinoxes (Swinbanks, 1979). Saltmarsh plant seedlings have been observed sprouting in Boundary Bay in March close to the time of the spring equinox, and so the long periods of continuous exposure which occur in the upper atmozone at this time have a high probability of coinciding with seedling germination. Thus there are reasonable physiological grounds for suggesting that the break in exposure duration and submergence frequency between the upper and lower atmozones is a causative factor in limiting the saltmarsh zone rather than a mere coincidence.

The lower limit of the algal mat zone coincides within the errors of surveying with the lower limit of the lower atmozone (Fig. 8). Apparently the cyanophyte algal mats thrive in an area subject to the prolonged periods of exposure associated with Level 1 exposures. Many blue-green algae are obligate photoautotrophs (Fogg et al., 1973)--i.e. they cannot grow without light. Phormidium sp. can grow very slowly in the dark on a medium of glucose and yeast autolysate (Allen, 1952), but for any blue-green algae to thrive, sufficient light is essential. However, as algal mats can be found growing on the crests of sand waves, well below the lower limit of the algal mat zone it would seem unlikely that the algal mat zone is light limited, but rather that desiccation for some reason is necessary for the algal mats to thrive. An ability to withstand desiccation is a characteristic feature of blue-green algae, and the vegetating cells of Oscillatoriaceae (the family to which Phormidium and Microcoleus belong) which have no perennating cells, survive desiccation better than other families of blue-green algae (Fogg et al., 1973). Although some species show great resistance to desiccation, growth of these does not occur at relative humidities of less than 80% (Hess, 1962), and therefore desiccation must only be indirectly beneficial.

It has been demonstrated that cerithid gastropods, such as Batillaria, destroy blue-green algal mats by their grazing activities (Garrett, 1970), and it has been suggested that algal mats are restricted to the uppermost intertidal to supratidal regions because grazing gastropods and burrowing organisms are absent or present in low densities in these areas (Garrett, 1970). In Boundary Bay Batillaria alone cannot limit the extent of the algal mat zone, because Batillaria densities are the same or of the same order of magnitude within the algal mat zone as without it (see average densities Figs. 9a & 9b). However, the grazing activities of Batillaria combined with the intense reworking activities of Abarenicola and Callianassa might be sufficient to limit the extent of the algal mats. The densities of Abarenicola and Callianassa increase abruptly near the lower limit of the algal mat zone (Figs. 15a & 15b, Figs. 17a & 17b). The algal mats and these organisms tend to be mutually exclusive, because the raised algal mat platforms are dry and inhospitable to the organisms, in particular Abarenicola, while the reworking and grazing activities of the organisms inhibit algal mat formation. If burrowing and grazing organisms were absent from Boundary Bay, algal mats would probably develop at lower intertidal levels as demonstrated by Garrett (1970). It is therefore suggested that the step in exposure duration between the amphizone and the atmozone sets the limit to the algal mat zone because desiccation associated with Level 1 exposures during neap tides prevents extensive population by burrowing organisms, in particular Abarenicola. The interaction between flora and fauna is an essential element in the restriction of the algal mat zone, but the abruptness of the zone's lower limit is caused by the step-like nature of intertidal exposure.

The upper limit of the eelgrass zone terminates at the upper limit of the lower amphizone and thus never experiences Level 2 exposures (Fig. 8). Keller and Harris (1966) found a direct correlation between the extent of

Z. marina coverage and elevation in Humboldt Bay, California. The eelgrass showed a pronounced upper limit at a level of 15% mean exposure 0.3 m above MLLW. They suggested that the upper limit of eelgrass is controlled by tidal exposure, because desiccation during exposure decreases the vigor and vegetative reproduction of the eelgrass. The upper limit of eelgrass in Boundary Bay lies at a much higher tidal elevation (mean sea level) and is exposed almost 50% of the time (Fig. 6). However, the uppermost part of the eelgrass zone in Boundary Bay consists entirely of the smaller species Z. americana. We therefore suggest that the upper limit of the eelgrass zone terminates at the upper limit of the lower amphizone because Z. americana cannot tolerate Level 2 exposures, which are always well in excess of half a lunar day and occur during daylight hours in summer, and Z. americana requires the influx of seawater brought by lower high water in order to survive. In Boundary Bay the upper limit of Z. marina does not appear to be controlled by elevation but rather seems to be strongly influenced by the distribution of tidal channels. This is well illustrated in the map of Z. marina distribution presented by O'Connell (1975). The tidal channels remain water-filled during low tide despite the fact that they lie well above sea level because water constantly drains into them. Z. marina growth extends up the floors and flanks of the channels and has thus attained elevations which in theory have as much as 30% exposure (Station A17 at - 0.5 m Geodetic Datum), but in fact usually remain under several centimeters of water throughout low tide, because of the presence of a topographic low and because the dense mat of Z. marina itself inhibits drainage.

The lower limit of the eelgrass zone on the tidal flats is not delimited by elevation. It may be limited by the presence or absence of sand waves or by the current or wave regime associated with sand waves (Fig. 2).



## SUMMARY

Each of the three floral/sedimentological zones lying between the saltmarsh zone and the lower sand wave zone has a distinctive macrofaunal assemblage, and as a result each zone has a characteristic assemblage of biogenic sedimentary structures (Fig. 22). Although living population densities cannot be correlated directly with trace fossil densities, it is assumed that the distribution patterns and assemblages of living organisms will be preserved in the trace fossil record. Topography of small and large scale creates lateral heterogeneity within the biofacies of each zone (Fig. 23). The topography may be physical or biogenic in origin. The characteristic biogenic sedimentary structures of each zone are as follows.

Algal Mat Zone

The raised algal mat platforms create lateral heterogeneity within this zone's biofacies, because they quickly become dry and inhospitable to organisms during low tide (Fig. 23a). The platforms have an internal stratification consisting of alternating sandy and organic rich layers, which are riddled with 'U' shaped burrows (up to  $100,000\text{ m}^{-2}$ ), suspected to be of fly larval origin. Batillaria pits also abound on the raised platforms. In water-filled depressions Spio are present in high densities ( $10^4\text{ m}^{-2}$ ), and Batillaria grazing trails are abundant. Callianassa and Mya burrows occur in this zone, but in very low densities. Abarenicola appears abruptly near the lower limit of the algal mat zone.

The mean grain size of the sands of this zone usually lie in the range of 3.1-3.3  $\phi$ . The sands are well sorted (Incl. Graphic Std. Dev. 0.35-0.50  $\phi$ ) and contain about 5% mud (range 3.6-8.0%).

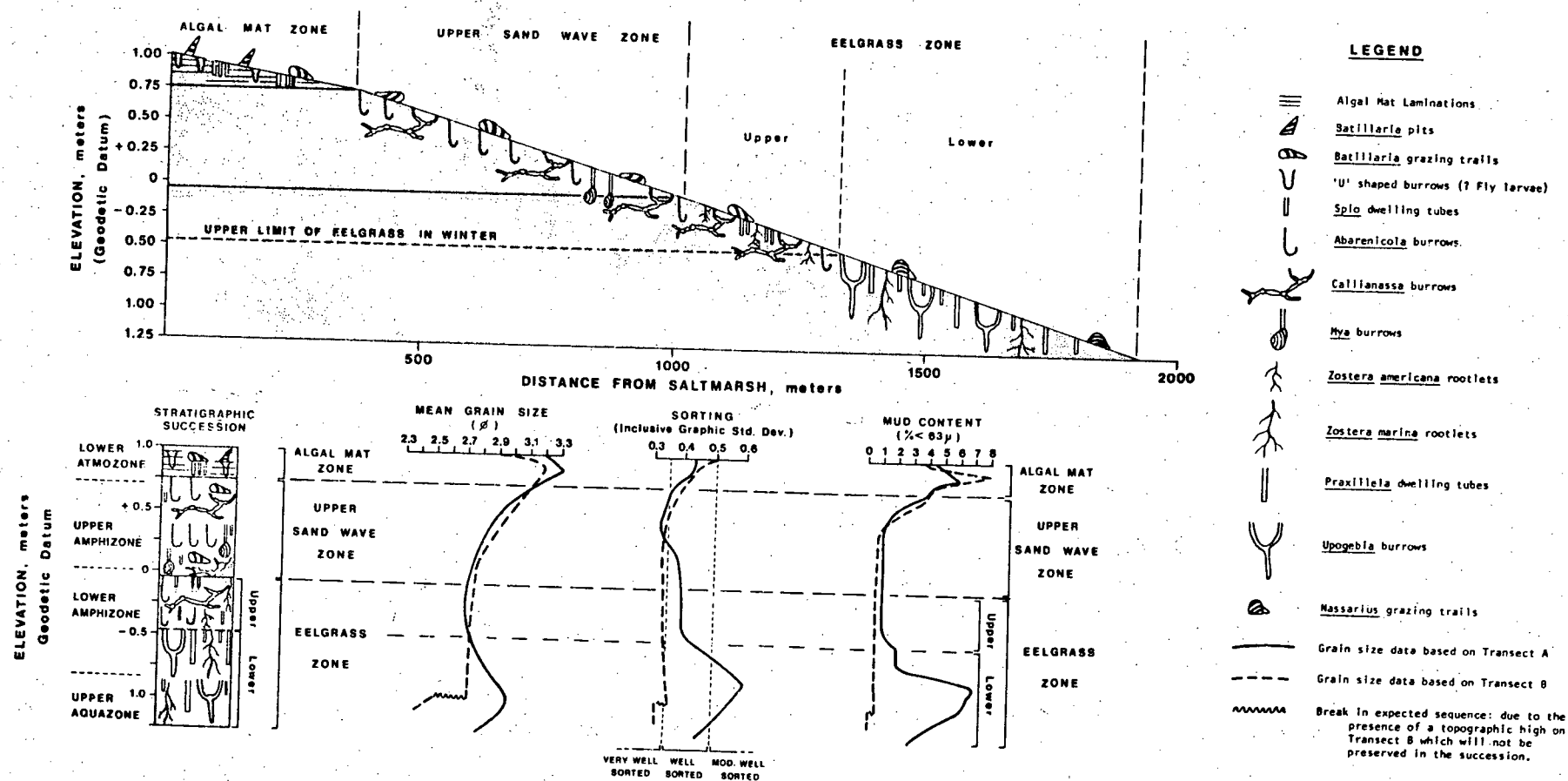


Figure 22. Zonation of biogenic sedimentary structures in three of the floral/sedimentological zones of Boundary Bay tidal flats, and the expected stratigraphic succession of biogenic sedimentary structures and grain size parameters, if the tidal flats are prograding seawards without subsidence.

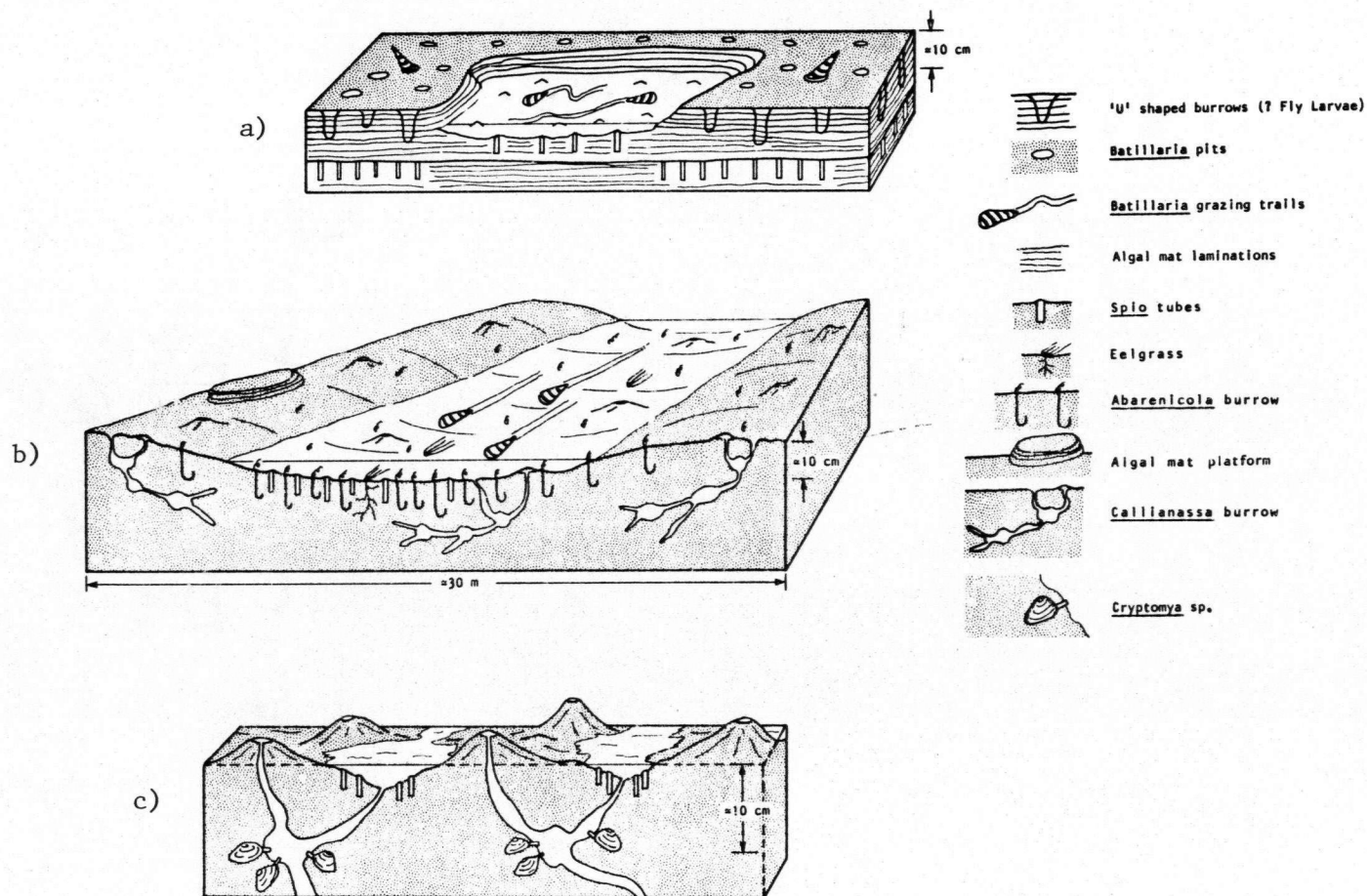


Figure 23. Lateral heterogeneity within zonal biofacies caused by topography of small and large scale.

a) Algal mat zone: Lateral heterogeneity created by upraised algal mat platforms.

b) Upper sand wave zone: Lateral heterogeneity created by sand waves.

c) Eelgrass zone: Lateral heterogeneity created by *Callianassa* mounds and burrows.

### Upper Sand Wave Zone

This zone is characterized by the presence of Abarenicola and by the lack of a floral cover. Mya attain their maximum density in the lower part of this zone. Lateral heterogeneity within the biofacies of this zone is created by the low amplitude sand waves (Fig. 23b). Abarenicola, Batillaria and Spio congregate in the water-filled troughs of the sand waves, and patches of Zostera americana are also present here. Weak currents produced by water draining along the axis of the sand wave troughs cause Batillaria to head upstream, producing grazing trails paralleling the current direction. On the sand wave crests, which dry out during low tide, Batillaria grazing trails are sinuous, pitting by Batillaria is evident, Abarenicola densities are low and Spio are absent. Algal mat platforms may be present on the crests. The distribution of Callianassa burrows is not influenced by the sand waves, because Callianassa is a deeper burrowing organism, and its burrow system is always water-filled, whether or not it occurs in the sand wave troughs..

The sands of this zone have a mean grain size in the range of 3.1-2.7  $\phi$ . They are well to very well sorted (Incl. Graphic Std. Dev. 0.33-0.39  $\phi$ ), and contain about 1% mud, except at the zones upper limit where values rise to 4%.

### Eelgrass Zone

The eelgrass zone can be subdivided into an upper and lower part. The upper eelgrass zone is characterized by a Zostera americana-Callianassa-Abarenicola-Batillaria community, while the lower eelgrass zone is characterized by a Zostera marina-Upogebia-Praxillela-Nassarius community. Callianassa attain their maximum densities in the upper eelgrass zone. Their sediment mounds and burrows create lateral heterogeneity within the biofacies of this zone (Fig. 23c). In the lower eelgrass zone Zostera marina growth is present throughout the year, and, if it forms an extensive and permanent

floral mat, mud accumulates in this zone.

The mean grain size in the eelgrass zone is in the range of 2.4-2.8  $\phi$ . The sands are very well to moderately well sorted (Incl. Graphic Std. Dev. 0.29-0.60  $\phi$ ), and in the upper eelgrass zone contain about 1% mud, while in the lower eelgrass zone mud contents can attain 7% if Z. marina forms an extensive floral mat, if not, values drop well below 1%.

The lower half of Figure 22 illustrates the expected stratigraphic succession of biofacies and grain size parameters if the tidal flats of Boundary Bay are prograding without subsidence, and a core were sunk in the algal mat zone. This succession might be expected in the western half of the Bay, where there is evidence that the saltmarsh is advancing (Kellerhals and Murray, 1969).

#### CONCLUSIONS

In Boundary Bay a distinct floral/faunal zonation exists, which is controlled primarily by exposure, although floral/faunal interactions also play an important role. The extent of exposure which a given location on the tidal flat experiences is a function of the relationship between elevation and tides, and is also a function of local topography, which may be of physical or biogenic origin. For tidal flats experiencing astronomically controlled tides, the intertidal zone can be divided into three distinct exposure zones. The duration of maximum continuous exposure or maximum continuous submergence 'jumps' on passing from one zone to the next. In Boundary Bay these exposure zones to a large extent delimit the floral zonation of the tidal flats on the macroscopic scale. However, on the more local scale, topography can be seen to profoundly influence faunal and floral distribution patterns, since topographic highs dry out rapidly during low tide, while depressions remain water-filled.

Boundary Bay tidal flats are exceptional, in comparison with those previously described in the literature, because grain size varies little over the bulk of the tidal flats. The flats are mantled with clean, well to very well sorted fine to very fine sand. The homogeneity in grain size continues to a depth of at least 30 cm, as revealed from box cores. Because of this homogeneity in grain size Boundary Bay tidal flats are to some extent comparable with rocky intertidal shorelines where precise elevational delimitation of floral/faunal zonation is well documented (Carefoot, 1977). In attempting to elucidate the effects of other parameters on faunal distribution patterns (e.g. grain size, mud content or salinity), one must first eliminate the elevation parameter. This can be done by setting up stations parallel to the waterline at some chosen tidal height, rather than using data collected from transects set up perpendicular to the shoreline. In addition to eliminating the elevation parameter, one must take care to compare stations with comparable topographic situations.

The most striking feature of Boundary Bay tidal flats is the fact that from shoreline to low water mark the tidal flats are mantled with sand. As a result the stratigraphic succession preserved by this tidal flat would consist of a monotonous sequence of sand, and the only means by which a detailed interpretation of the succession could be made, would be through the study of biogenic sedimentary structures (both floral and faunal), and by grain size analysis techniques.

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Part 3

SEDIMENT REWORKING AND THE BIOGENIC FORMATION  
OF CLAY LAMINAE BY ABARENICOLA PACIFICA

## ABSTRACT

An estimated  $4.25 \times 10^8$  Abarenicola populate the tidal flats of Boundary Bay on the southern flank of the Fraser Delta and annually rework about one million cubic meters of sand. In tidal pools, where Abarenicola attain densities of  $200 \text{ m}^{-2}$ , the worms completely rework the substrate they live in to a depth of 10 cm in 100 days.

In the laboratory Abarenicola can separate a sand/clay mixture, by floating the clay out in suspension in the head shaft irrigation current. The clay then settles as a biogenically formed lamina, which is subsequently buried and reworked by the worm. In the natural intertidal environment the clay would be carried away by tidal currents, and by using this process Abarenicola could 'clean' mud out of a mud/sand mixture creating a better sorted sand.

## INTRODUCTION

The topic of bioturbation and biodeposition has recently been receiving increasing attention in the literature (Rhoads and Stanley, 1965; Rhoads and Young, 1970; Aller and Dodge, 1974; Risk and Moffat, 1977). Much of the classic work in this field has been by German and Dutch workers (Schwarz, 1932; Van Straaten, 1952; Reineck, 1958; Schäfer, 1972). Organisms can size-sort sediment and create biogenic graded bedding (Van Straaten, 1952; Rhoads and Stanley, 1965; Featherstone and Risk, 1977). By constantly reworking sediments, organisms can drastically alter its physical properties (e.g., relief, water content, compressibility, etc.). This has both sedimentological and biological consequences. For example, deposit feeders through their burrowing and feeding activities can produce an unstable substrate that is easily reworked by currents and which thereby tends to exclude filter feeding organisms from the area (Rhoads and Young, 1970; Aller and Dodge, 1974).

During a study of biosedimentological zonation on Boundary Bay tidal flats (Swinbanks, 1979) on the southern flank of the Fraser Delta (Fig. 1), one of the organisms studied which proved to be especially interesting was Abarenicola pacifica Healy and Wells. This polychaete produces the most visible evidence of bioturbation in Boundary Bay, continually excreting mounds of loosely coiled sediment onto the surface. By constantly reworking the surface sediments Abarenicola may limit the extent of the algal mat zone - one of the five major floral/sedimentological zones of the tidal flats (Swinbanks, 1979) (Fig. 1). It is thus of interest from both the ecological and sedimentological point of view to determine the rate at which this organism reworks sediment.

Abarenicola pacifica is the Pacific coast equivalent of the well known lugworm, Arenicola marina, which is found on the Atlantic coasts of North

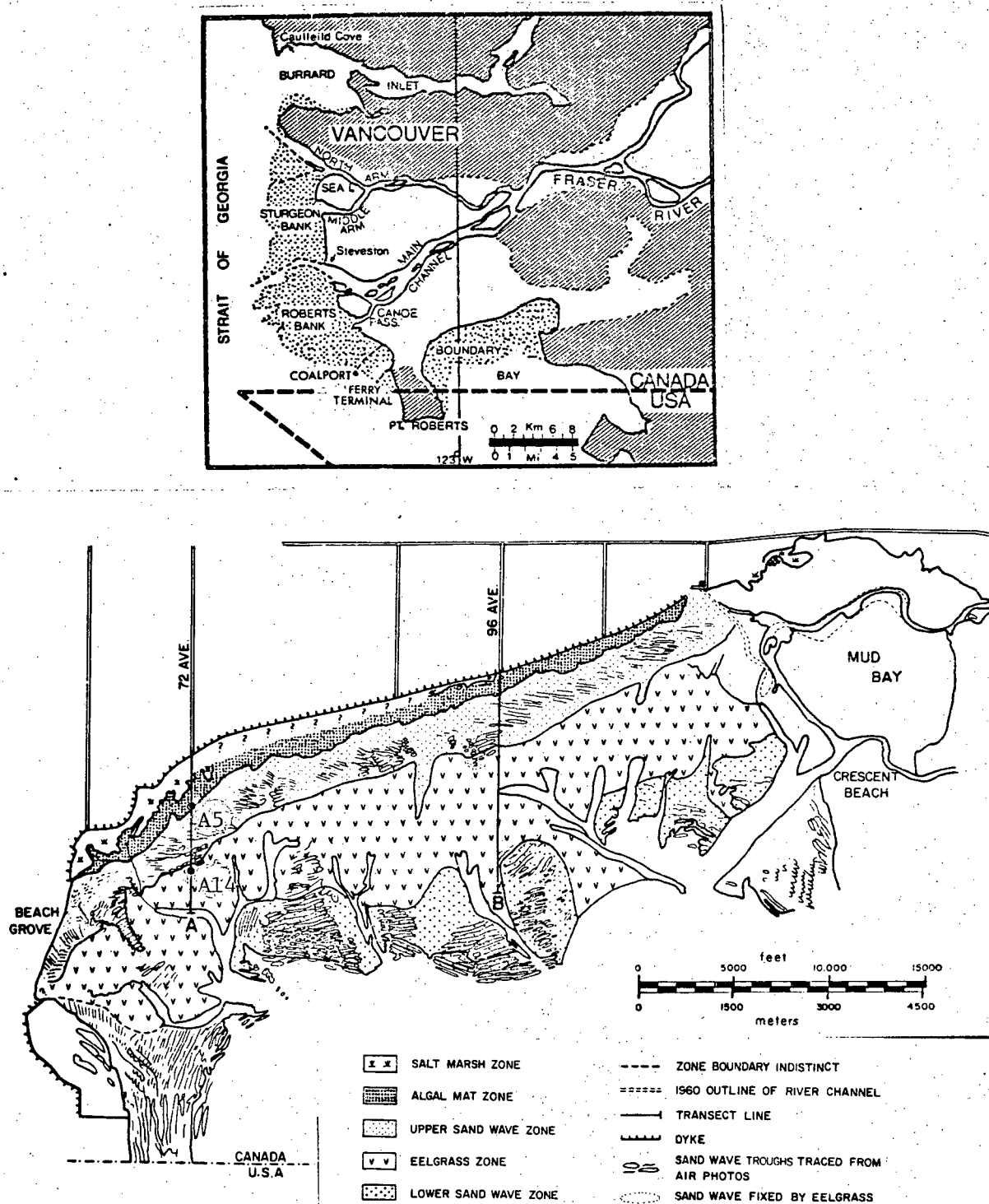


Figure 1. Location of study area. Upper map shows the general location of Boundary Bay on the Fraser Delta and the lower maps the floral/sedimentological zones of the tidal flats. The two transects A and B were set up in 1976 (Swinbanks, 1979).



America and Europe, and which is mentioned in several intertidal studies by sedimentologists (Van Straaten, 1952; Reineck, 1958; Evans, 1965).

Abarenicola pacifica is a deposit feeder but there is some evidence that, as in the case of Arenicola marina, it may also suspension feed by filtering the sea water that it circulates through its burrow for respiration purposes (Hobson, 1967). It constructs a 'J' shaped burrow with a vertical tail shaft, and horizontal gallery that ends in a feeding chamber above which lies a cone of collapsed sediment on which it feeds (Hylleberg, 1975; Swinbanks, 1979). Hylleberg (1975) suggested that Abarenicola 'garden' the sediment by irrigating its burrow, creating an oxidizing micro-environment in which the micro-organisms (e.g., ciliates, flagellates and nematodes), on which it feeds, flourish. Hylleberg (1975) found that Abarenicola locally increases the percentage of coarse grains around its feeding chamber much as reported by Van Straaten (1952) for Arenicola marina and by Rhoads and Stanley (1965) for Clymenella torquata. Hylleberg (1975) attributed this to Abarenicola selectively feeding on sediment less than 80  $\mu\text{m}$  in size. Another mechanism of biogenic size-sorting, caused by Abarenicola irrigating its burrow, is reported here.

There are five floral/sedimentological zones on the Boundary Bay tidal flats (Fig. 1). These are, from the shoreline seawards, the saltmarsh zone, the algal mat zone, the upper sand wave zone, the eelgrass zone and the lower sand wave zone. Abarenicola is most abundant in the upper sand wave zone and appears abruptly near the lower limit of the algal mat zone. Its density rises from much less than  $0.5 \text{ m}^{-2}$  to about  $20 \text{ m}^{-2}$  in the distance of less than 100 m. There are no changes in grain size parameters (mean size, sorting or mud content) over this interval (Swinbanks, 1979). Hobson (1967) and Healy and Wells (1959) consider that sediment type rather than intertidal exposure governs the distribution of Abarenicola pacifica and Abarenicola clapedi

vagabunda Healy and Wells in False Bay on San Juan Island, A. pacifica

preferring muddy substrates and A. vagabunda clean sand. In Boundary Bay A. pacifica is abundant in pure sands containing only about 1% mud, and the abrupt upper limit to their distribution occurs at a constant elevation that is probably determined by exposure (Swinbanks, 1979).

#### METHODS

Two transects running north/south from the saltmarsh edge to low water mark were established in the summer of 1976 (Swinbanks, 1979) (Fig. 1). Stations marked with wooden stakes were placed at 91.4 m (300 ft) intervals and their elevations determined by surveying. The rate at which Abarenicola reworks sediment was determined in June, 1976, November, 1976 and August, 1978. A 1 m<sup>2</sup> area was staked out at stations A5 to A14 on transect A (Fig. 1) just as the waterline retreated from the area. All Abarenicola casts were carefully removed and counted. The stations were reoccupied about 10 hours later just before the tide returned and the volume of casts accumulated was measured with a graduated cylinder. To distinguish 'wet' sites from 'dry' a depression about 1 cm deep was made in the sand with a finger after about 10 hours of exposure. If the depression immediately filled with water the site was considered 'wet.'

In the laboratory Abarenicola was kept and observed in sandwich tanks using the running sea water facilities of the Pacific Environment Institute, West Vancouver, during the winter of 1977. Worms were placed in wet sieved Boundary Bay sand (>63 µm), which had been homogenized with about 10% (by weight) finely powdered (<63 µm) montmorillonite. Abarenicola's ability to size sort sediment was clearly visible using this technique as concentrations of the fine grained white montmorillonite stood out in contrast to the dark grey sand.

## RESULTS

Field ResultsSediment Reworking Rates

The rate at which Abarenicola reworks sediment during various times of the year is presented in Tables I and II. In the upper sand-wave zone (stations A5 to A12), the factor which seems to influence the rate of sediment turnover most is the wetness of the sediment. The highest rates were recorded in tidal pools where the worms remain under water during low tide. They excrete  $5.1 \pm 2.4$  wet ml worm<sup>-1</sup> day<sup>-1</sup> (1 wet ml=1.5 g dry weight) on average. Rates were lower in sediment which remained wet but not under water, the average rate being  $1.8 \pm 0.9$  wet ml worm<sup>-1</sup> day<sup>-1</sup>, and lowest in dry sediment, averaging  $0.5 \pm 0.6$  wet ml worm<sup>-1</sup> day<sup>-1</sup>. In the lower intertidal regions (Stations A13 and A14) rates were an order of magnitude higher, averaging  $29 \pm 18$  wet ml worm<sup>-1</sup> day<sup>-1</sup>. The rates of sediment turnover at stations A5 to A12 do not decrease greatly between summer and winter. The wet rate in June averaged  $2.5 \pm 0.5$  wet ml worm<sup>-1</sup> day<sup>-1</sup> while in November it dropped to  $0.9 \pm 0.4$  wet ml worm<sup>-1</sup> day<sup>-1</sup>, but the under water rate did not decrease (June,  $4.4 \pm 2.7$  wet ml worm<sup>-1</sup> day<sup>-1</sup>; November,  $6.6 \pm 2.3$  wet ml worm<sup>-1</sup> day<sup>-1</sup>). On the other hand for the worms producing high rates of sediment turnover in summer at A13 and A14, there is such a marked decrease in rate of turnover in winter that fecal casts are very hard to find. When present they only contain 1 or 2 ml of sediment as opposed to 20 to 50 ml in summer.

Budget of Sediment Turnover

Taking into account the above variable rates, an annual budget of sediment turnover by Abarenicola can be calculated utilizing density data

TABLE I

Rates of Sediment Turnover by Abarenicola

June 28, 1976  
Mean Air Temperature 18.5 °C (range 16-21 °C)

Station	State of Substrate	Rate <sup>-1</sup> (wet ml worm <sup>-1</sup> day <sup>-1</sup> )	N
A5	dry	0.02	43
A6/A7	dry	0.72	102
A8	dry	0.08	18
*A9 1/3	wet	3.05	37
A11	dry	0.30	10
A13	u.w.	18.00	5

\* Between A9 and A10 30.5 m (100 ft) from A9.

June 30, 1976  
Mean Air Temperature 17 °C (range 13-20 °C)

Station	State of Substrate	Rate <sup>-1</sup> (wet ml worm <sup>-1</sup> day <sup>-1</sup> )	N
A5	u.w.	8.4	63
A6	u.w.	2.8	54
A7	u.w.	4.0	43
A8	u.w.	2.5	19
A9	dry	1.4	130
A10	wet	2.6	66
A11	wet	1.9	96
A12	wet	2.4	52
A13	u.w.	21.8	18
A14	u.w.	19.6	23

N = number of fecal casts in sampled area (1 m<sup>2</sup>)  
u.w. = under water

Note: Air temperature data based on records during the hours of sampling at Vancouver International Airport approximately 20 km from the study site (source: Monthly meteorological summary, Atmospheric Environment Service, Fisheries and Environment Canada).

TABLE II

Rates of Sediment Turnover by Abarenicola

November 8, 1976  
 Mean Air Temperature 9.5 °C (range 9-10 °C)

Station	State of Substrate	Rate (wet ml worm <sup>-1</sup> day <sup>-1</sup> )	N
A5	wet	1.4	30
A5/A6	wet	0.4	52
A6	wet	1.2	47
A5	u.w.	8.2	28
A6	u.w.	5.0	25

August 22, 1978  
 Mean Air Temperature 17.5 °C (range 16.5-18.5 °C)

Station	Substrate Temperature (°C) (2 cm depth)	State of Substrate	Rate (wet ml worm <sup>-1</sup> day <sup>-1</sup> )	N
A10	19-21	u.w.	5.1	211
A13	20-22	u.w.	56.0	9

N = number of fecal casts in sampled area (1 m<sup>2</sup>)  
 u.w. = under water

Note: Air temperature data based on records during the hours of sampling at Vancouver International Airport approximately 20 km from the study site (source: Monthly meteorological summary, Atmospheric Environment Service, Fisheries and Environment Canada).

collected by Swinbanks (1979). The following assumptions and estimates are made (Table III):

(1) Most Abarenicola occupy the upper sand wave zone which lies between mean sea level and +0.75 m Geodetic Datum and has an area of  $0.8 \times 10^7 \text{ m}^2$ . The area is exposed on average 70% of the time (estimated from mean exposure curve presented by Swinbanks, 1979). In summer during exposure about one third of this area remains under water due to the presence of tidal pools. The remaining two thirds is 'wet' during exposure, except during daylight summer exposure when one third is 'wet' and the other 'dry.' This was estimated from 77 random quadrats taken on transect A in June, 1976, of which 24 were under water, 27 were 'wet' and 26 'dry.'

(2) The average density of Abarenicola at wet or under water sites, which constitute two thirds of the area above mean sea level, is  $57 \text{ m}^{-2}$ , while the average density in dry areas, which constitute one third of the area is  $10 \text{ m}^{-2}$ . Hence the under water + wet population amounts to  $3 \times 10^8$  individuals, while the dry population is  $0.25 \times 10^8$  individuals.

(3) In the upper sand wave zone, Abarenicola turns over about  $5.1 \text{ ml worm}^{-1} \text{ day}^{-1}$  when under water, throughout the year. At wet sites in summer they average  $2.5 \text{ ml worm}^{-1} \text{ day}^{-1}$  and in winter  $0.9 \text{ ml worm}^{-1} \text{ day}^{-1}$ . The summer dry rate is  $0.5 \text{ ml worm}^{-1} \text{ day}^{-1}$ .

(4) There is an estimated population of  $10^8$  Abarenicola in the eelgrass and lower sand wave zones below mean sea level, which turn over sediment at an average under water rate of  $29 \text{ ml worm}^{-1} \text{ day}^{-1}$  during summer. The rate of sediment turnover in winter is negligible.

(5) 'Summer' conditions last from April to September and 'winter' conditions from October to March.

The total annual budget is about  $1 \times 10^6 \text{ m}^3$  (Table III). Of this budget more than half is reworked in the area below mean sea level during summer.

TABLE III

Annual Budget of Sediment Turnover for Abarenicola in Boundary Bay

Zone	State of Tide	No. of days	Rate (ml worm <sup>-1</sup> day <sup>-1</sup> )	Population	Turnover (m <sup>3</sup> )
UPPER	IN	110	u.w. 5.1	3.25 x 10 <sup>8</sup> (total pop.)	1.82 x 10 <sup>5</sup>
	OUT	255	u.w. 5.1	1.50 x 10 <sup>8</sup> (tidal pools)	1.95 x 10 <sup>5</sup>
SAND	OUT	255 {	127.5 winter wet 0.9	1.50 x 10 <sup>8</sup>	0.17 x 10 <sup>5</sup>
WAVE			127.5 summer wet 2.5	1.50 x 10 <sup>8</sup> ('wet' pop.)	0.48 x 10 <sup>5</sup>
ZONE	OUT	255 {	127.5 winter wet 1.00	0.25 x 10 <sup>8</sup>	0.03 x 10 <sup>5</sup>
			127.5 summer dry 0.25	0.25 x 10 <sup>8</sup> ('dry' pop.)	0.01 x 10 <sup>5</sup>
..... Mean Sea Level .....					4.46 x 10 <sup>5</sup>
EELGRASS	IN/OUT	182.5	u.w. 29	10 <sup>8</sup>	5.30 x 10 <sup>5</sup>
ZONE	Total Budget				9.76 x 10 <sup>5</sup>

To place this budget in perspective, it can be compared with the annual sediment discharge of the Fraser River which amounts to about  $20 \times 10^6 \text{ m}^3$  (Mathews and Shephard, 1962).

On the smaller scale, Abarenicola can attain densities as high as  $200 \text{ m}^{-2}$  in tidal pools, and the worms turn over sediment at the under water rate of about  $.5 \text{ ml worm}^{-1} \text{ day}^{-1}$ . Each day a layer of sediment about 1 mm thick is extruded onto the surface by Abarenicola. This is equivalent to a layer about eight grains thick. In 100 days Abarenicola reworks all the sediment it lives in to a depth of 10 cm. However, it should be remembered that this rate is under optimum conditions.

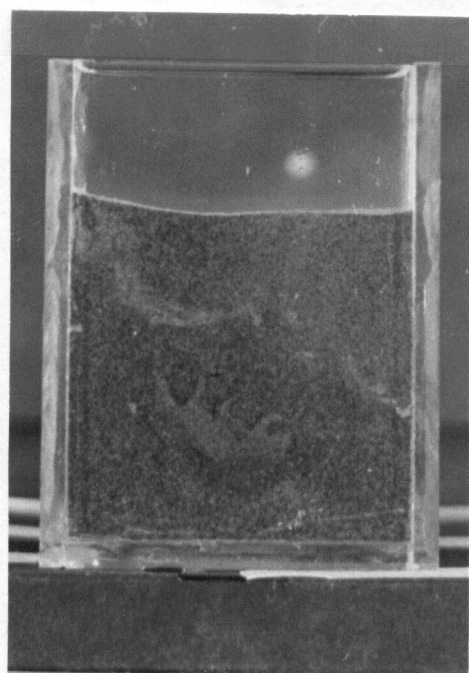
### Laboratory Results

In the laboratory Abarenicola demonstrates an amazing capacity to size-sort sediment. When placed in a mixture of homogenized sand and clay Abarenicola quickly segregates the two through its irrigation activities (Fig. 2). Water is drawn in through the tail shaft and returns to the surface through the head shaft (Fig. 3). Fine grained clay particles float to the surface carried in suspension by the head shaft current and in the low energy environment of the laboratory the clay settles out on the substrate forming a thick lamina within 24 hours (Fig. 2b). Within a few days the lamina is buried by fecal casts excreted through the tail shaft, and is then deformed by the feeding and respiration activities of the worm (Fig. 2c).

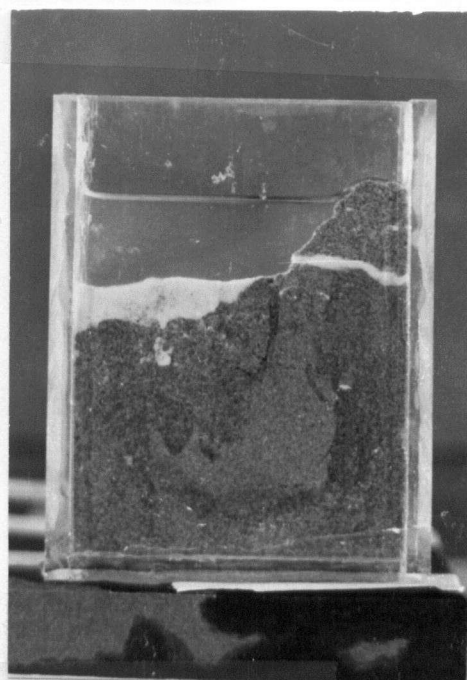
### DISCUSSION

The rates of sediment turnover reported here are comparable with those determined by Hobson (1967) and Healy and Wells (1975) for A. pacifica, with the exception of the very high rates recorded in the eelgrass zone (Tables I

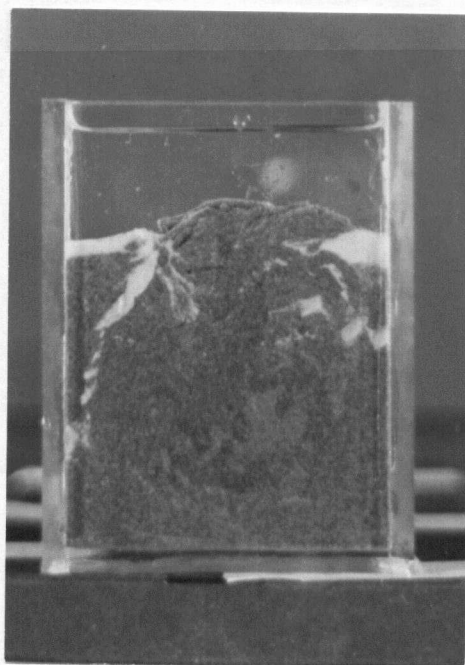




(a)



(b)



(c)

Figure 2. Grain size sorting by Abarenicola:

- a) Start of the experiment. An individual Abarenicola ( $\approx 2$  g) was placed in a homogenized mixture of sand ( $> 63\mu\text{m}$ ) and montmorillonite ( $< 63\mu\text{m}$ ).
- b) After 24 hours a thick, biogenically formed lamina of montmorillonite (white) has developed as a result of the irrigation activities of the worm.
- c) After three days the lamina has been buried by fecal casts and the lamina has been deformed and bioturbated by the feeding and irrigation activities of the worm.

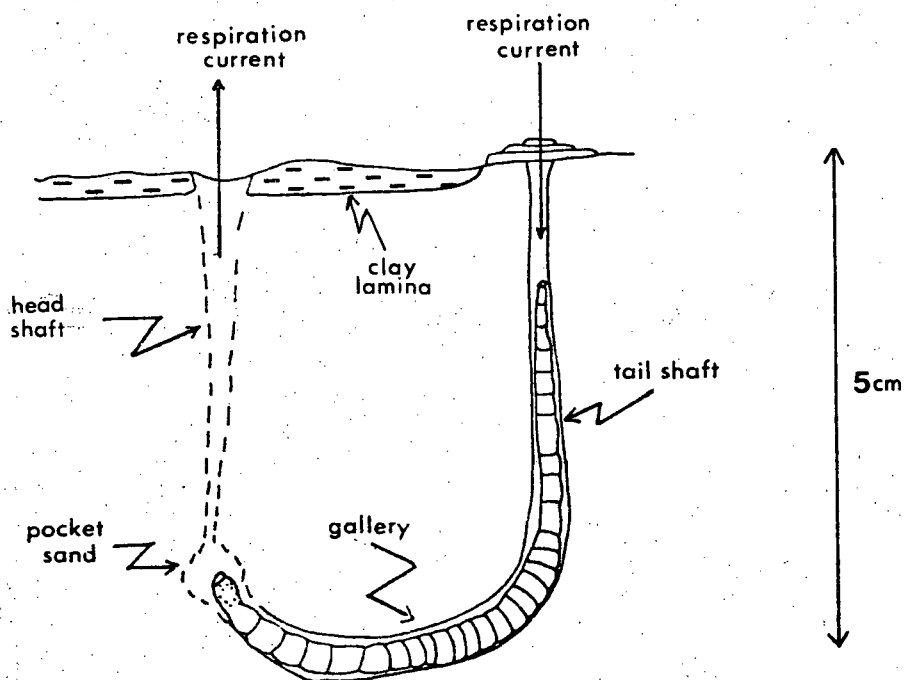


Figure 3. Sketch of a comparable situation to that illustrated in Figure 2b. The important features of the Abarenicola burrow are labelled and the direction of flow of the respiration current which irrigates the burrow is indicated. A clay lamina has developed as a result of fine grained clay particles floating out in suspension in the head shaft irrigation current and then settling on the substrate.

and II; stations A13 and A14). These high rates, ranging between 18-56 ml worm<sup>-1</sup> day<sup>-1</sup>, are a puzzle which remains unsolved. The worms in the eelgrass zone appear to be larger and this may account for the higher rates. It may be that Abarenicola migrates to lower intertidal levels as it gets older and larger as reported for Arenicola marina by Werner (1954a, b). But why do reworking rates decrease so dramatically from an average of 29 ml worm<sup>-1</sup> day<sup>-1</sup> during summer to at most 1 or 2 ml worm<sup>-1</sup> day<sup>-1</sup> during winter, while in the upper sand wave zone rates only decrease slightly or not at all (Tables I and II)? The possibility that another species of Arenicolidae is present should not be ruled out. Of nineteen specimens collected in the vicinity of A13 seventeen proved to be Abarenicola pacifica upon dissection, having between 4 to 6 pairs of esophageal caeca each. However, two specimens had only one large pair of esophageal caeca each, which is diagnostic of the genus Arenicola (Smith and Carlton, 1975). Arenicola marina in the Dutch Wadden Sea demonstrate seasonal variation in reworking rates very comparable to those reported above for the eelgrass zone (26-29 ml worm<sup>-1</sup> day<sup>-1</sup> in summer, av. air temp. 17°C, 2.4 ml worm<sup>-1</sup> day<sup>-1</sup> in winter, av. air temp. 3°C, Cadée, 1976).

The phenomenal rates at which Abarenicola rework sediment in Boundary Bay probably has a considerable influence on the sedimentology and ecology of the tidal flats. The rates of biogenic reworking of up to 1mm per day are far in excess of estimated rates of sedimentation by physical processes. Kellerhals and Murray (1969) estimated a long term sedimentation rate of 0.41 mm year<sup>-1</sup>, based on radio-carbon dating, and a short-term rate of 5 mm year<sup>-1</sup>, based on the thickness of seasonal algal mat laminae. As Swinbanks (1979) has suggested the intense reworking activities of Abarenicola may act to limit the extent of the algal mat zone - one of the five major floral/sedimentological zones of the Boundary Bay tidal flats (Fig. 1). The worms may inhibit the formation of blue-green algal mats by their constant

turnover of surface sediments or through burial of algae by feces.

Abarenicola has the potential of generating biogenic graded bedding and biogenically formed clay laminae through its irrigation activities. In the intertidal environment where the surface is constantly reworked by the inflow and outflow of water, the lamina of clay seen in Figure 2 would probably be washed away as fast as it forms, and using this process Abarenicola could conceivably 'clean' the mud out of a loose mud/sand mixture, creating a better sorted sand. The high degree of sorting of sands in the upper sand wave zone in Boundary Bay (Incl. Graphic Std. Dev. 0.30-0.39  $\phi$ ; Swinbanks, 1979) may at least in part be due to the reworking activities of this worm. This is a quite a separate process from that of rejection of coarse grains during feeding, reported by Hylleberg (1975) for Abarenicola, by Rhoads and Stanley (1965) for Clymenella and by Van Straaten (1952) for Arenicola. But the two processes should produce the same result as they both transport fine grains towards the surface either in the head shaft irrigation current or as feces.

#### ACKNOWLEDGEMENTS

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Part 4A

ENVIRONMENTAL CONTROLS ON THE DISTRIBUTION  
OF THALASSINIDEAN BURROWING SHRIMPS  
ON FRASER DELTA TIDAL FLATS, BRITISH COLUMBIA

A Marine Tidal Flat Between Two Man-Made Causeways  
on Southeastern Roberts Bank

## ABSTRACT

The thalassinidean burrowing shrimps Callianassa californiensis and Upogebia pugettensis are abundant on a sandy tidal flat, which lies between two man-made causeways on the south-eastern tidal flats of the Fraser Delta-front, attaining densities as high as 446 burrow openings  $m^{-2}$ . This tidal flat is 'marine' in character and can be divided into four major floral/sedimentological zones. These are, from the shoreline seawards, the saltmarsh zone, the algal mat zone, the sandflat zone and the eelgrass zone. Thalassinidean burrowing shrimps are most abundant in the sandflat zone.

At high intertidal levels Callianassa distribution is limited by the presence of the saltmarsh, the lower limit of which lies at the lower limit of the upper atmozone, while dense eelgrass cover limits Callianassa distribution at low intertidal levels. The upper limit of the eelgrass zone lies at the upper limit of the lower aquazone. Callianassa are abundant ( $>50$  burrow openings  $m^{-2}$ ) in sediments which range from 5-50% in mud content and from 2.6-4.0  $\phi$  in median grain size.

Upogebia extend up to the base of the upper amphizone (about mean sea level), a level above which the maximum duration of anoxia due to exposure probably exceeds the lethal limit for postmolt Upogebia. Upogebia show a distinct preference for muddy substrates and only attain high densities ( $>20$  burrow openings  $m^{-2}$ ) in sediments containing more than 40% mud. The relationship between percent mud and Upogebia density can be approximated by a straight line, the slope of which is dependent on tidal elevation.

There is some evidence to suggest that Callianassa and Upogebia densities are negatively correlated at tidal elevations where both Upogebia and Callianassa densities have the potential of being high. It is speculated that this may be a consequence of increased mortality amongst postlarval



suspension feeding Upogebia resulting from the surface reworking activities of adult deposit-feeding Callianassa, and/or as a result of predation by the carnivorous planktic larvae of Upogebia on the planktic larvae of Callianassa. It may be that this negative interaction between Upogebia and Callianassa overrides and masks a possible preference on the part of Callianassa for muddy substrates.

Callianassa reworks sediment at the rate of  $18 \pm 9$  ml/shrimp/day.

An estimated 100 million Callianassa on the intercauseway tidal flat rework about 0.2 million cubic metres of sand during the three months of summer.

In the area of their peak density (446 burrow openings  $m^{-2}$ ) Callianassa.

rework the sediment they live in to a depth of 50 cm in about five months.

It is suggested that bioturbation of a shallow subsurface horizon of clayey mud by the deep burrowing of Upogebia has locally increased the mud content of surface sediments on the southeastern side of the sandflat zone, resulting in an anomalous patch of muds within this otherwise sandy zone.

## INTRODUCTION

Thalassinidean burrowing shrimps produce the very distinctive trace fossils Ophiomorpha and Thalassinoides (Weimer and Hoyt, 1964; Frey and Howard, 1975; Pemberton, 1976). The burrows of these shrimps extend deep into the substrate and, as a result, stand very good chances of being preserved as trace fossils in the geological record. Their potential as paleoenvironmental indicators has already been pointed out (Weimer and Hoyt, 1964; Dewindt, 1974), but such potential will remain limited as long as data on the influence of pertinent environmental factors on thalassinidean shrimp distribution is lacking. The primary aim of this paper is to assess the effects of various environmental factors on the distribution of Callianassa californiensis Dana and Upogebia pugettensis (Dana) on a marine tidal flat that lies between two man-made causeways on the southeastern Fraser Delta - the Tsawwassen ferry terminal causeway and the Coalport causeway (Fig. 1). The Coalport causeway has cut off the supply of brackish silt-laden waters from the Fraser River to this tidal flat, and has thus probably enhanced its 'marine' characteristics (Levings and Coustalin, 1975). Because of the relatively stable salinity regime of the tidal flat, the combined effects of tidal elevation, grain size and bio-interactions on thalassinidean shrimp distribution can be systematically broken down into their component effects. Bio-interactions include the effects of floral cover (saltmarsh, algal mats and eelgrass) and any ammensalistic interactions between Upogebia, a suspension feeder, and Callianassa, a deposit feeder. Rhoads and Young (1970) introduced the concept of trophic group ammensalism to describe the negative interaction between deposit feeders and suspension feeders in a subtidal environment, where the unstable bottom created by the reworking activities of deposit feeders were tending to exclude suspension feeding

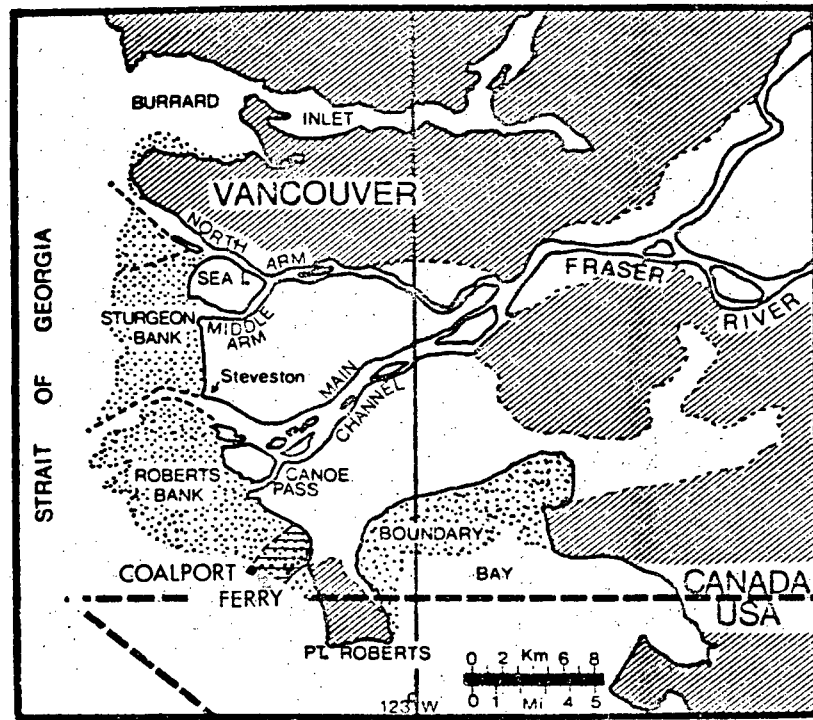


Figure 1. Location of the study area is indicated by horizontal cross-hatching. Tidal flats are stippled, land area of Recent alluvium is blank, and older deposits diagonally cross-hatched. (adapted from Luternauer and Murray, 1973).

organisms. As an essential part of the study of the interactions between Callianassa and Upogebia the rates at which these shrimps rework sediment were measured.

Armed with the information from this tidal flat, in Part 4B the complexities of the environment of central and northern Roberts Bank is tackled, where salinity becomes the overriding factor among the variables influencing thalassinidean shrimp distribution, due to the influx of freshwater from the Fraser River. The environment of Roberts Bank divides naturally into a brackish environment to the northeast, and a marine environment to the southeast and it was felt appropriate to split Parts 4A and B in this way.

The presence of Callianassa californiensis on the active tidal flats of the Fraser Delta was first reported by Bawden et al. (1973) and Luternauer and Murray (1973) and again by Levings and Coustalin (1975). The distribution of Callianassa and Upogebia in Boundary Bay on the inactive southern flank of the Fraser Delta (Fig. 1) has been described qualitatively (Kellerhals and Murray, 1969; O'Connell, 1975) and quantitatively (Swinbanks, 1979). Thalassinidean burrowing shrimps are frustrating organisms to study because they prove so difficult to catch, as others have noted (Risk et al., 1978). With experience one is quickly able to recognize the very characteristic burrows, burrow entrances, mounds, fecal pellets and discarded exoskeletons (exuviae) of these shrimps. Callianassa burrows usually have two entrances to each system although occasionally they may have three and rarely four openings, while Upogebia burrows usually have two (Thompson, 1972; Swinbanks, 1979). Thus, one can quantitatively assess the distribution of the shrimps by counting burrow entrances at the surface rather than catching the shrimps themselves. It would be more desirable to obtain direct shrimp counts and shrimp biomass data, but to do so would have severely limited the geographical

extent of this survey.

A number of studies of Callinassa californiensis and Upogebia pugettensis have been made by biologists. MacGinitie (1930, 1934) recounts in vivid detail the burrowing, feeding, reproduction and day-to-day lifestyles of both shrimps. MacGinitie and MacGinitie (1968) list nine commensal organisms, including pea-crabs, amphipods, bivalves, goby fish and polychaetes, which use the burrows of Callinassa as a protective haven or as a sediment-water interface on which to feed. L. Thompson and Pritchard (1969) have carried out physiological studies on the osmoregulatory capacities of both C. californiensis and U. pugettensis as have Torres et al. (1977). R. Thompson and Pritchard (1969) have studied anoxia tolerance in both shrimps. Thompson (1972) has studied U. pugettensis in detail for a doctoral thesis.

#### METHODS

Three transects, A, B and C, were established perpendicular to the shoreline on the inter-causeway tidal flat (Fig. 2) in June and July, 1977. In addition to these, two transects, D and E, were established between transects A and B roughly parallel to the shoreline, because qualitative observations indicated that lateral changes in grain size were pronounced in this region. Stations were taped at 100 m intervals on the transects and marked by wooden stakes. The elevations of all stations on transects A, B and C were determined by surveying from three bench marks which lay close to the ends of each line (Fig. 2). Elevations at stations were determined by standard leveling techniques using a T2 transit (Scientific Instruments Ltd., Ottawa, Ontario), which is capable of determining elevation differences to an accuracy of 5 mm over a distance of 200 m (the maximum sighting distance employed). A cross survey between transects A and B

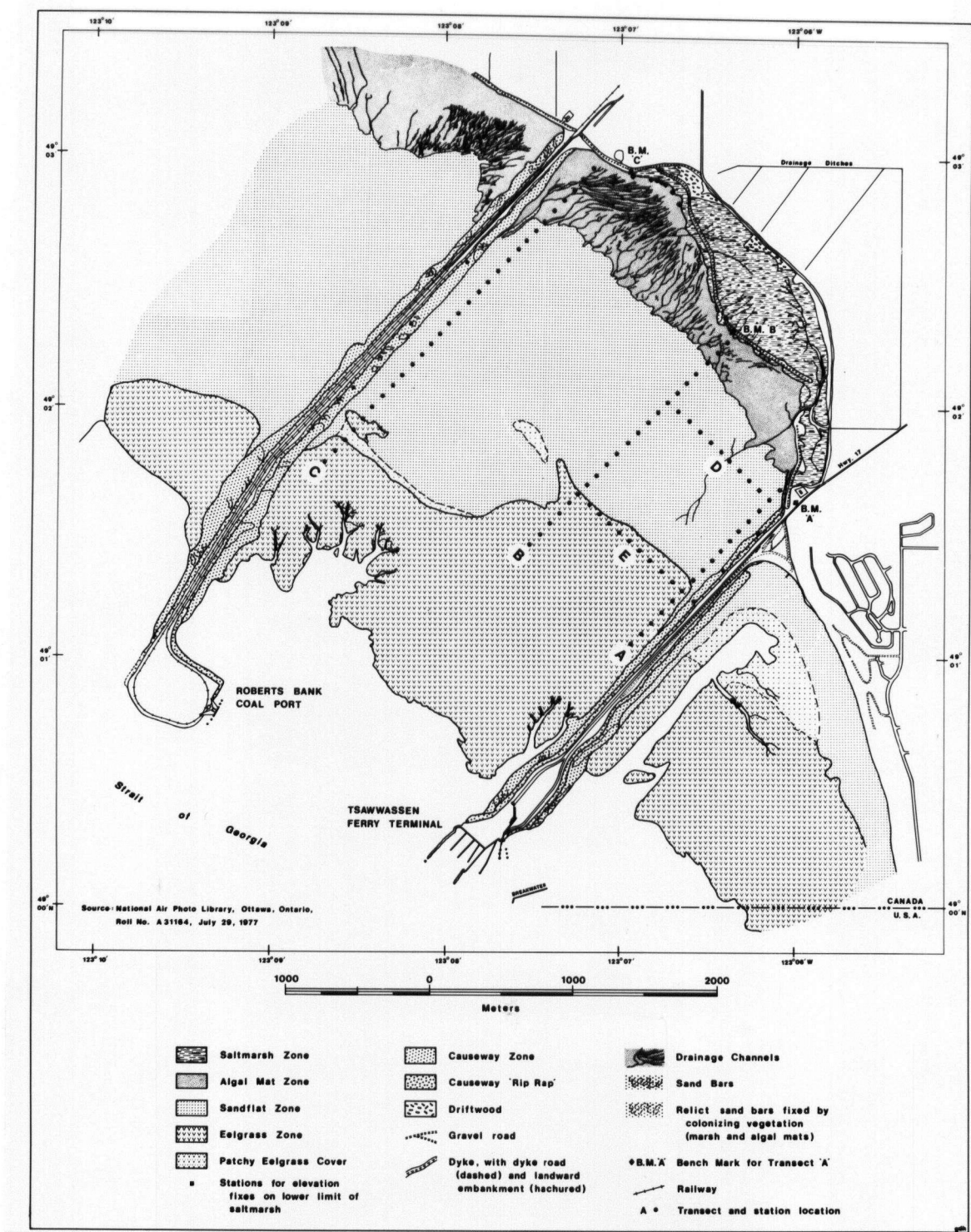


Figure 2. The floral/sedimentological zones of the inter-causeway tidal flat with the locations of transects, stations and bench marks indicated.

was made along transect D, tying bench mark B (Fig. 2) to bench mark A by surveying over a distance of approximately 2 km. The discrepancy between the expected elevation for the bench mark A and the observed elevation was 6 cm (observed 6 cm higher than expected). This gives an estimate of the accuracy of the surveying technique over a typical transect length, and provided elevation data for transect D. A further check of the survey data using observed tidal heights at Tsawwassen indicates that the data is accurate to about  $\pm 4$  cm (range 0.2-9.4 cm, N=19, Appendix 3). Transect E was not surveyed because observations indicated that it lay almost parallel to the waterline and the stations on the transect were therefore of very similar elevation. The survey results confirm this conclusion as the elevations of stations B16 and A11 at either end of transect B/A only differ in elevation by  $13 \pm 2.5$  cm. In addition to the transects mentioned above six stations were established adjacent to the causeways 20 m from the edge of the 'rip rap,' (Fig. 2). They were not surveyed.

At all stations shrimp burrow opening densities were determined by sampling eight times at each station with a  $0.25 \text{ m}^2$  quadrat. Upogebia burrows were easily distinguished from those of Callinassa, because of their firm mud lining, lack of constricted apertural necks, and distinctive geometry (Swinbanks, 1979). Surface grain size samples were obtained at all stations using a 2 cm deep rectangular box, and surface substrate salinities were recorded at low tide using a refractometer (Endeco type 102). Twenty-one substrate salinity profiles were taken on transects A, B and C sampling at 2.5 cm, 5 cm, 7.5 cm, 10 cm, 15 cm and 45 cm over the period July 1-7, 1977, using a sampler which draws interstitial waters from these depths (Appendix 5). Fortunately, because of the sandy nature of the substrate, interstitial waters were clear and salinity could be measured directly with a refractometer.

In order to determine the rate at which the shrimps turnover sediment,

protected enclosures were constructed and placed around a number of burrow openings (usually about 10) in order to prevent currents from washing away the mounds which accumulate outside the burrow entrances. The enclosures consisted of open ended metal boxes 50 x 50 x 50 cm. They were pushed about 10 cm into the substrate. Twelve holes (5 mm diameter) placed around the box at the level of the sediment-water interface allowed easy inflow and outflow of water and prevented 'geysers' from forming on flood tide. A layer of gravel was used to mark the initial level of the sediment-water interface. Preliminary tests indicated that the boxes could only be left in for one tidal cycle (25 hours), because, if wave action at the beginning of flood tide was significant (>10 cm amplitude) waves breaking over the box would redistribute the accumulated mounds to the sides of the enclosure and on the subsequent ebb tide sand would drain out of the boxes. For this reason the boxes were emplaced just before the flooding waterline reached the station and data was collected the following day, if undisturbed mounds were found within the box (i.e., there had been no significant wave action at the late stages of ebb).

In the laboratory, grain size samples were washed free of salt, wet sieved through a 63  $\mu\text{m}$  sieve to extract the silt/clay fraction and dry sieved at 0.5  $\phi$  intervals. Approximately 10 g of sample was used.

The distinctive floral/sedimentological zones of the inter-causeway tidal flat were mapped using low level colour aerial photographs (scale 1:12,000) of July 29, 1977 (A31164, National Air Photo Library, Ottawa, Canada). Detailed descriptions of these zones are included in this paper because it is essential to place the thalassinidean shrimp distribution data within the overall zonal framework of the tidal flat, as the two are intimately inter-related.



## THE INTER-CAUSEWAY TIDAL FLAT

The first study of animal-sediment relationships carried out on the inter-causeway tidal flat was that of Levings and Coustalin (1975). They made extensive baseline studies on all the tidal flats of the Fraser Delta-front, concentrating on the near surface benthic organisms (sampling depth 2 cm). Their results demonstrated that the number of species of organisms on this tidal flat is the highest for the whole delta-front; cumaceans were recorded at almost all stations. Both indicate that marine influences are prominent over the entire tidal flat (Levings and Coustalin, 1975). The Canadian National Harbours Board has recently proposed to expand the Coalport, and an environmental impact study has been carried out (Beak-Hinton, 1977). The report includes detailed maps and descriptions of the eelgrass bed and saltmarsh on this tidal flat. Hillaby and Barrett (1976) have also studied and mapped the saltmarsh. R. Moody (1978) studied an eelgrass bed on the southern side of the ferry causeway. His study included monthly monitoring of salinity and turbidity levels adjacent to the eelgrass bed.

### Floral/Sedimentological Zones

Field observations and aerial photographs of the inter-causeway tidal flat reveal four major floral/sedimentological zones which can be recognized on the basis of their distinctive floral cover and/or drainage and sediment characteristics (Fig. 2). These are, from the shoreline seawards, the salt-marsh zone, the algal mat zone, the sandflat zone and the eelgrass zone. There are also two distinctive zones of minor areal extent, which parallel the two causeways, here called the 'causeway zones' (Fig. 2). The sediments

in the causeway zones are coarser and contain less mud than the adjacent tidal flat, sand bars are present, the beach profile is much steeper than elsewhere, and, at the seaward end of the causeways, these zones lack any eelgrass cover, despite lying at elevations which could be colonized by eelgrass. The sediments of the causeway zones have in part been derived from sand fill during causeway construction. Shoreward of the causeway zones a narrow strip of 'rip rap' parallels each causeway.

Figure 3 presents the elevational limits of the four major floral/sedimentological zones with respect to Geodetic Datum and with respect to the average exposure zone limits for observed tides between 1968-1978 at the Tsawwassen tide gauge. Swinbanks (1979) advocates the subdivision of the intertidal region into exposure zones on the basis of critical tidal levels at which the maximum duration of exposure or submergence changes abruptly in a step-like fashion. Exposure zone terminology (atmozone, amphizone, aquazone) has been introduced and defined elsewhere (Swinbanks, 1979). The elevation of the saltmarsh/algal mat zone boundary was determined at 7 locations (Fig. 2), where the marsh showed signs of prograding (i.e., clumps forming seaward of the marsh and no evidence of erosion). The upper limit of the algal mat zone lies at  $+0.88 \pm 0.04$  m (range 0.83-0.92 m, N=7) Geodetic Datum, which is 13 cm lower than in Boundary Bay (Swinbanks, 1979) (Fig. 1). The saltmarsh plants grow on mounds and plateaus which are elevated about 20 cm above this level, and thus the lower limit of the saltmarsh lies at  $+1.07$  m (range 1.066-1.071 m, N=2) Geodetic Datum, which is almost identical in elevation to the lower limit of the saltmarsh in Boundary Bay ( $+1.12$  m Geodetic Datum, Swinbanks, 1979), and as in Boundary Bay, lies very close to the lower limit of the upper atmozone (Fig. 3), which has lain at  $+1.23 \pm 0.08$  m (range 1.04-1.38 m) Geodetic Datum for the past ten years at Tsawwassen (Swinbanks, 1979). This is the tidal elevation at which the maximum duration

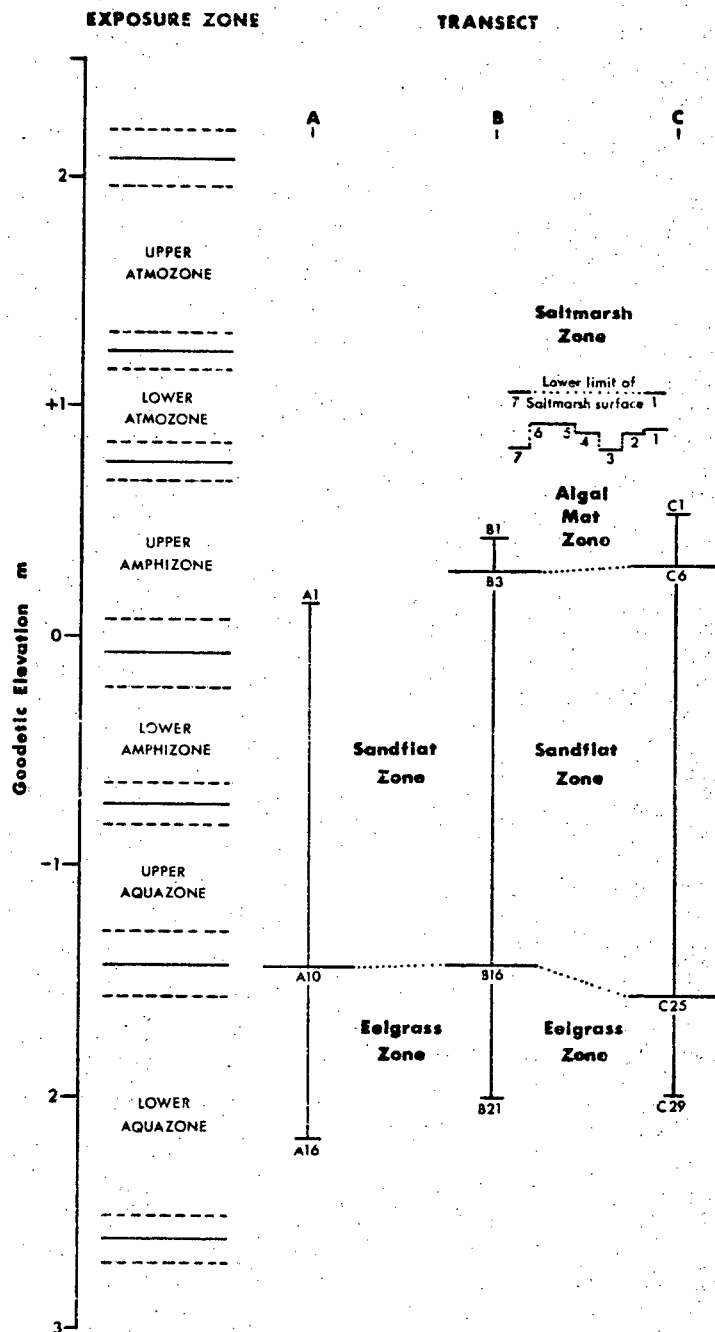
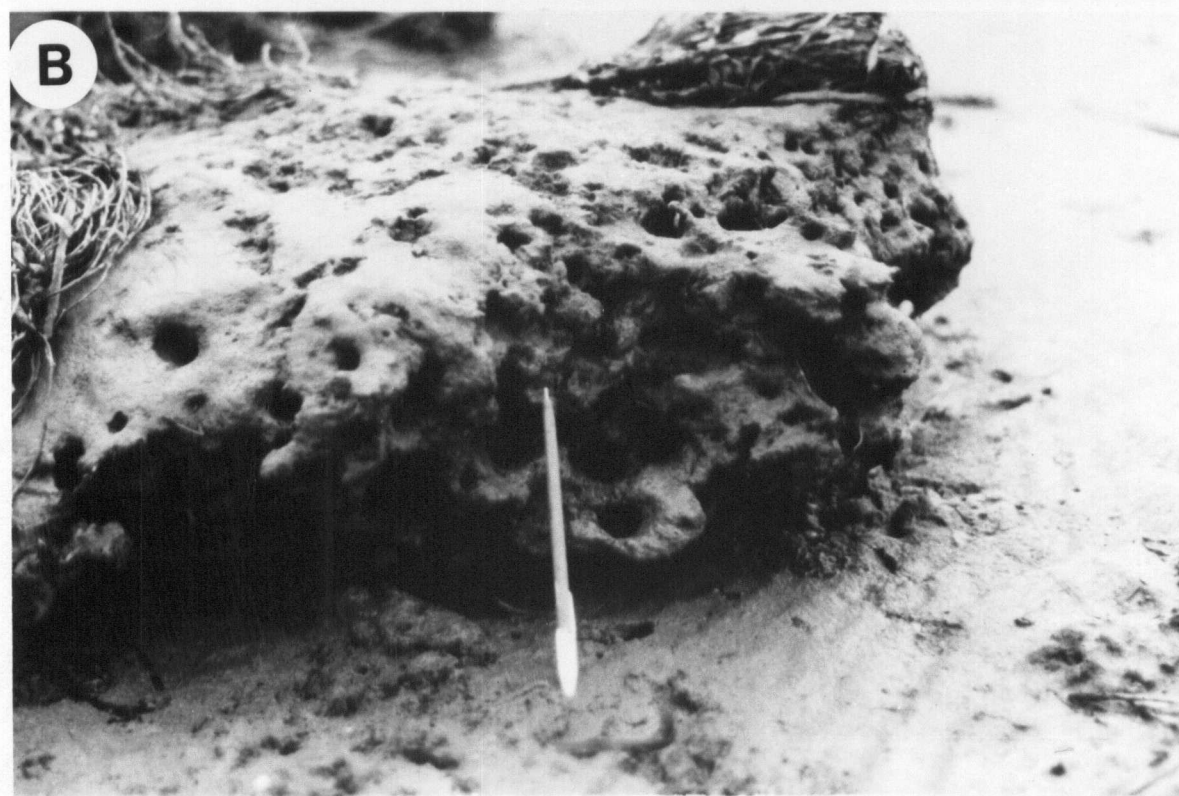
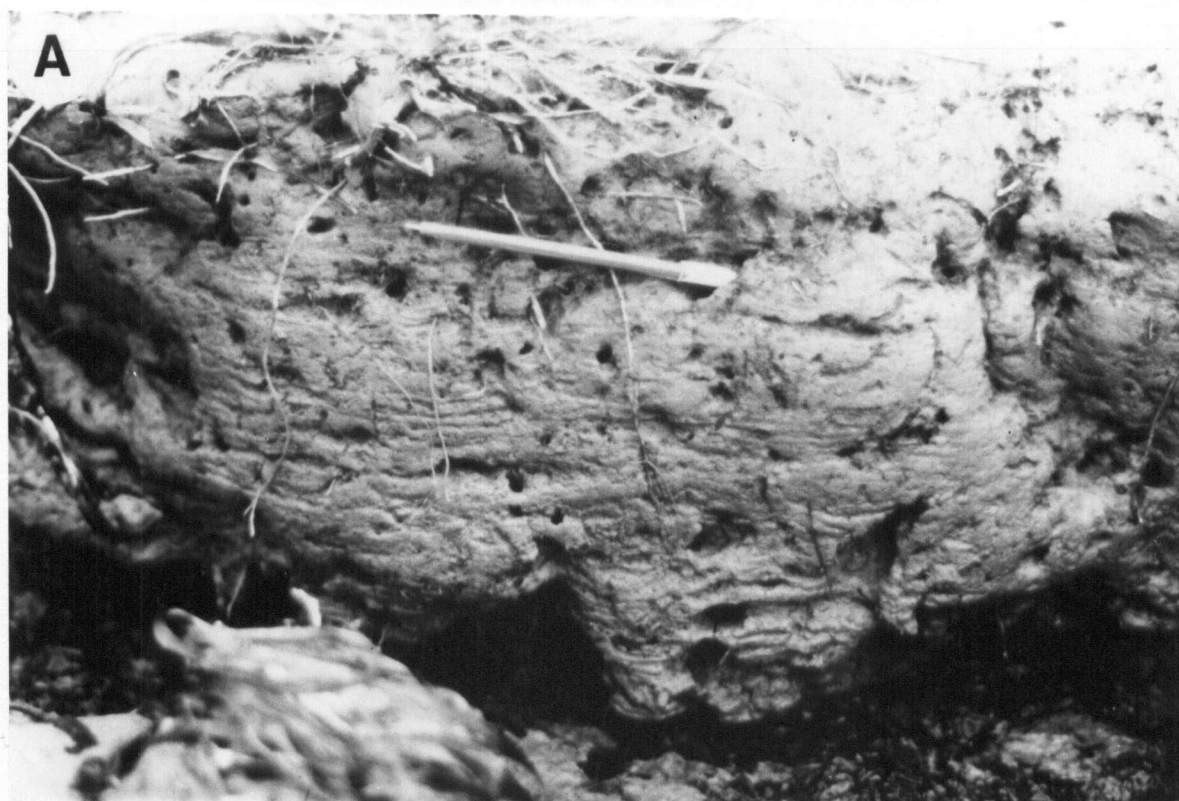


Figure 3. The elevational limits of the four major floral/sedimentological zones on the inter-causeway tidal flat with respect to Geodetic Datum and the average exposure zone limits for observed tides between 1968-78 at the Tsawwassen tidal gauge (source: Swinbanks, 1979). The dotted envelopes indicate one standard deviation from the mean level of the exposure zone boundary. The exposure zone limits for the lower aquazone are based on only two years of records (1976-78) because these boundaries are significantly modulated by an 18.6 year declinational cycle in the moon (Swinbanks, 1979). The elevation of the saltmarsh/algal mat zone boundary was determined at seven points between transects B and C (Fig. 2).

of exposure jumps from about 10 to 20 days (Swinbanks, 1979). The saltmarsh is characterized by a dense growth of halophytic vegetation with Triglochin maritima and Salicornia virginica dominating in the lower regions (Beak-Hinton, 1977). The saltmarsh is dissected by deeply incised tidal channels 1-2 m deep, which have remained stable in position for decades (Beak-Hinton, 1977). The sediments of the saltmarsh consist of laminated silts riddled with rootlets (Figs. 4a, 4b).

The algal mat zone is lower atmozonal to upper amphizonal in exposure and extends down to about +0.30 m Geodetic Datum (Fig. 3), thus attaining a lower elevation than in Boundary Bay, where the algal mat zone is restricted to lower atmozonal elevations (Swinbanks, 1979). The sediments within the zone are muds or muddy sands. Mud contents decrease rapidly seaward from about 90% to 20% (Fig. 5). The zone is dissected by an extremely dense network of dendritic tidal channels which drain water from the impermeable muds (Fig. 6a). The channels terminate abruptly at the lower limit of the zone. They are up to 1 m in depth and are lined with sand and shell deposits (valves of Mya arenaria, many still in growth position). Blue-green algal mats (mainly Phormidium sp. with minor Oscillatoria sp. and Spirulina sp.) bloom in summer on the plateaus between the channels. The algal mats in the upper half of the zone become extensively cracked in summer and the algal mats blister and curl (Fig. 6b). Crabs (Hemigrapsus oregonensis) infest the cracks and undermine the algal mats to such an extent that algal mat 'cakes' can be peeled from the substrate (Fig. 6c); Hemigrapsus burrows up into the algal mat cakes from below (Figs. 6c, 6d). In winter a film of mud and very fine sand washed in by winter storms buries the algal mats and fills the cracks and crab burrows. Thus, the plateaus between tidal channels consist of finely laminated sediments with black organic rich laminae and mud laminae cross-cut by casts of cracks and crab burrows (Fig. 6d). Tidal pools are

- Figure 4. a) Laminated silts of the saltmarsh. The coarser laminae stand out in relief. Pen is 15 cm long.
- b) The weathered surface of the saltmarsh reveals that the saltmarsh deposits are riddled with rootlets, which have weathered out as holes here. Pen is 15 cm long.



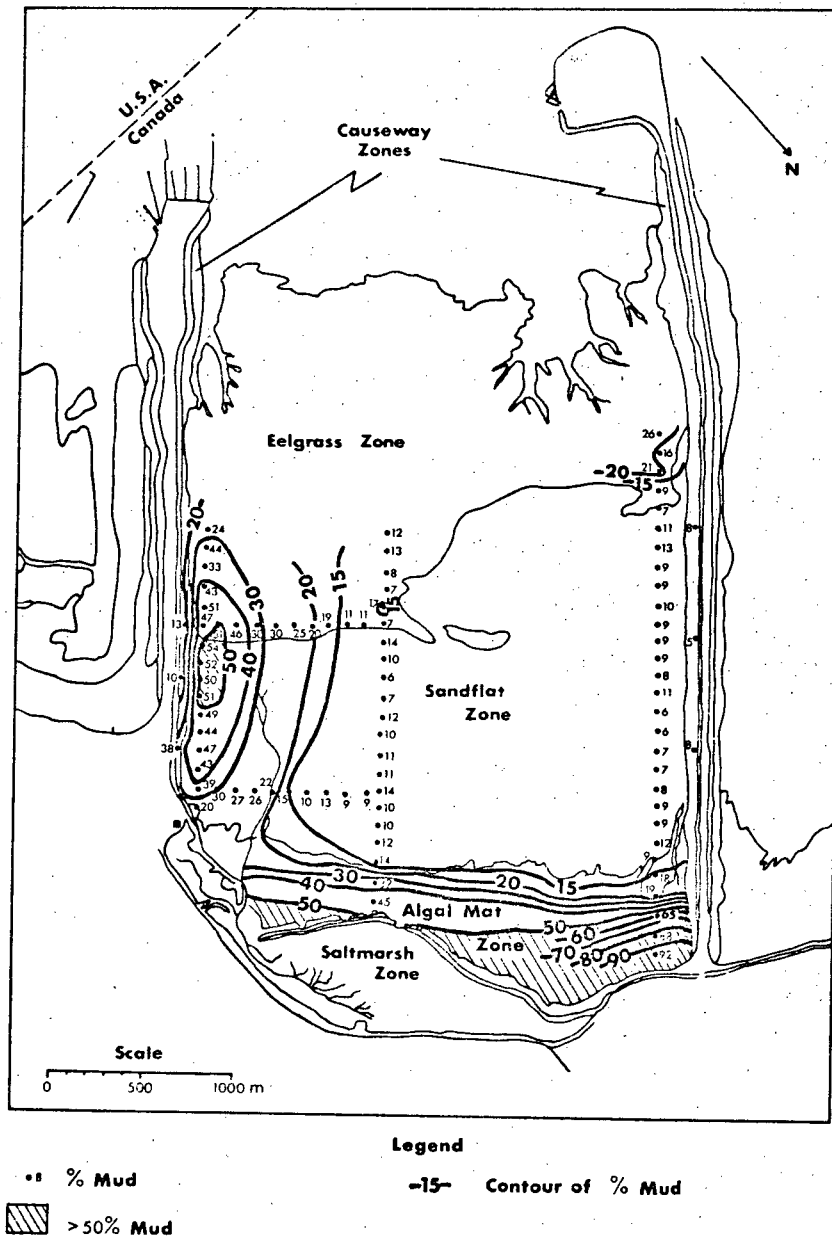
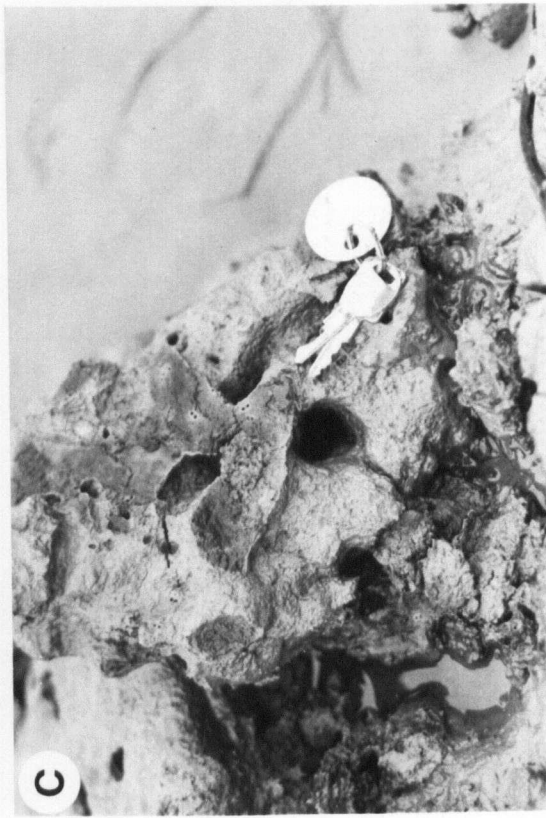


Figure 5. The mud contents of surface sediments. Numbers next to stations indicate the percent mud at each station. The general trends of the contours between transects have been determined by qualitative field observations.

- Figure 6. a) The algal mat zone. The channel in the foreground is about one meter wide. Taken on flood tide, just as the channels are beginning to fill. Mudcracked plateaus lie between the channels, and water-filled depressions are present on the plateaus.
- b) Mudcracked surface of the algal mat zone. The algal mats blister and curl under the effects of desiccation, and cracking produces isolated 'algal mat cakes.'
- c) Undersurface of an 'algal mat cake,' riddled by crab burrows.
- d) Laminated sediments of an algal mat cake, cross-cut by a crab burrow (Hemigrapsus oregonensis).





present in depressions on the plateaus. Filamentous green algae (mainly Rhizoclonium sp. with minor Enteromorpha sp.) bloom around the moist edges of the pools in summer, while the polychaete worms Abarenicola pacifica and Spio sp. are abundant in the pools - Swinbanks (1979) provides descriptions of the burrows of these worms. Whereas the algal mats are firm and easy to walk on, the tidal pools are underlain by soft dilatant muds. In the lower algal mat zone blue-green algal mats become patchy in distribution, and the dominant algal form is a brown film of diatoms (Plurosigma sp., Gyrosigma sp., Navicula sp. and Nitzschia sp.).

The sandflat zone is predominantly lower amphizonal to upper aquazonal in exposure (Fig. 3). As the name implies, the zone is flat, lacking in tidal channels and dominated by very fine to fine sands, although a small area of muds is present in the middle of transect A (Fig. 5). The zone generally lacks any floral cover although a patch of Zostera americana (dwarf eelgrass) is present between stations C11 and C17 and smaller patches are present elsewhere. The characteristic feature of this zone is the very high density of thalassinidean burrowing shrimps which it supports. Unlike the zones of non-vegetated sand in Boundary Bay (Swinbanks, 1979), this zone lacks sand wave bedforms.

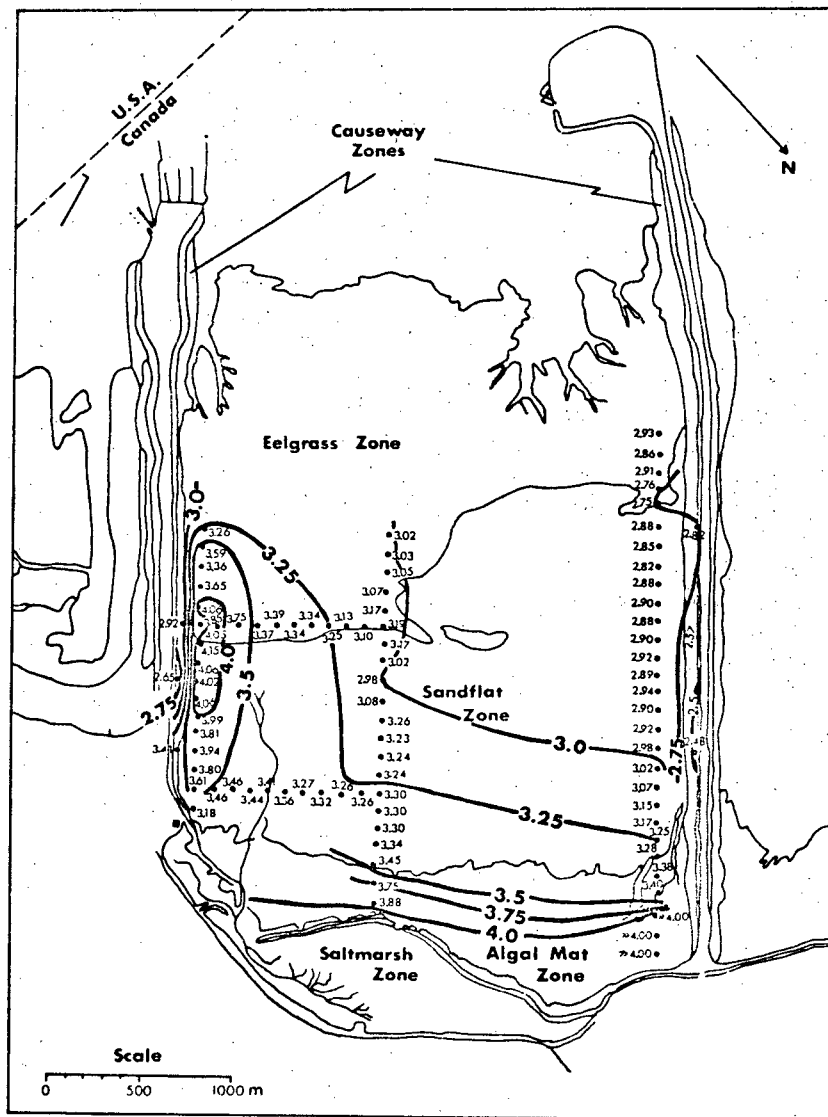
The eelgrass zone is exclusively lower aquazonal in exposure. Its upper limit terminates at the upper limit of the lower aquazone at about -1.5 m Geodetic Datum (Fig. 3), a level below which the maximum duration of submergence begins to increase abruptly by a series of steps, the first being a jump from about 10 to 20 days of continuous submergence (Swinbanks, 1979). The eelgrass consists entirely of the larger species Zostera marina. Z. marina beds attain higher elevations (up to -0.5 m Geodetic Datum) in Boundary Bay by extending as fingers up the broad depressions of tidal channels which remain water-filled during low tide (Swinbanks, 1979). The

upper limit of the eelgrass bed studied by Moody (1978) on the southern side of the ferry causeway is bounded by a 'causeway zone.' Moody (1978) reported an anomalously low elevation for the upper limit of the eelgrass bed in his study area (-2.10 m Geodetic Datum; +0.85 m Tsawwassen Chart Datum; Moody, 1978). The sediments within the eelgrass zone are fine sands on transects B and C and very fine sands and muds on transect A (Fig. 7). On the Coalport side of the tidal flat the eelgrass zone is currently being eroded by a dendritic drainage channel system, which extends from the head of a borrow pit dredged during construction of the Coalport in 1969 (Beak-Hinton, 1977). Since Coalport construction, the eelgrass zone has been advancing shorewards at the rate of about  $25 \text{ m yr}^{-1}$  (Beak-Hinton, 1977), but there is no historical data on the density of eelgrass cover.

#### Grain Size of Surface Sediments

The general grain size characteristics of each zone seaward of the saltmarsh have already been described. Grain size coarsens seawards on transects B and C (Fig. 7), which is a typical characteristic of tidal flats (Klein, 1971). The steepest gradient in grain size occurs from upper amphizonal elevations upwards; i.e., above about mean sea level (just below the lower limit of the algal mat zone) much as reported by Swinbanks (1979) for Boundary Bay. Transect A does not follow this trend and a puzzling patch of mud is present in the middle of the transect. The six samples taken from the two 'causeway zones' illustrate the anomalous nature of these zones, as the sediments have coarser median grain sizes and/or lower mud contents than the immediately adjacent tidal flats (Figs. 5, 7).

Box cores revealed little evidence of stratification except that already mentioned in the algal mat zone. However, on transect C in the eelgrass zone,



### Legend

-3.5- Contour of Median Grain Size φ

Figure 7. The median grain size (φ) of surface sediments. The numbers next to stations indicate median grain size (φ) at each station.

black organic rich sediments were underlain at a few centimeters depth by clean, light coloured sands probably indicating the recent landward encroachment of the eelgrass zone (Beak-Hinton, 1977). On transect A stations A1 to A4 are underlain at about 30-40 cm depth by a thin peat horizon which in turn is underlain by blue-grey clayey muds. Beyond station A4 the peat horizon was not detected, but instead the surficial muddy sands or muds were directly underlain at about 40 cm depth by the blue-grey clayey muds. This blue-grey clayey mud horizon was traced as far seawards as A7.

### Salinity and Turbidity

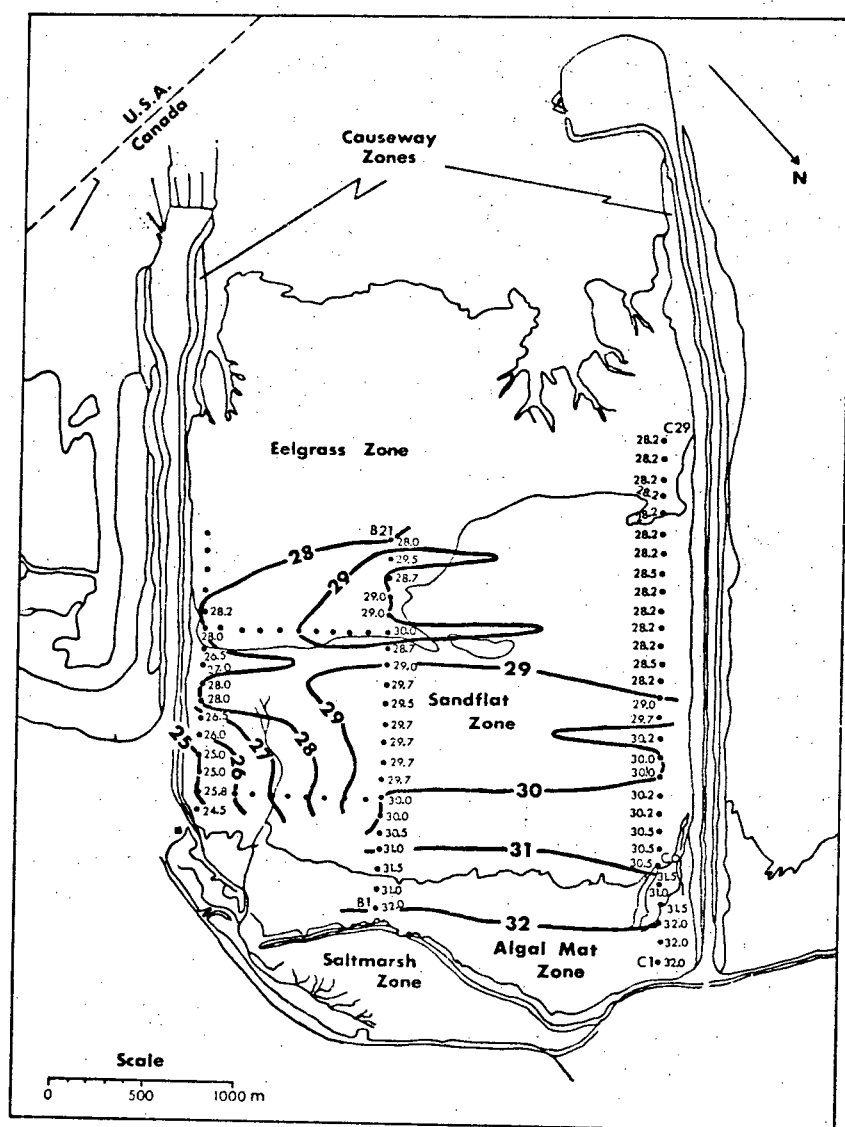
Aerial photographs clearly indicate that the Coalport causeway deflects the turbid, silt-laden waters of the Fraser plume away from this tidal flat and the inter-causeway waters are now clearer than they were (e.g., A37170-39 National Air Photo Library, Ottawa, Canada). R. Moody (1978) has monitored the salinity of surface waters immediately south of the ferry terminal causeway on a monthly, bi-monthly and diurnal basis over a 10-month period. On 18 out of the 20 days sampled surface water salinities were greater than or equal to 20‰ (range 20-28‰). On two days, one in August the other in October, salinity dropped to between 14 and 15.5‰ (Moody, 1978). Moody (1978) has demonstrated that the turbidity of surface waters increases during the summer months when the Fraser is in freshet, as indicated by a decrease in secchi disc depth from about 5 m in winter to 2 m in summer (May-September). Levings and Coustalin (1975) took three surface substrate salinity measurements in the inter-causeway area in February, 1974. Their values ranged between 26.5‰ and 27‰.

Surface substrate salinities were monitored over the period July 1-7, 1977 at 64 stations on transects A, B, C and D, and on August 13, 1977 surface

substrate salinities were measured at all 67 stations on transects A, B and C in a three-hour period. Values ranged between 22 and 32‰ (Appendix 5 ). Results for August 13 are typical (Fig. 8). The results show little lateral variability in salinity over the tidal flat apart from a slight increase in salinity shorewards, probably due to evaporation (e.g., the salinity of surface waters at C6 increased ~~from 30.5‰ to 31.5‰ over the three-hour sampling interval~~). Anomalously low salinities were recorded in the vicinity of station A2. This is possibly a result of groundwater seepage from the shore along the impermeable peat and mud horizon previously mentioned. A substrate salinity profile taken at station A2 detected low salinity water (10‰) associated with this horizon (Appendix 5 ). Twenty-two substrate salinity profiles taken on transects A, B and C were almost all isohaline (Appendix 5 ). Figure 9 shows a typical example. On June 8, 1978 three salinity profiles of the water column, taken in the inter-causeway area at high tide, were virtually isohaline with salinities between 22-24‰. (Part 4B).

#### DISTRIBUTION OF THALASSINIDEAN SHRIMPS

Thalassinidean shrimp burrows dominate the sandflat zone (Figs. 10, 11). Callianassa are abundant throughout the zone (Fig. 10) while Upogebia only attain high densities ( $>20$  burrow openings  $m^{-2}$ ) in the muddy sediments on the ferry terminal side of the sandflat zone (Fig. 11). Callianassa attain a maximum density of  $172 \pm 22$  burrow openings  $m^{-2}$  (equivalent to about 70 shrimps  $m^{-2}$ ) in the sandflat zone. However, the highest densities of Callianassa were recorded in the narrow 'causeway zone' next to the ferry terminal, where burrow opening densities attain  $446 \pm 31 m^{-2}$  (equivalent to about 180 shrimps  $m^{-2}$ ). The presence of the saltmarsh limits Callianassa distribution at upper intertidal levels. Callianassa densities are low in the algal mat



Legend		Sampling Times
-32-	Contour of substrate salinity ‰	C6 - C29 1130 - 1200
• 29.0	Transect station with salinity measurement indicated ‰	B21 - B1 1225 - 1305
		A12 - A1 1320 - 1350
		C6 - C1 1415 - 1425

Figure 8. Surface substrate salinities as measured on transects A, B and C August 13, 1977 at low tide between 11:30 and 14:25 in the order indicated. Numbers next to stations indicate salinity.

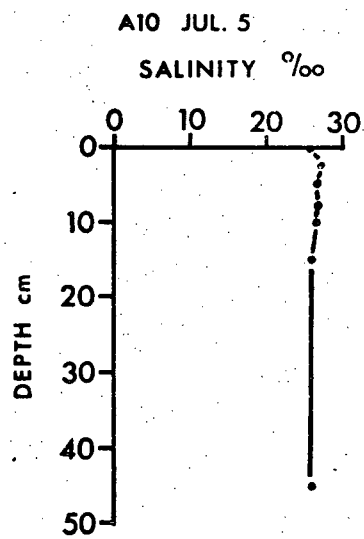
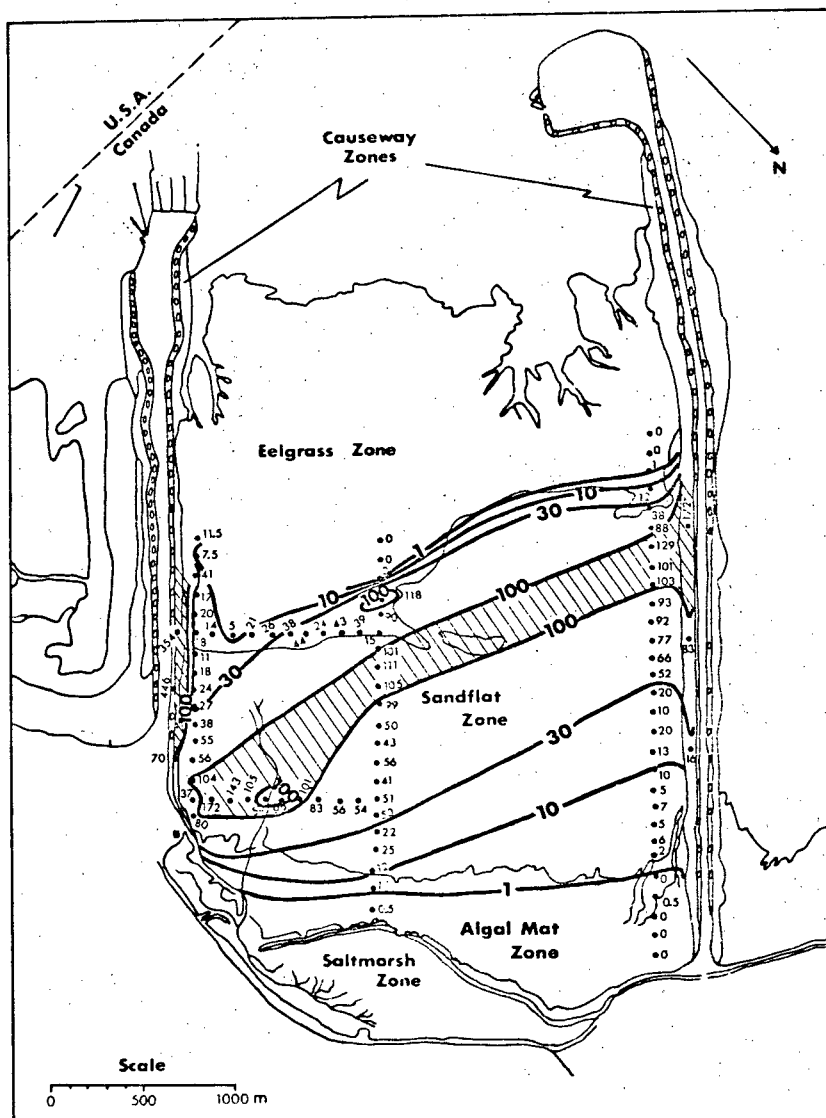


Figure 9. Typical substrate salinity profile from the inter-causeway area.





#### Legend

- 10- Contour of burrow opening density  $m^{-2}$  for *Callianassa*
- $>100 m^{-2}$
- Causeway 'Rip Rap'

Figure 10. Distribution of *Callianassa* burrow openings in contoured map form. General trends of contours between transects determined by qualitative field observation.

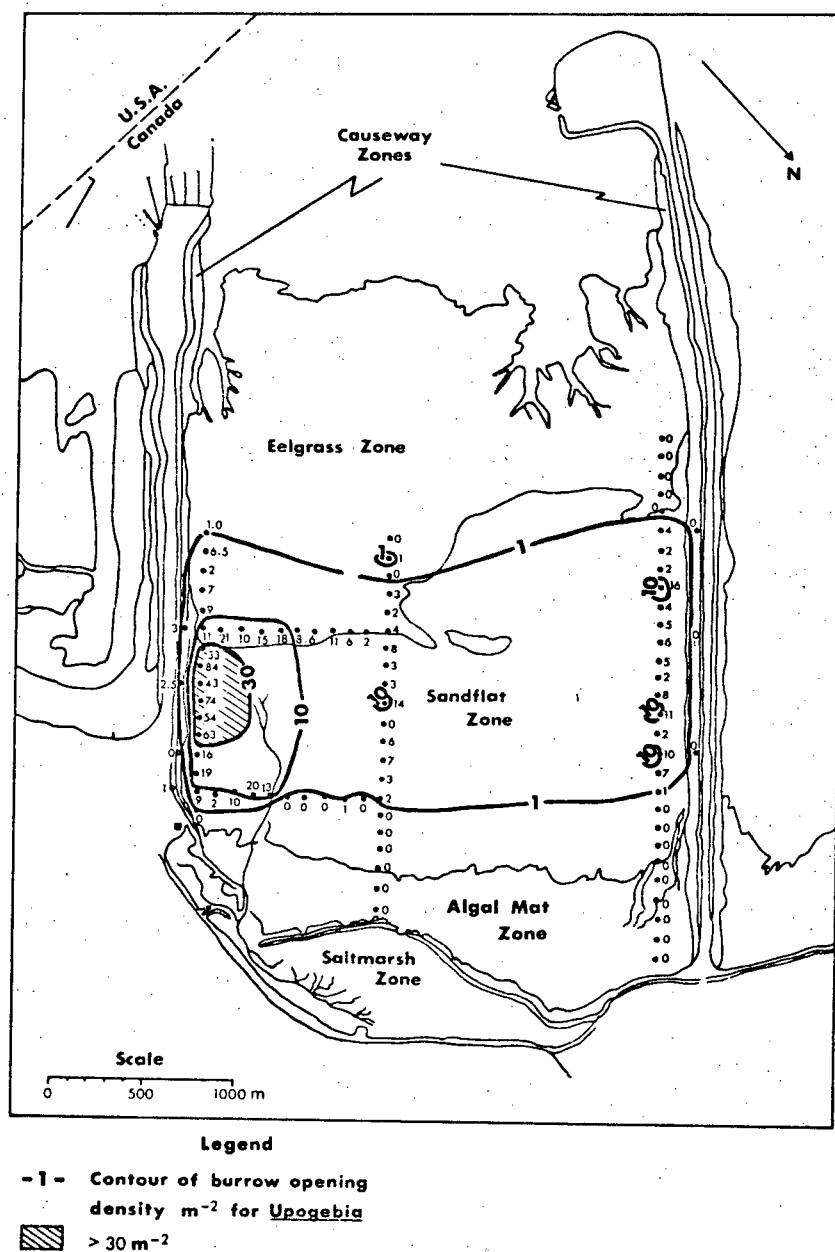


Figure 11. Distribution of *Upogebia* burrow openings in contoured map form.

zone. At low intertidal levels Callianassa densities decrease dramatically on transects B and C where eelgrass forms a dense and continuous mat (Fig. 10).

Upogebia has not been observed in the algal mat zone. Upogebia attains its highest elevations on transect A extending up to the base of the upper amphizone (about mean sea level).

A comparison of Figure 5, showing mud distribution, with Figure 11, showing the distribution of Upogebia, clearly demonstrates a preference on the part of Upogebia for mud. This has been pointed out qualitatively by biologists many times in the past (Stevens, 1928; MacGinitie, 1930; L. Thompson and Pritchard, 1969; Thompson, 1972, for U. pugettensis; Ott et al., 1976, for U. litoralis). In the following section the relationship will be analyzed quantitatively.

#### Influence of Grain Size on Thalassinidean Shrimp Distribution

The inter-causeway tidal flat forms an almost ideal environment in which to study the relationship between grain size and thalassinidean shrimp distribution because: (1) Lateral variations in salinity and turbidity have been reduced to a minimum by causeway construction. (2) The tidal flat shows considerable variation in grain size parameters in a direction parallel to the shoreline, enabling comparison of stations of similar elevation but different grain size. (3) Thalassinidean shrimp densities are high, thus allowing easy resolution of trends.

Upogebia--Figure 12a compares the density of Upogebia burrow openings with median grain size and Figure 12b with mud content, regardless of station elevation. It is apparent that high densities ( $>20 \text{ m}^{-2}$ ) of Upogebia are associated with the finer grained sediments (median  $>3.8 \phi$ ) containing more

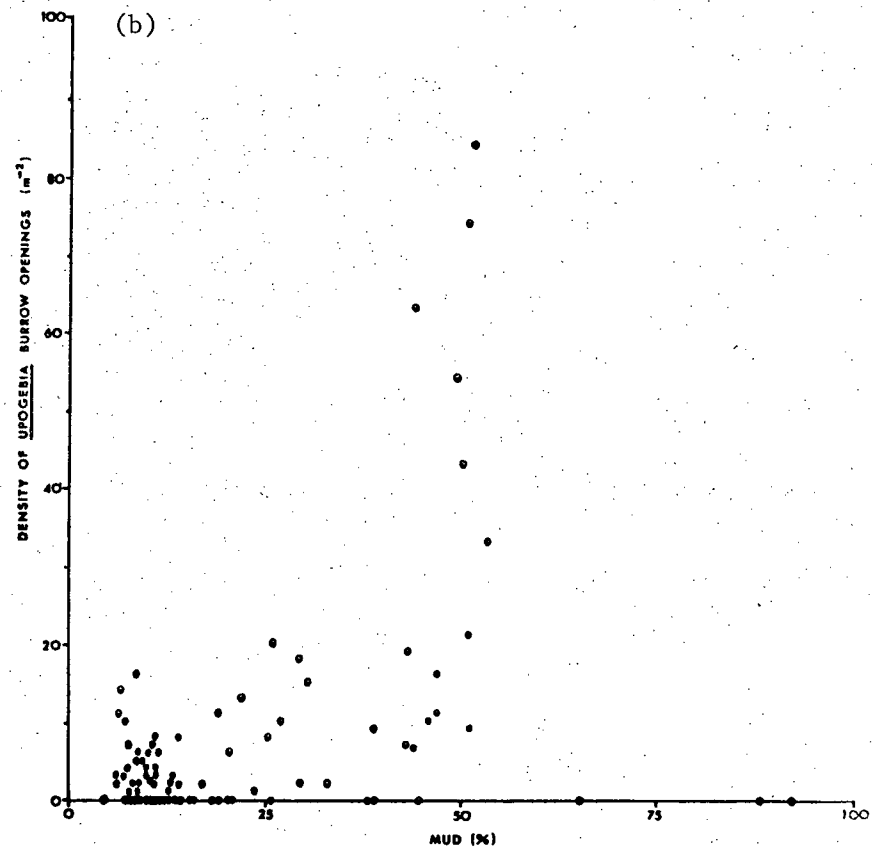
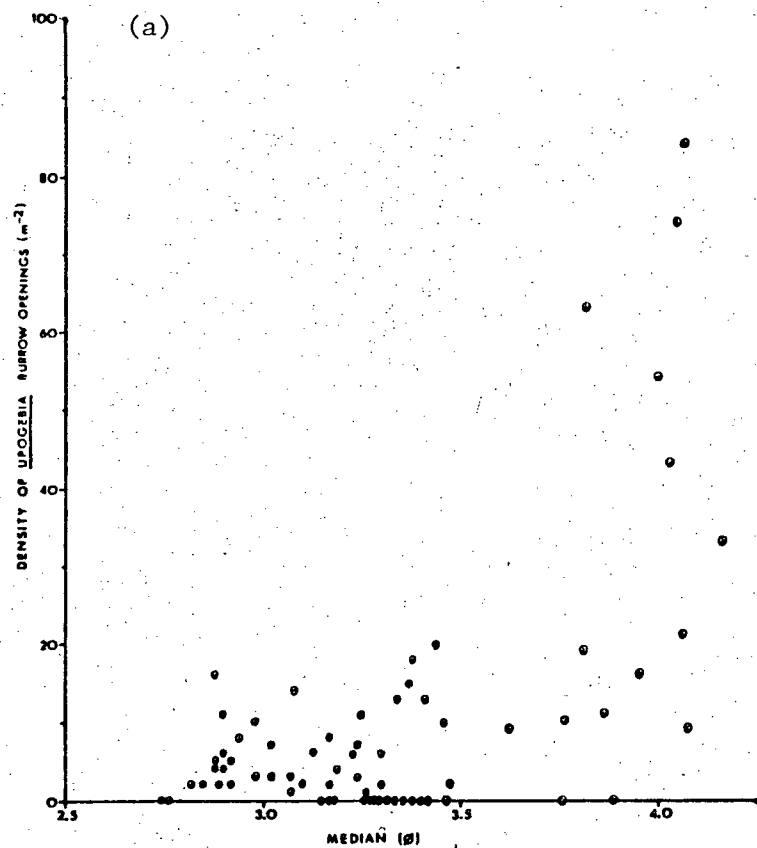


Figure 12. a) Density of *Upogebia* burrow openings vs median grain size ( $\phi$ ), regardless of elevation.  
 b) Density of *Upogebia* burrow openings vs mud content (%), regardless of elevation.

than about 40% mud. However, Upogebia density is also a function of elevation, and this obscures the trends in Figure 12. To overcome this problem the stations were classed into 0.25 m elevation class intervals from -2.20 m to +0.05 m (Geodetic Datum). The results for mud content are presented in Figure 13. Very similar results were obtained for median grain size (Appendix 6). For all class intervals higher densities of Upogebia occur in the muddier finer grained sediments. The trend can be approximated by a straight line, the slope of which is dependent on elevation. The slope of the line is minimized at the upper and lower limits of Upogebia's distribution, and maximized at the elevations of highest Upogebia density. Correlation coefficients are quite high, many exceeding 0.9 and 13 out of 18 are significant at the 95% confidence level (r test).

Callianassa--A similar analysis of the data for Callianassa was carried out. For unclassified data no trends are apparent. Callianassa attains high densities ( $>50$  burrow openings  $m^{-2}$ ) in sediments which range in median grain size from 2.57  $\phi$  to 3.94  $\phi$ , and in mud content from 4.5% to 47% (Appendix 6). On breaking the data down into 0.25 m elevation class intervals no consistent correlation can be discerned. Figure 14 presents the results for mud content. Very similar results were obtained for median grain size (Appendix 6). At low elevations (e.g., Fig. 14D) Callianassa densities decrease with increasing mud content and decreasing grain size, but as elevation increases the slope of the regression line decreases and at high elevations the trend is reversed with high Callianassa densities occurring in the muddier finer grained sediments (e.g., Fig. 14H). Callianassa densities are very low ( $<0.5$  burrow openings  $m^{-2}$ ) in the muddiest sediments on the tidal flat, which occur high on transect C (Stations C1-C3), where mud contents range between 65% and 92%. However, it is difficult to know whether the low densities are a function of

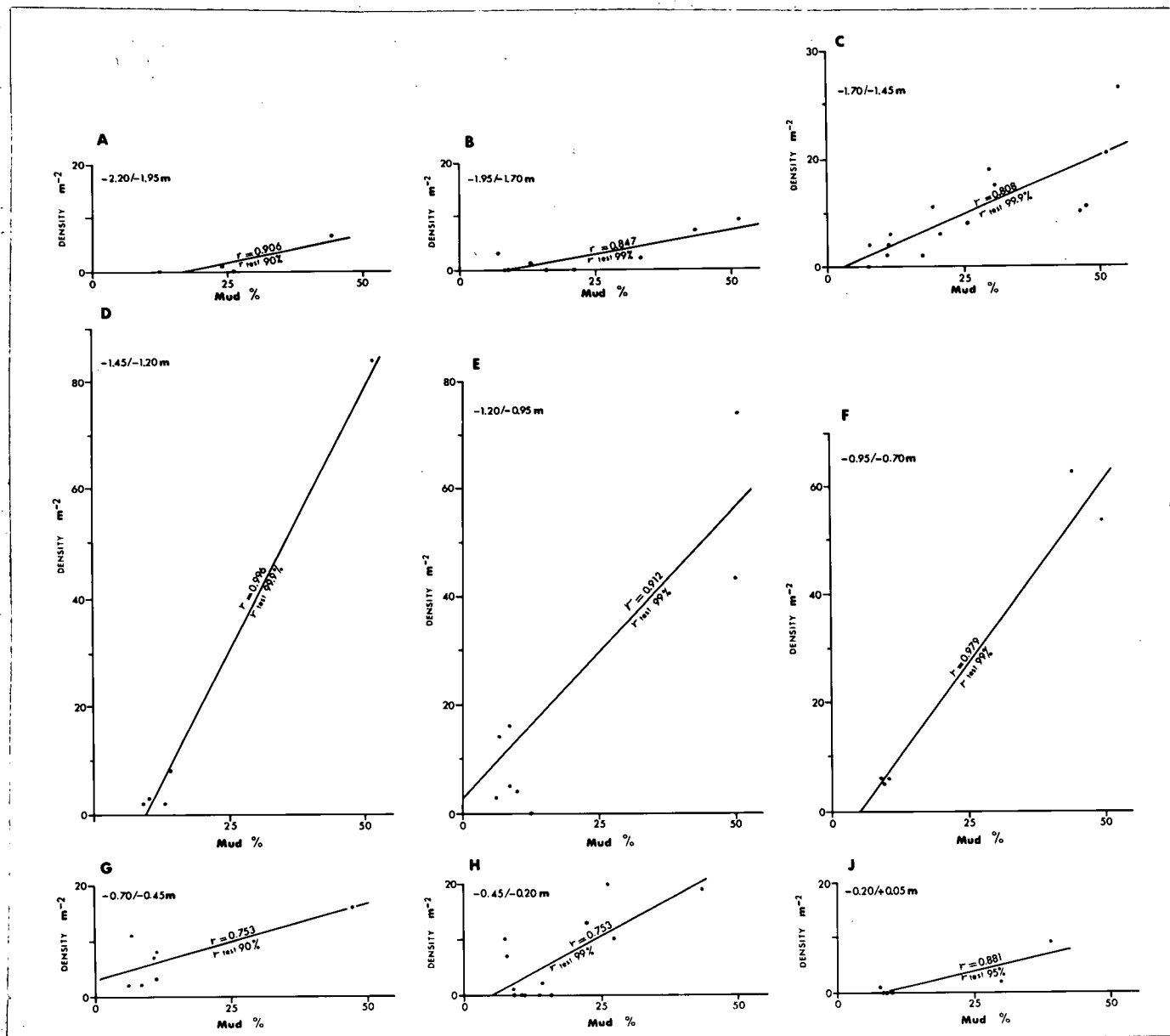
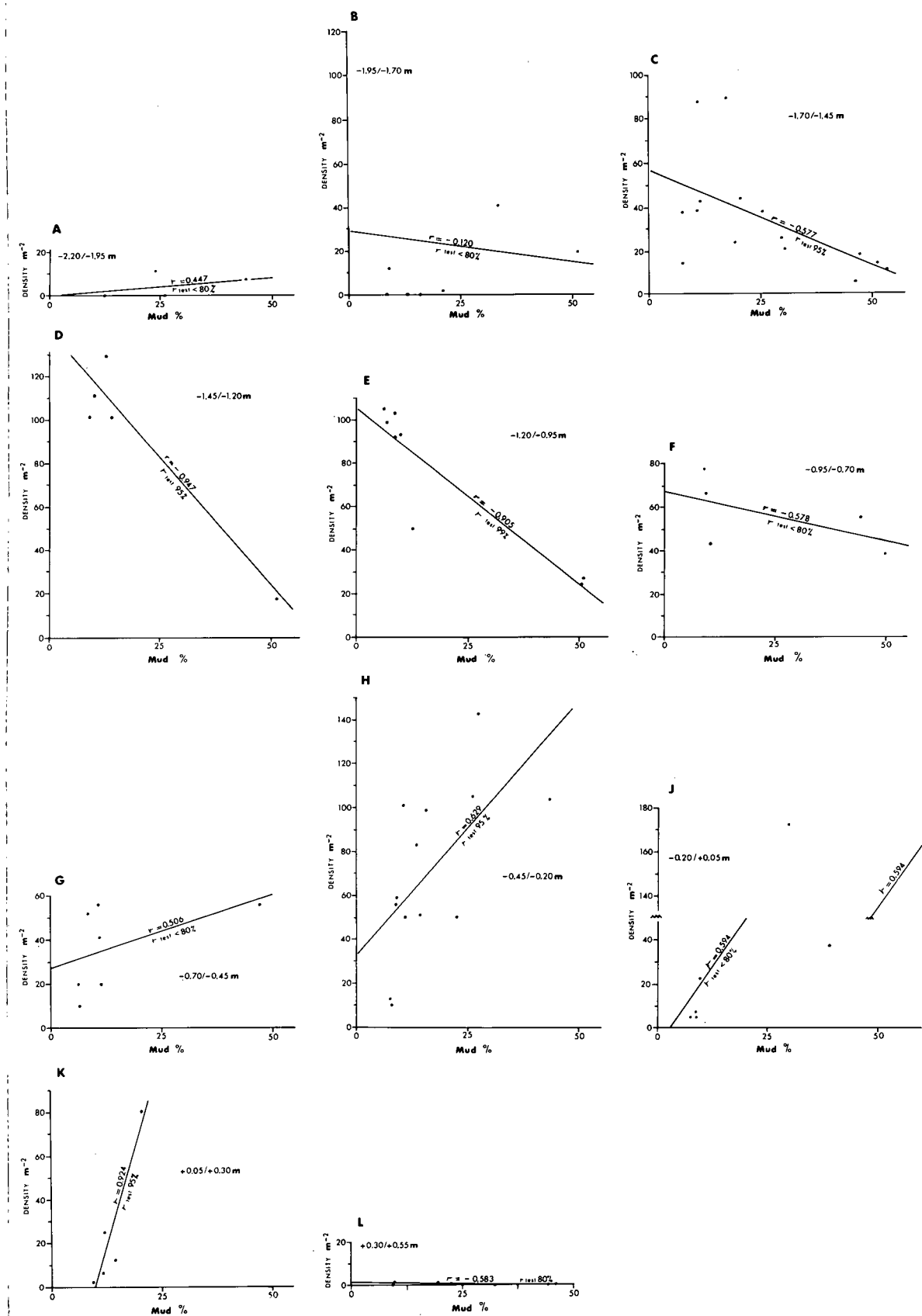


Figure 13. Relationship between mud content (%) and *Upogebia* burrow opening density, with data grouped into 0.25 m elevation class intervals. Best-fit linear regression lines are indicated, along with their correlation coefficients ( $r$ ) and confidence levels ( $r$  test). Elevation (Geodetic Datum) increases from A to J.

Figure 14. Relationship between mud content (%) and Callianassa burrow opening density, with data classed into 0.25 m elevation class intervals. Best-fit linear regression lines are indicated, along with their correlation coefficients ( $r$ ) and confidence levels ( $t$  test). Elevation (Geodetic Datum) increases from A to L.





grain size or elevation.

### Thalassinidean Shrimp Interrelationships

Callianassa and Upogebia burrows occur side by side (Fig. 10, 11).

Upogebia is a suspension feeder (MacGinitie, 1930; Thompson, 1972), while Callianassa is a deposit feeder (MacGinitie, 1934). They occupy very similar niches within the intertidal environment. Do the two shrimps interact? Is there any evidence of competition or trophic group ammensalism (Rhoads and Young, 1970)?

Linear regression analysis was carried out on Callianassa and Upogebia density data which had been classed into 0.25 m elevation class intervals (Fig. 15). Three out of nine of the class intervals have correlation coefficients which are significant at the 95% confidence level ( $r$  test), while a fourth is significant at the 90% confidence level. In all four cases the correlation coefficients are negative. Examination of Figure 15 reveals that it is only at elevations where both Upogebia and Callianassa have the potential of attaining high densities that a negative correlation between Callianassa and Upogebia density is apparent.

### BIOGENIC REWORKING OF SEDIMENT

Sediment reworking rates were monitored within protected metal enclosures during the summer of 1978 (Table I). The rate at which Callianassa reworks sediment is quite variable, ranging between 9 to 33 ml/shrimp/day (assuming there are 2.5 burrow openings per shrimp). The average rate is  $18 \pm 9$  ml/shrimp/day. These rates are comparable with the rate of 25 ml/shrimp/day reported by Ott et al. (1976) for Callianassa stebbingi, but is appreciably

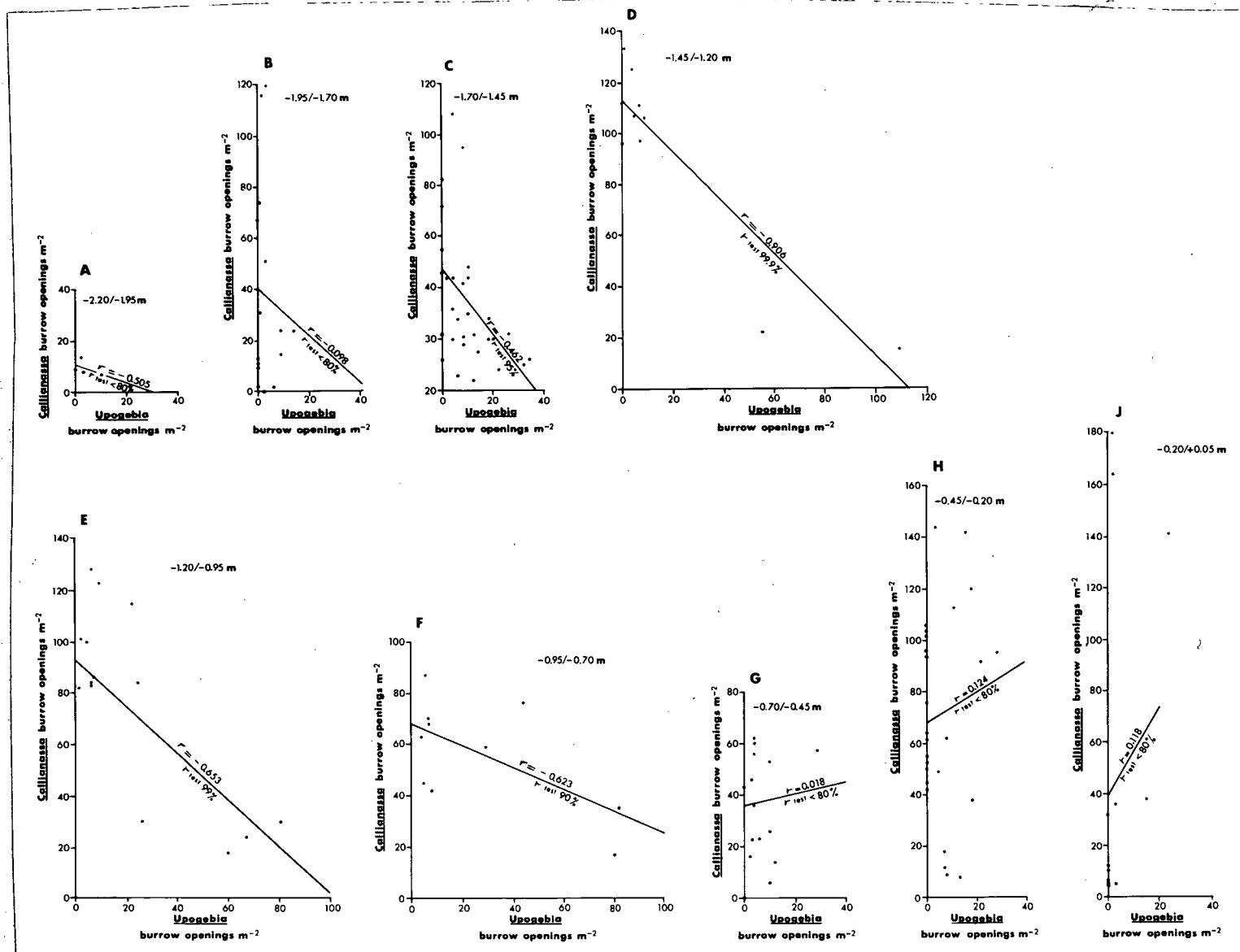


Figure 15. Relationship between *Upogebia* burrow opening density and *Callianassa* burrow opening density with the data classed into 0.25 m elevation class intervals. Best-fit linear regression lines are indicated along with their correlation coefficients ( $r$ ) and confidence levels ( $r$  test). Elevation (Geodetic Datum) increases from A to J.

TABLE I

Rates of biogenic reworking of sediment by Callianassa and Upogebia, as measured in protected metal enclosures on the surface of the substrate

Date	Station	Temperature of substrate and sea water ( $^{\circ}\text{C}$ )	Exposure Duration (hours)	Burrow Openings ( $0.25 \text{ m}^{-2}$ )		Rate (ml/shrimp/day)	
				*C.	*U.	*C.	*U.
Jul 31/Aug 1 1978	C23	27, 26 (2 cm)** 23, 24 (10 cm)** 22, 22 (S.W.)***	3.5	17	--	27	--
"	C15	27, 28 (2 cm) 24, 25 (10 cm) 22, 22 (S.W.)	6.5	6	--	22	--
"	C12	27, 29 (2 cm) 25, 26 (10 cm) 22, 22 (S.W.)	7.0	3	5	33	0
Aug 4/Aug 5 1978	C23	26, 29 (2 cm) 24, 24 (10 cm) 22, 22 (S.W.)	3.3	13	--	11	--
Aug 30/Aug 31 1978	C17	25, 20 (10 cm) 19, 18 (S.W.)	5.4	8	--	14	--
"	A7	25, 19 (10 cm) 19, 18 (S.W.)	4.2	--	15	--	0
Sept 3/Sept 4 1978	C21	19, 20 (10 cm) 18, 18 (S.W.)	2.0	11	--	9	--
"	C17	19, 20 (10 cm) 18, 18 (S.W.)	4.0	10	--	13	--
Average						$18 \pm 9$	0

\* C. = Callianassa    U. = Upogebia

\*\* 2 cm = Substrate temperature at 2 cm.

\*\*\* S.W. = Flooding sea water at 50 cm depth.

Note: All rates were determined on the basis of 25 hours observation (i.e., one lunar day).  
At each station temperatures were measured at the beginning and end of each experiment.  
Characteristics of the stations used to determine these rates are given in Appendix 7.

less than the estimate of 50 ml/shrimp/day made by MacGinitie (1934) for Callianassa californiensis; MacGinitie (1934) gave no details of the technique used to determine rates.

The population of Callianassa on the inter-causeway tidal flat was estimated to be about 100 million (actual estimate  $1.08 \times 10^8$ ). This was done by dividing Figure 10 into areas of comparable shrimp density and computing shrimp populations for each area, by determining the average burrow opening density for the area multiplying this density by the area and assuming a burrow opening to shrimp ratio of 2.5 to 1. During the summer (June 21-September 21), when substrate temperatures are probably comparable to those presented in Table I, this population of Callianassa turns over about 0.2 million cubic meters of sand, and in areas of highest shrimp density ( $178 \text{ m}^{-2}$ ) Callianassa reworks the sediment it lives in to a depth of 50 cm in about five months.

Upogebia did not produce any measurable mounds of sediment within 25 hours (Table I). However, this does not mean that Upogebia does not rework sediment. Both Thompson (1972) and Ott et al. (1976) have noted in the laboratory that Upogebia constantly tends to its burrow and transports sediment from one part of the system to another, by excavating sediment in one place and tamping it into the walls in another. Figure 5 illustrates that there is an anomalous patch of muds in the middle of transect A, which is hard to account for in terms of physical processes, and is associated with high densities of Upogebia (Fig. 11). As shall be seen in Part B, Upogebia constructs a muddy inner lining to its burrow, which is 1-4 mm thick. A blue-grey clayey mud horizon has been detected at about 40 cm depth on transect A and can be traced at least 600 m seawards as far as A7. Upogebia burrows, which extend down to about 60 cm depth, cross into this horizon (Fig. 16). Perhaps the anomalously high mud contents of the sediments on

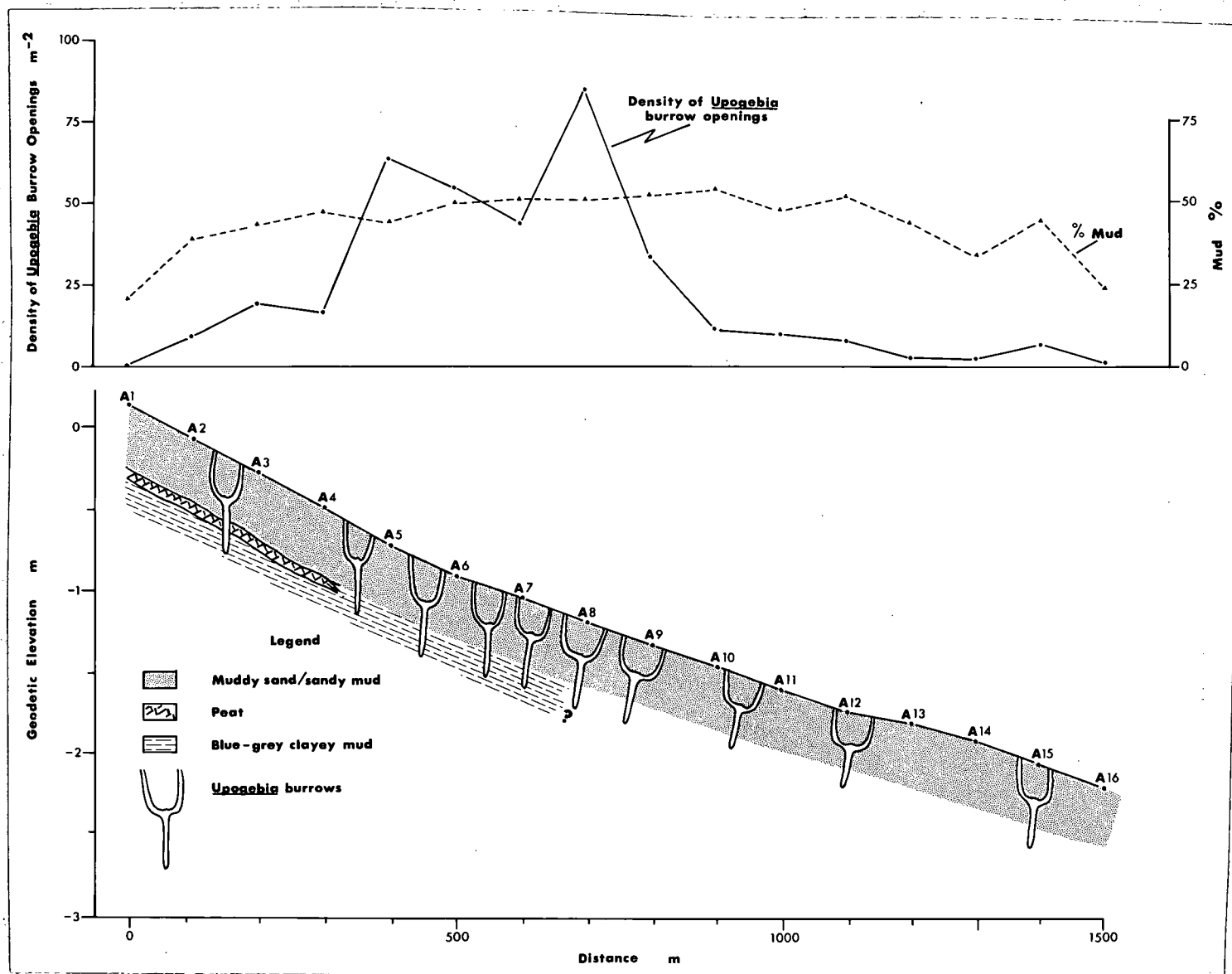


Figure 16. The near-surface stratigraphy of the tidal flat on transect A. *Upogebia* burrows extend down into a blue-grey clayey mud horizon (the vertical dimensions of the burrows are drawn to scale). This bioturbation may account for the anomalously high mud contents of the surface sediments.

transect A are the result of intense bioturbation by Upogebia, which can attain densities of 84 burrow openings  $m^{-2}$  in this area (Fig. 16). Upogebia in constructing burrows have possibly transported mud from the blue-grey clayey mud horizon at depth and incorporated it into the burrow walls near the surface, thereby increasing the mud content of the surface sediments.

## DISCUSSION

The ranges of salinity encountered within the inter-causeway area are within the tolerance limits of both Callianassa and Upogebia, the lower lethal limit for Callianassa being 10‰ and for Upogebia 3.5‰ (L. Thompson and Pritchard, 1969). Callianassa is probably protected from any transient incursions of low salinity water by high salinity interstitial waters at depth which are free to enter its unlined burrow (L. Thompson and Pritchard, 1969). Thus, in the inter-causeway area, salinity does not influence thalassinidean shrimp distribution.

### Upper Limits of Thalassinidean Shrimp Distribution

The presence of the saltmarsh limits Callianassa distribution at upper intertidal levels. As in Boundary Bay the lower limit of the saltmarsh lies at the lower limit of the upper atmozone. This is the tidal level at which the maximum duration of exposure jumps from about 10 to 20 days, and this period of exposure occurs at the time of the spring equinox (Swinbanks, 1979). As Swinbanks (1979) has suggested, based on the saltmarsh studies of Chapman (1974), this prolonged period of exposure may be essential for successful seedling germination. Apart from being excluded by the dense vegetative cover of the saltmarsh Callianassa probably cannot survive at the upper atmozonal elevations of the marsh because the maximum duration of exposure exceeds

Callianassa's tolerance of exposure. More than about 5 days of anoxia is lethal to Callianassa (R. Thompson and Pritchard, 1969).

On transect A, Upogebia extends up to the base of the upper amphizone (about mean sea level). Upogebia burrow waters can become anoxic within one hour of exposure (R. Thompson and Pritchard, 1969). The maximum duration of exposure within the lower amphizone is less than half a lunar day (Swinbanks, 1979), whereas within the upper amphizone the maximum duration of exposure lies between 0.7 and 1.0 lunar days (i.e., 17-25 hours, Swinbanks, 1979), which is within the range of exposure to anoxia lethal to postmolt Upogebia (range 12-42 hours, R. Thompson and Pritchard, 1969). Hence, Upogebia probably attains its absolute physiological limit in elevation on transect A by extending up to the base of the upper amphizone.

#### Lower Limits of Thalassinidean Shrimp Distribution

Ott et al. (1976) suggest that dense meadows of seagrass (Cymodocea) limit the distribution of Upogebia litoralis and Swinbanks (1979) suggests that Callianassa distribution may be limited in Boundary Bay by the dense floral cover of Z. marina in the lower eelgrass zone. Further evidence for Z. marina limiting Callianassa distribution is found in the inter-causeway area on transects B and C. On these transects Callianassa density decreases dramatically to less than  $0.5 \text{ m}^{-2}$ , where Z. marina coverage becomes dense and continuous. In the absence of eelgrass, Callianassa extend to lower intertidal levels (Part 4B). The dense rootlets of Z. marina may hinder the mining activities of Callianassa and/or the dense floral cover, black organic rich surface sediments and dense rootlets may discourage settlement by postlarval Callianassa. There is no evidence that Upogebia is limited by Z. marina. In Boundary Bay Upogebia is abundant in dense Z. marina beds

(Swinbanks, 1979).

Upper Limit of Eelgrass--Moody (1978) attributes the anomalously low elevation (-2.10 m Geodetic Datum, 1% mean exposure) for the upper limit of eelgrass adjacent to the 'causeway zone' south of the ferry causeway to more rapid desiccation associated with the sandy substrate. However, eelgrass attains much higher elevations on sandy substrates in the inter-causeway area (-1.43 m Geodetic Datum, 7.8% mean exposure, Transect B; -1.56 m Geodetic Datum 6.4% mean exposure, Transect C) and attains the same elevation on muddy substrates (-1.45 m Geodetic Datum, Transect A), disproving Moody's (1978) theory that the upper limit of eelgrass is influenced by grain size. Desiccation may be enhanced by the steepened profile associated with the 'causeway zone,' but probably much more important is the increased effects of wave action on the steepened profile as evidenced by the presence of sand bars (Fig. 2). The 'rip rap' adjacent to this area had to be replaced with coarser material after causeway construction, because it was being transported by wave-induced longshore currents (A. Tamburi, Western Canada Hydraulics, oral commun. 1978). Eelgrass is absent in the presence of sand waves in Boundary Bay (Swinbanks, 1979). Eelgrass cannot tolerate wave shock (Beak-Hinton, 1977). The upper limit of eelgrass bounded by the 'causeway zones' is probably determined by wave shock, rather than exposure.

The inter-causeway area may be the only area on the Fraser Delta where the factor determining the upper limit of Z. marina may be a simple function of tides and elevation, because the area is not subject to strong wave action (as evidenced by the lack of sand waves), lacks tidal channels (in which submergence duration is enhanced), and has a relatively stable salinity regime. The upper limit lies at the upper limit of the lower aquazone that has lain at  $-1.51 \pm 0.14$  m Geodetic Datum for the past two years (Swinbanks, 1979). This is the level below which the maximum



duration of submergence jumps from about 10 to 20 days, and this period of prolonged submergence always occurs at the time of the spring and autumn equinoxes (Swinbanks, 1979). Until now biologists have suggested that the upper limit to Z. marina is determined by desiccation due to exposure, rather than being any function of submergence (Keller and Harris, 1966; den Hartog, 1970; Moody, 1978). However, there are no jumps in exposure duration within the aquazone and therefore there is no way of accounting for the abrupt termination of the eelgrass zone in terms of exposure. Perhaps spring is a critical time of the year when eelgrass puts on renewed growth after winter dormancy, and seedling germination and/or vegetative reproduction requires continuous submergence without exposure in order to succeed. Could the advance of the upper limit of Z. marina in the inter-causeway area over the past eight years (Beak-Hinton, 1977) be a result of the fact that the upper limit of the lower aquazone has risen about 30 cm over the past ten years from -1.80 m (Geodetic Datum) in 1968/70 to -1.51 m (Geodetic Datum) in 1976/78, due to an 18.6 year cycle in the moon's declination (Swinbanks, 1979)? These ideas are designed to provoke thought and further study of the elevational limits of eelgrass, rather than to offer answers.

#### Factors Influencing Thalassinidean Shrimp Density

Callianassa does not exhibit a clear preference for a particular grain size of sediment, and is abundant in sediments ranging from sandy muds to pure sands. Callianassa densities are low in the muds and muddy sands of the algal mat zone, but rather than being a result of substrate selection by Callianassa, this is probably because drainage enhanced exposure on the plateaus between tidal channels results in a mudcracked, inhospitable environment that can only be colonized by blue-green algae and crabs. Upogebia shows

a distinct preference for muddy substrates (probably because it lines its burrow with mud (Swinbanks, 1979; Part 4B)). A durable mud-lined burrow is probably essential for Upogebia's suspension feeding and respiration activities.

There is some evidence to suggest that Callianassa and Upogebia densities are negatively correlated at tidal elevations where densities of both shrimps are high, suggesting that they may be competing for available space. Significantly, the four elevation class intervals which show high negative correlation coefficients between Callianassa and Upogebia density (Figure 15C, D, E and F) are the same four which have high negative correlation coefficients between Callianassa density and mud content (Fig. 14C, D, E and F). The negative correlations between Callianassa density and mud content could be the result of a positive correlation between Upogebia density and mud content, combined with a negative correlation between Callianassa density and Upogebia density, rather than being the result of a preference on the part of Callianassa for sandy coarser grained substrates. Conversely, the negative correlation between Callianassa density and Upogebia density could be the result of a positive correlation between Upogebia and mud content combined with a negative correlation between Callianassa and mud content, rather than being the result of any negative interaction between Callianassa and Upogebia. But if we accept the explanation that Callianassa shows a preference for sandy coarser grained substrates at the elevations of these four class intervals, we must also accept that this trend is completely reversed at higher elevations with Callianassa exhibiting a preference for muddier, finer grained sediments (Fig. 14H). Such a reversal of preference is hard to explain. This contradiction does not arise if we accept the former explanation that Callianassa and Upogebia exhibit a negative interaction where densities of both shrimps can be high, because then we need only accept that Callianassa

may be positively correlated to mud content. This positive correlation is only exhibited at high intertidal elevations where Upogebia is absent or is only present in low densities. At intertidal elevations where Upogebia and Callianassa densities can be equally high, Callianassa's preference for muddy substrates is overridden and suppressed by a negative interaction between Callianassa and Upogebia combined with a strong preference on the part of Upogebia for muddy substrates.

Accepting the above explanation of the correlations what form does the competition between Callianassa and Upogebia take? It may be a form of trophic group ammensalism (Rhoads and Young, 1970), as Upogebia is a suspension feeder (MacGinitie, 1930; Thompson, 1972), while Callianassa is a deposit feeder (MacGinitie, 1934). Perhaps the reworking activities of Callianassa are detrimental to Upogebia. In constantly piling up sediment in mounds on the surface Callianassa may increase mortality among postlarval Upogebia, which construct small 'Y' shaped burrows a few centimeters deep in the surface sediments for the purposes of suspension feeding (Thompson, 1972). Aller and Dodge (1974) have suggested that the reworking activities of Callianassa in a tropical lagoon produce an unstable bottom which cannot be colonized by most kinds of suspension feeding organisms. Shifting, unstable bottoms cause high mortality for settled suspension feeding larvae of bivalves (Levinton and Bambach, 1970), and high fluxes of resuspended sediment may clog filtering mechanisms of suspension feeders and prevent efficient feeding (Loosanoff, 1962). The planktic larvae of Upogebia are carnivorous (Thompson, 1972), and perhaps the larvae of Upogebia feed on those of Callianassa. The negative correlation between Callianassa and Upogebia could be a result of one or both of these suggested factors.

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Part 4B

ENVIRONMENTAL CONTROLS ON THE DISTRIBUTION  
OF THALASSINIDEAN BURROWING SHRIMPS  
ON FRASER DELTA TIDAL FLATS, BRITISH COLUMBIA

The Marine to Brackish Tidal Flats  
of Central and Northern Roberts Bank



## ABSTRACT

The thalassinidean burrowing shrimps Callianassa californiensis and Upogebia pugettensis are abundant on the 'marine' tidal flats of the southeasternmost section of central and northern Roberts Bank on the Fraser Delta-front. Northwestward toward the distributaries of the Fraser River, there is an abrupt transition from 'marine' to brackish conditions in the vicinity of Canoe Pass, and thalassinidean shrimp densities decrease dramatically. A technique for contouring this transition in salinity regime, based on the percent thickness of the salt wedge, is outlined. Accompanying this transition is a complete restructuring of the floral/sedimentological zonation of the tidal flats. The 'marine' tidal flats can be divided into four floral/sedimentological zones. These are, from the shoreline seawards, the saltmarsh zone, the algal mat zone, the sandflat zone and the eelgrass zone. Thalassinidean burrowing shrimps are most abundant in the sandflat zone. On the brackish tidal flats a brackish marsh zone displaces the saltmarsh and algal mat zones and the upper half of the sandflat zone, while a sandflat/mudflat zone crosscut by both active and relict channels displaces the eelgrass zone and the lower half of the sandflat zone. The brackish marsh extends to much lower tidal elevations than the saltmarsh, almost reaching the upper limit of the aquazone. In response to these changes, the peak in Callianassa distribution moves to lower intertidal levels, because of the presence of low salinity water at higher tidal levels and because of the disappearance of eelgrass in lower intertidal regions. The lower limit of the brackish marsh forms the upper limit to Callianassa distribution. In close proximity to the major channels of the Fraser River, Callianassa are absent.

Callianassa burrow opening density is positively correlated to the salinity of surface substrate waters. Upogebia, although physiologically

better adapted to cope with fluctuating salinities, demonstrates lower tolerance of brackish water in its distribution than Callianassa, probably because the function of its mud-lined burrow as a conduit for suspension feeding and respiration exposes Upogebia to low salinity surface waters, while Callianassa, in its unlined burrow used for deposit feeding, is protected from surface waters by high salinity interstitial waters. The distinction between mud-lined, permanent dwelling burrows and unlined, temporary feeding burrows is, therefore, considered to be of great significance from the paleoenvironmental point of view. The abundance of each of the two types of burrow in the geological record could be used as a qualitative indication of paleosalinity, burrows of the former being more sensitive than those of the latter. Both Upogebia and Callianassa are probably capable of producing trace fossil burrows resembling either Ophiomorpha or Thalassinoides, depending on whether the knobbly outer or smooth inner burrow wall, respectively, is accentuated during fossilization; therefore, the distinction between Ophiomorpha and Thalassinoides is considered to be of little significance. In the high energy environment and unstable salinity regime of northern and central Roberts Bank, Callianassa constructs burrows with long constricted apertural necks which extend about 30 cm down into the substrate. This is thought to reflect a change in feeding mode, with Callianassa abandoning near-surface feeding because of the instability of the surface environment.

## INTRODUCTION

The primary aim of these two papers (Part 4A, and B) is to assess the effects of various environmental factors on the distribution of the thalassinidean burrowing shrimps, Callianassa californiensis Dana and Upogebia pugettensis (Dana), on Fraser Delta tidal flats, in the hope that their distinctive burrows may be used as paleoenvironmental indicators in ancient deltaic sequences. Thalassinidean shrimps are known to occur as far back as the Cretaceous (Borradaile, 1903). The studies of thalassinidean shrimp distribution on the inter-causeway tidal flat on southern Roberts Bank (Part 4A) and in Boundary Bay (Swinbanks, 1979) dealt with areas experiencing relatively stable, 'marine,' salinity regimes. The aim of this paper is to examine shrimp distribution on the tidal flats of central and northern Roberts Bank, north of the Coalport causeway (Fig. 1), where the influx of freshwater from the Fraser River system is an added environmental factor influencing shrimp distribution. The following questions are considered to be the points of most interest: (1) Which shrimp is most sensitive to changes in salinity regime? (2) To what extent does the nature and function of the burrow system affect the shrimps' capacity to tolerate reduced salinities? (3) Could the distinctive burrows of these shrimps be used as paleosalinity indicators?

To assess the effects of reduced salinities on thalassinidean shrimp distribution it is necessary to have a sound understanding of the effects of other parameters (e.g., elevation, grain size and floral cover). Such data have been obtained in the studies of Boundary Bay (Swinbanks, 1979) and of the inter-causeway tidal flat (Part 4A). Secondly, it is necessary to have physiological data on the responses of Upogebia and Callianassa to reduced salinities, and knowledge of their ethology, particularly in regard to feeding and respiration. Such data are available in the studies of L.

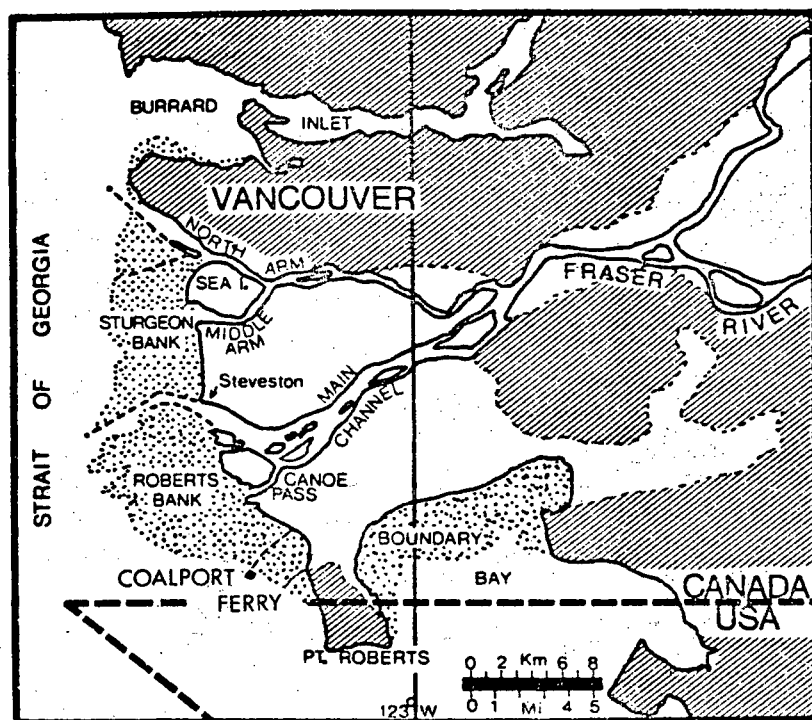


Figure 1. Location of study area. Tidal flats are stippled, land area of Recent alluvium is blank, and older deposits cross-hatched (adapted from Luternauer and Murray, 1973).

Thompson and Pritchard (1969), R. Thompson and Pritchard (1969), Thompson (1972) and MacGinitie (1930, 1934). Felder (1978) has recently studied the osmoregulatory capacities of three species of Callinassidae (C. major, C. islagrande and C. jamaicense) and related this to their distribution on the Louisiana and Mississippi coast. Unfortunately Felder (1978) did not include descriptions of the feeding or respiratory activities of the three shrimps, nor did he include descriptions of their burrows, although, of course, the burrows of C. major are well known to geologists, as they are a modern equivalent of Ophiomorpha (Weimer and Hoyt, 1964).

Previous studies of Roberts Bank have established that there is a change from brackish to more marine conditions in going from north to south. Levings and Coustalin (1975) recorded higher numbers of benthic species on a transect immediately north of the Coalport causeway (Fig. 1) than on any transects further to the north, and cumaceans were abundant at many of the stations (up to  $15,872 \text{ m}^{-2}$ , Levings and Coustalin, 1975), both of which indicates that the portion of Roberts Bank immediately north of the Coalport causeway still has the 'marine' characteristics of the inter-causeway area (Part 4A).

Amphithoc valida, an amphipod which prefers more saline conditions, is also abundant in the area immediately north of the causeway (Dr. M. Pomeroy, Pacific Environment Institute, West Vancouver, oral commun. 1978). Moody (1978) has mapped and studied the marsh at Brunswick Point immediately south of Canoe Pass (Fig. 4). This is a typical brackish marsh. The upper marsh is dominated by Carex lyngbyei while the lower marsh consists of Scirpus americanus and Scirpus maritimus. However, towards the Coalport causeway the areal extent of the marsh decreases abruptly and only a narrow fringe of marsh is present, with Distichlis sp. and Salicornia sp. in the upper parts and Triglochin maritima in the lower (Moody, 1978). These marsh plants are typical of the saltmarshes of the inter-causeway and Boundary Bay

areas (Kellerhals and Murray, 1969; O'Connell, 1975; Parsons, 1975; Hillaby and Barrett, 1976; Beak-Hinton, 1977; Swinbanks, 1979). Accompanying this marsh transition, surface substrate salinities increase from <3‰ in the brackish marsh to as high as 21‰ in the saltmarsh (Moody, 1978). The highest salinities were recorded on the transects closest to the Coalport causeway (Moody, 1978).

## METHODS

Seventy-five stations were sampled at low tide by hovercraft and helicopter on a grid of approximately 1 km extending from the marsh perimeter down to about 0.6 m Chart Datum on the dates indicated in Figure 2. Nineteen stations lying on the same grid system between Canoe Pass and the Tsawwassen ferry terminal were occupied by hovercraft on June 8, 1978 at high tide, and salinity profiles were taken with a Beckman RS5-3 portable inductive salinometer, sampling at 0.25 m intervals. Eleven of these stations were reoccupied on the same day (June 8) to obtain substrate salinity and shrimp density data at low tide. Hovercraft stations were located using Decca radar and are accurate to within a radius of about 50 m. Helicopter stations were plotted on a recent aerial photograph (A37597-146, National Air Photo Library, June, 1978) with a scale of 1 to 72,000, after being located visually from the air, and are accurate to within a radius of about 100 m.

Using a topographic map (Swan Wooster, 1967) of 0.6 m contour interval (Fig. 3) the hovercraft and helicopter stations were grouped into 0.6 m elevation class intervals. Some of the contours on this map may be inaccurate, particularly in the vicinity of the main channel of Canoe Pass, as this channel has changed direction since 1967. However, it is the best elevation data available. The Chart Datum for the contours on the map is -2.63 m Geodetic Datum. The tidal data used in this paper was derived from the tide gauge at

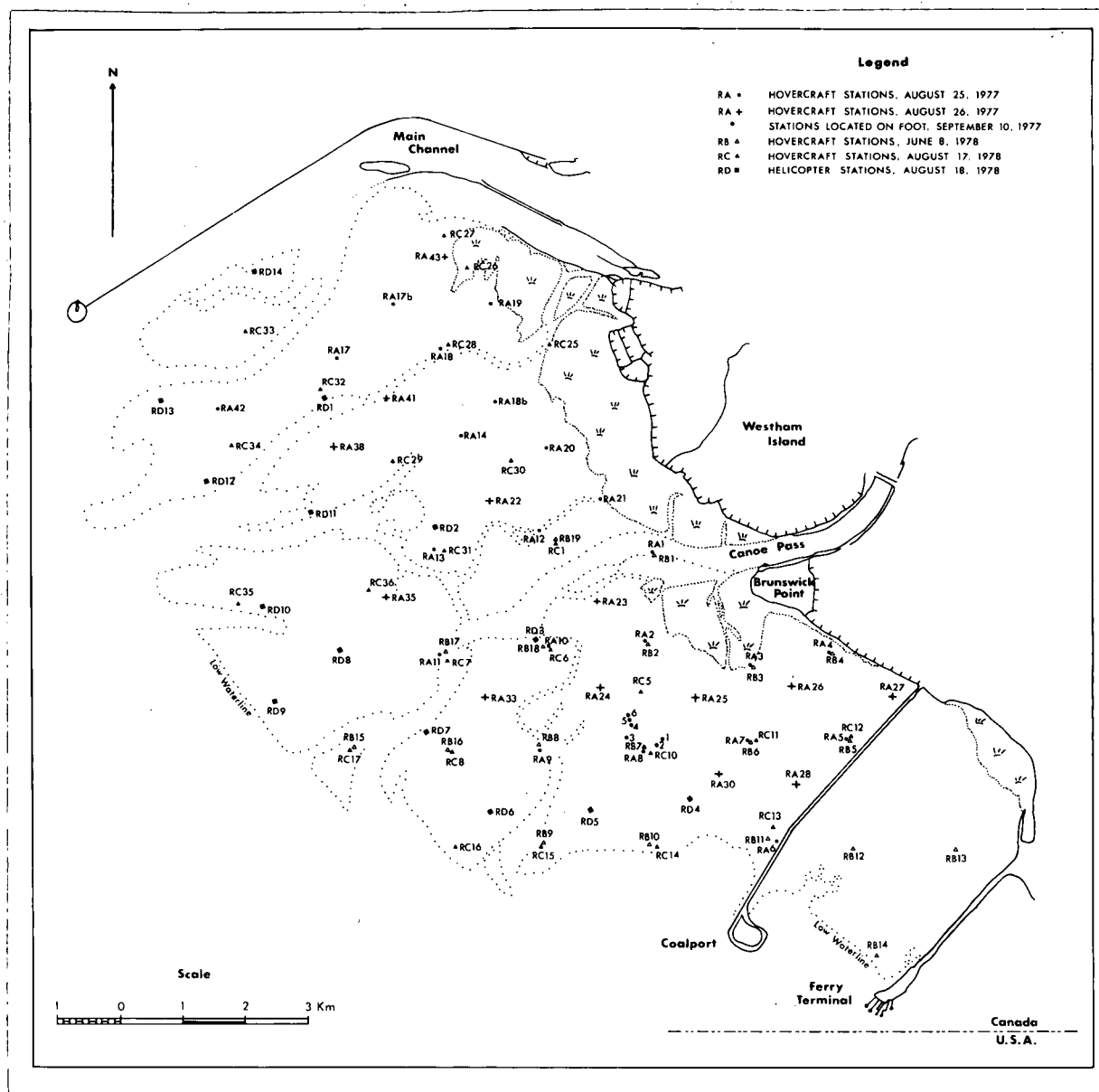


Figure 2. Locations of stations sampled by hovercraft, helicopter and on foot in 1977 and 1978.



Figure 3. Topographic map of Roberts Bank in 1967. The datum for contours in this map is -2.63 m Geodetic Datum. Contours in meters (source: Swan Wooster, 1967).



the Tsawwassen ferry terminal, where present-day Chart Datum is -2.95 m Geodetic Datum. To avoid confusion as to datum, throughout the remainder of this paper elevations will be given with respect to Geodetic Datum, which remains fixed in time and space. Where reference is made to Chart Datum the datum referred to is present-day datum at Tsawwassen.

At all stations, shrimp burrow opening densities were determined by sampling eight times at each station with a  $0.25 \text{ m}^2$  quadrat. Surface grain size samples were obtained at all stations using a 2 cm deep rectangular box. Unfortunately, the twenty-six grain size samples collected on August 17, 1978 were lost. Surface water salinities were recorded at all stations at low tide using a refractometer (Endeco type 102). The geometry of shrimp burrows was studied using a box core (15 x 20 cm by 30 cm deep), resin casts (Shinn, 1968) and simple excavation with a spade.

In addition to the stations mentioned above, six stations were located on foot on Roberts Bank between Canoe Pass and the Coalport causeway (Fig. 2) specifically to monitor the effects of changing substrate salinity on shrimp distribution at a fixed tidal level. On September 10, 1977 at slack water low tide (observed tidal height: +1.4 m Chart Datum or -1.55 m Geodetic Datum) surface substrate salinities were monitored with a refractometer at approximately 100 m intervals in close proximity to the waterline walking from the Coalport causeway towards Canoe Pass. An area showing a pronounced salinity gradient was located where salinities dropped from 24.5‰ to 12.5‰ over a distance of about 0.75 km. Six stations with sandy substrates showing a range in surface salinities were located within a few meters of the waterline and marked with wooden stakes, and mapped using a Brunton compass (Fig. 2). The following day surface salinities, salinity profiles, grain size samples and shrimp burrow density data were collected at these stations. Sixteen quadrat readings were taken at each station, with a  $0.25 \text{ m}^2$  quadrat

to obtain accurate estimates of shrimp burrow density.

In the laboratory, grain size samples were washed free of salt, wet sieved through a 63  $\mu\text{m}$  sieve to extract the silt/clay fraction, dried and the percent mud values calculated. The data from the inter-causeway area (Part 4A) has demonstrated that percent mud values are perfectly adequate for assessing the relationships between thalassinidean shrimp distribution and grain size.

The distinctive floral/sedimentological zones of the Roberts Bank tidal flats were mapped using a high level, colour, aerial photograph taken in June, 1978 (A37597-146, National Air Photo Library, Ottawa, Canada) in conjunction with low level, colour, aerial photographs (Scale 1:12,000) taken in July, 1977 (A31164, National Air Photo Library).

#### NORTHERN AND CENTRAL ROBERTS BANK

It is essential to place the thalassinidean shrimp distribution data within the overall framework of floral/sedimentological zones on the tidal flats as the two are intimately interrelated (Part 4A). In the case of these marine to brackish tidal flats, it is also necessary to describe in detail the lateral changes in salinity regime which occur on the tidal flats, as this influences shrimp distribution. For these reasons extensive descriptions of both follow.

#### Floral/Sedimentological Zones

Figure 4 is a map of the floral/sedimentological zones of Roberts Bank north of the Coalport causeway. Two zonation schemes have to be employed to subdivide the intertidal region; one for the 'marine' area in the vicinity of the Coalport causeway and one for the brackish area from Brunswick Point

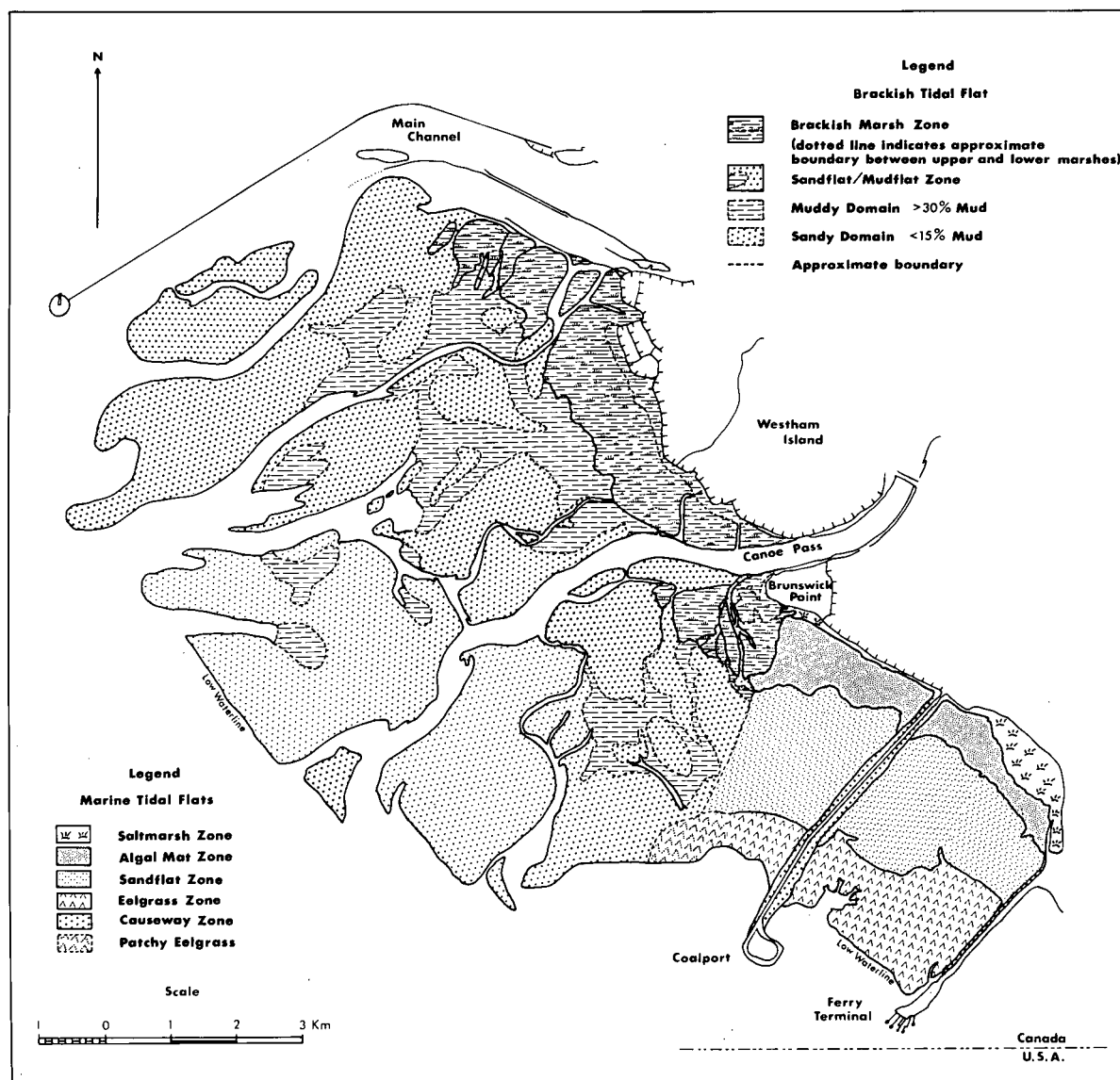


Figure 4. Floral/sedimentological zones of Roberts Bank, prepared from a colour aerial photograph of June, 1978 (A37597-146, N.A.P.L., Ottawa, Canada).

northwards. The transition between the two environments is not gradual but abrupt. In the area southeast of Brunswick Point a four-fold zonation is present which is very similar to that of the inter-causeway area (Part 4A). The zones are, from the dyke seawards, the saltmarsh zone, the algal mat zone, the sandflat zone and the eelgrass zone.

In contrast to the inter-causeway area, the algal mat zone is dominated by filamentous green algae (mostly Rhizoclonium sp.) with only minor filamentous blue-green algae (Oscillatoria sp.). The filamentous green algal mats are coated with a brown film of diatoms (Navicula sp., Nitzschia sp. and Pinnularia sp.). The green algae are probably better adapted than cyanophytes to cope with the reduced light availability and unstable salinities north of the causeway (Dr. M. Pomeroy, Pacific Environment Institute, oral commun. 1978). In addition, tidal channels in the inter-causeway algal mat zone are more deeply entrenched resulting in desiccation on plateaus between channels favourable to blue-green algal mat development.

The elevational limits of the saltmarsh and algal mat zones are very similar to those in the inter-causeway area (Table I). These elevations were determined by overlaying the topographic map (Fig. 3) on Figure 4, and linearly interpolating between contours to determine the elevational ranges of each boundary. The accuracy of this technique was checked by determining the elevational limits of zone boundaries in the inter-causeway area on transects A, B and C (Part 4A), and then this data was compared with the surveyed data presented in Part 4A. The average discrepancy between the surveyed data and that from the topographic map is  $\pm 11$  cm (range +22 cm to -16 cm) (Table I). Thus the map gives a reasonable estimate of elevation. The lower limit of the saltmarsh is, if anything, slightly higher than in the inter-causeway area, lying at +1.02 to +1.29 m Geodetic Datum, while the lower limit of the algal mat zone is possibly slightly lower, lying close to

TABLE I

Elevation ranges for zone boundaries on the 'marine' tidal flats as determined from a topographic map. The accuracy of elevations obtained from the map is checked by comparing with surveyed elevation data obtained in the inter-causeway area (Part 4A).

ZONE BOUNDARY	GEODETIC ELEVATION (m)			
	North of Coalport (Map)	Inter-Causeway Area (Map) (Surveyed) (Discrepancy)		
Saltmarsh Zone/ Algal Mat Zone	+1.02 +1.29		+0.80 +1.00	+0.83 +1.07 -0.03 -0.07
Algal Mat Zone/ Sandflat Zone	+0.13 -0.13	B C	+0.16 +0.15	+0.29 +0.31 -0.13 -0.16
Sandflat Zone/ Eelgrass Zone	-1.74 (highest elevation)	A B C	-1.34 -1.21 -1.52	-1.45 -1.43 -1.56 +0.11 +0.22 +0.04
			Average	±0.11

Note: A, B and C (refer to transects A, B and C) in the inter-causeway area.

0.0 m Geodetic Datum. The highest level that the eelgrass zone attains is -1.74 m Geodetic Datum, which is appreciably lower than in the inter-causeway area (Table I), and, unlike its counterpart in the inter-causeway area, the upper limit is not delimited by elevation, but veers off towards low water mark in a westerly to south westerly direction as Canoe Pass is approached. The eelgrass cover also becomes patchier in this direction (Fig. 4).

From Brunswick Point northwards, the intertidal region can be divided into two major zones, the brackish marsh zone and the sandflat/mudflat zone (which is equivalent to the intertidal portion of the 'main platform,' Luternauer and Murray, 1973). The Brunswick Point marsh can be subdivided into an upper and lower part on the basis of Moody's (1978) map. The Westham Island marsh can tentatively be divided into an upper and lower part on the basis of information provided by Burgess (1970), who noted an abrupt change in elevation of between 0.15 m to 0.45 m over a distance of 1.5-3.0 m, which marks the boundary between the upper marsh, dominated by Carex lynbyei, and the lower marsh, dominated by Scirpus americanus. This break appears to be marked in aerial photographs by a line of driftwood and changes in drainage channel direction. Moody (1978) determined that this break occurs at about +0.10 m Geodetic Datum in the Brunswick Point marsh, while Burgess (1970) estimated it to occur at 0.0 m Geodetic Datum. The boundary between upper and lower marshes thus lies close to the boundary between the upper and lower amphizones at  $-0.08 \pm 0.15$  m Geodetic Datum, a level above which the maximum duration of exposure jumps from less than 0.5 lunar days to greater than or equal to 0.7 lunar days (Swinbanks, 1979). The elevation of the lower limit of the lower marsh was determined at several localities by overlaying the topographic map (Fig. 3) on Figure 4 (Table II). At Brunswick Point the marsh extends down to -0.20 m Geodetic Datum (Table II). This

TABLE II

## Elevation of the Lower Limit of the Brackish Marsh

LOCATION	ELEVATION RANGES (Geodetic Datum, m)
<u>Brunswick Point</u>	
E/W boundary parallel to Canoe Pass	-0.08 to -0.20
NW/SE boundary	-0.20 to +0.10
SSW/NNE boundary (brackish marsh/algal mat zone)	+0.04 to +1.02
<u>Westham Island</u>	
Canoe Pass to Main Channel	-0.20 to -0.52

compares with Moody's (1978) figure of  $-0.13$  m Geodetic Datum. However, this boundary is not delimited by elevation, but rises from Canoe Pass towards the Coalport causeway, and in the area where the marsh transforms to a saltmarsh the boundary rises abruptly towards the NNE from about  $+0.04$  m to  $+1.02$  m Geodetic Datum (Table II). The lower limit of the marsh at Westham Island ranges irregularly between about  $-0.20$  to  $-0.52$  m Geodetic Datum just above the upper limit of the aquazone ( $-0.74 \pm 0.10$  m Geodetic Datum, Swinbanks, 1979). Burgess (1970) estimated that the lower limit of the marsh extends down to  $-0.9$  m Geodetic Datum. However, Burgess (1970) did not specify whether he was referring to the main body of the marsh or to the isolated little clumps of marsh plants which lie below the boundary mapped in Figure 4. The lower limit of the brackish marsh lies at least 1 to 1.5 m below that of the saltmarsh, and the brackish marsh laterally replaces the algal mat zone and the upper part of the sandflat zone of the 'marine' tidal flats. This is clearly illustrated in a high level aerial photograph (Fig. 5) taken on a flooding tide, when the waterline lay at about  $-0.12$  m Geodetic Datum (estimated from tide tables for Pt. Atkinson). The waterline in this photo has reached the lower limit of the marsh at Westham Island, is just below the lower limit of the marsh at Brunswick Point and is approaching the algal mat zone in the area south of Brunswick Point and in the inter-causeway area, while in Boundary Bay it lies at the upper limit of the eelgrass zone (which consists of Z. americana in the upper regions; Swinbanks, 1979).

The Brunswick Point marsh has been undergoing rapid expansion since the late 1940's (Moody, 1978). It has been suggested that this is a result of the deposition of large quantities of sediment in front of the marsh by a major flood in 1948, forming an elevated region which marsh plants could colonize (A. Tamburi, Western Canada Hydraulics, oral commun. 1978).

Below the brackish marsh zone lies the sandflat/mudflat zone which can





Figure 5. High level aerial photograph of the Fraser Delta. The waterline lies at about  $-0.12$  m Geodetic Datum on a flooding tide, and lies above the lower limit of the marsh at Westham Island (centre) is approaching the algal mat zone in the inter-causeway area and lies at the upper limit of the eelgrass zone in Boundary Bay (refer to Fig. 1 for location). Water is beginning to flood into the distributary channels of the Brunswick Point marsh from Canoe Pass.

be subdivided into 'muddy domains' and 'sandy domains.' The muddy domains consist of sediments containing more than about 30% mud (range 29.4-86%) while the sediments of the sandy domains contain less than about 15% mud (range 0.21-14.3%). This was determined by overlaying percent mud values for 48 samples from the sampling grid (Fig. 6), over the air photos - a technique developed by Medley and Luternauer (1976). The muddy domains dominate near the fringe of the marsh, but are also present at lower elevations associated with topographic depressions and in particular with relict channels. The increase in mud content shorewards is clearly apparent in Figure 6 but the coarse sampling grid in most cases fails to detect the muddy domains in lower intertidal regions. The main channel of Canoe Pass has changed direction in the recent past. This can be seen by comparing the Swan Wooster (1967) topographic map (Fig. 3) with the map compiled from present-day aerial photographs (Fig. 4). The channel on the Coalport side of the present main channel, which was a major channel of Canoe Pass, is rapidly necking off in the upstream direction, and will probably be abandoned and infilled with mud in the near future. To the east of this channel lies an elongate depression that is probably the relic of a former channel which suffered a similar fate.

### Salinity

The Fraser River reaches its peak discharge in June and July (Fig. 7). Aerial photographs indicate that the turbid water of the Fraser plume is dispersed over all parts of northern and central Roberts Bank (e.g., Fig. 5, A30339-116, National Air Photo Library), but it is impossible to tell the thickness of the plume or the salinity of its water from the photographs. Strait of Georgia waters off the Fraser Delta-front are stratified into a brackish surface layer and an underlying salt wedge (Waldichuk, 1957). The



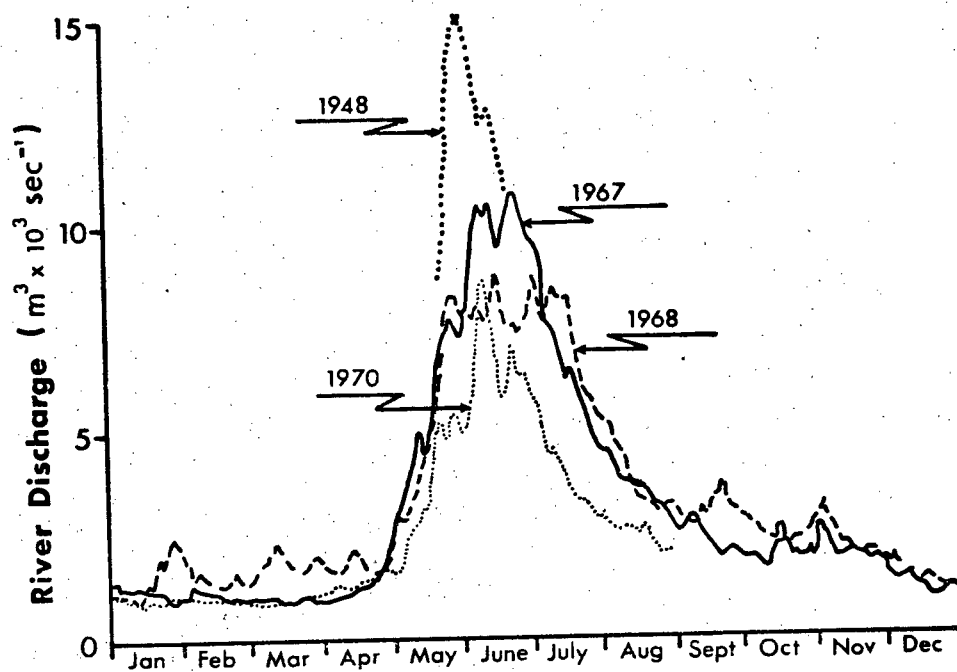


Figure 7. Discharge curves for the Fraser River including the freshet portion of the runoff for 1948, a severe flood year in the Fraser Valley (adapted from R. Thompson, unpublished data).

salt wedge intrudes the distributary channels of the Fraser on flood tides by under-running river water, extending as far as 20 km upstream of the inner tidal flats during the winter, but extends no further than the inner edge of the flats during the summer freshet (Ages and Woollard, 1976).

Figure 8 presents (a) typical distribution pattern of surface substrate salinity on central and northern Roberts Bank. Similar contour patterns were obtained for data collected in August, 1977 (Appendix 8 ) and February, 1974 (Leyings and Coustalin, 1975; Appendix 8 ), although the absolute values at equivalent stations varied quite considerably, probably due to differing wind conditions and river discharge during the preceding high tide. There are two features which all the results have in common: (1) there is a general increase in salinity seaward as one goes to lower intertidal levels (2) a higher salinity region is always present immediately northwest of the Coalport causeway.

How do substrate salinities at low tide relate to salinities in the water column at high tide? It was suspected that surface substrate salinities should closely reflect surface water salinities at high tide on ebb, as surface substrate waters should be derived from the last water to drain off the tidal flat. To test this hypothesis and to better define the transition from marine to brackish conditions between Tsawwassen and Canoe Pass, salinity profiles were recorded at high tide on ebb at nineteen stations in this area within a 3.3 hour period on June 8, 1978. In the vicinity of Canoe Pass, profiles were isohaline and almost pure freshwater, while immediately north of the Coalport causeway profiles were isohaline and 'marine' in salinity (Fig. 9a). Between these two extremes lay a region where a distinct halocline was developed (Fig. 9a). Figure 9a contours surface water salinities at high tide on ebb, while Figure 9b contours surface substrate and surface shallow water (<0.7 m) salinities on approaching low tide (the shallow water salinity profiles were

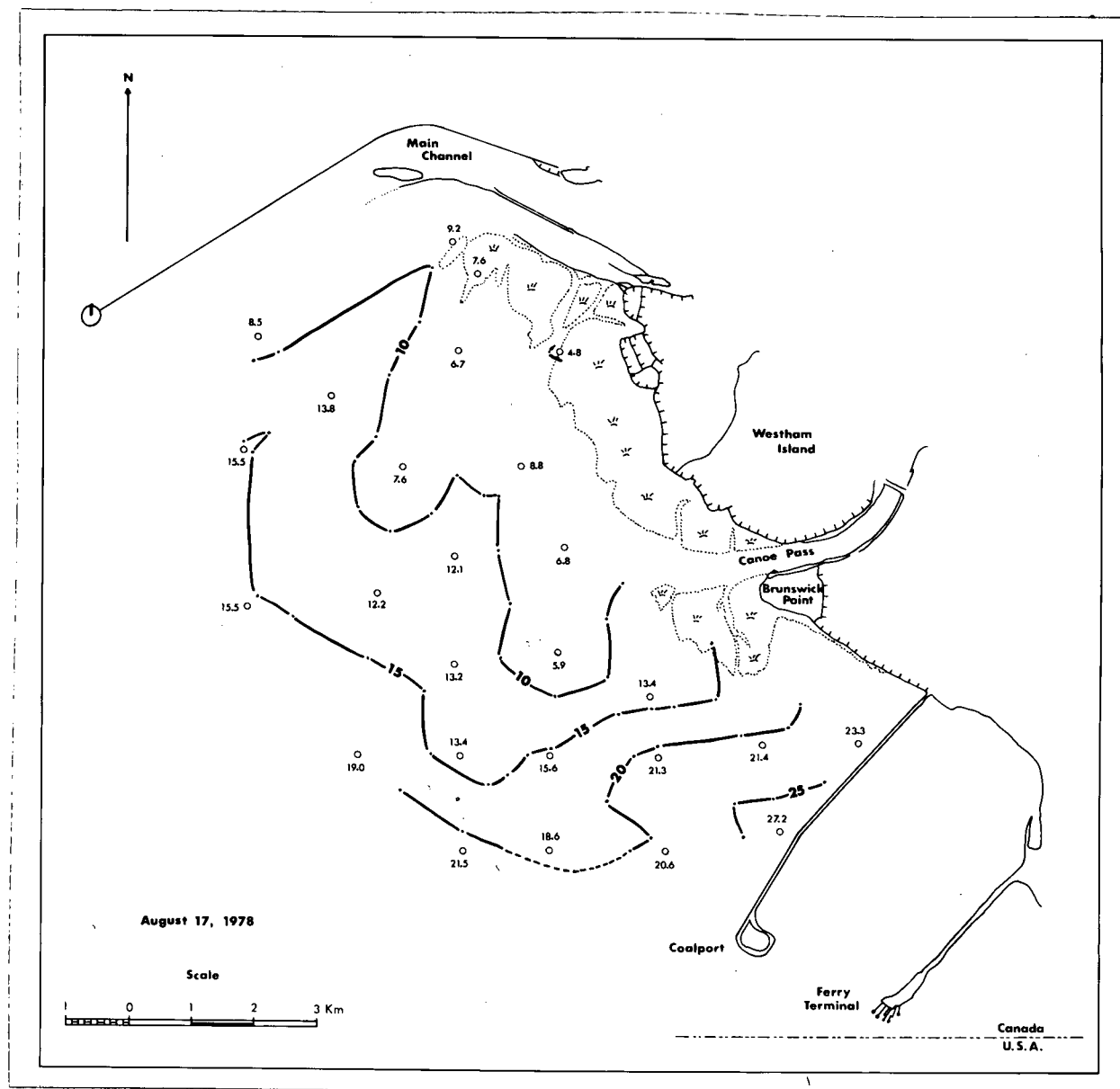


Figure 8. Surface substrate salinities on Roberts Bank at low tide on August 17, 1978. Mechanical contouring employed.

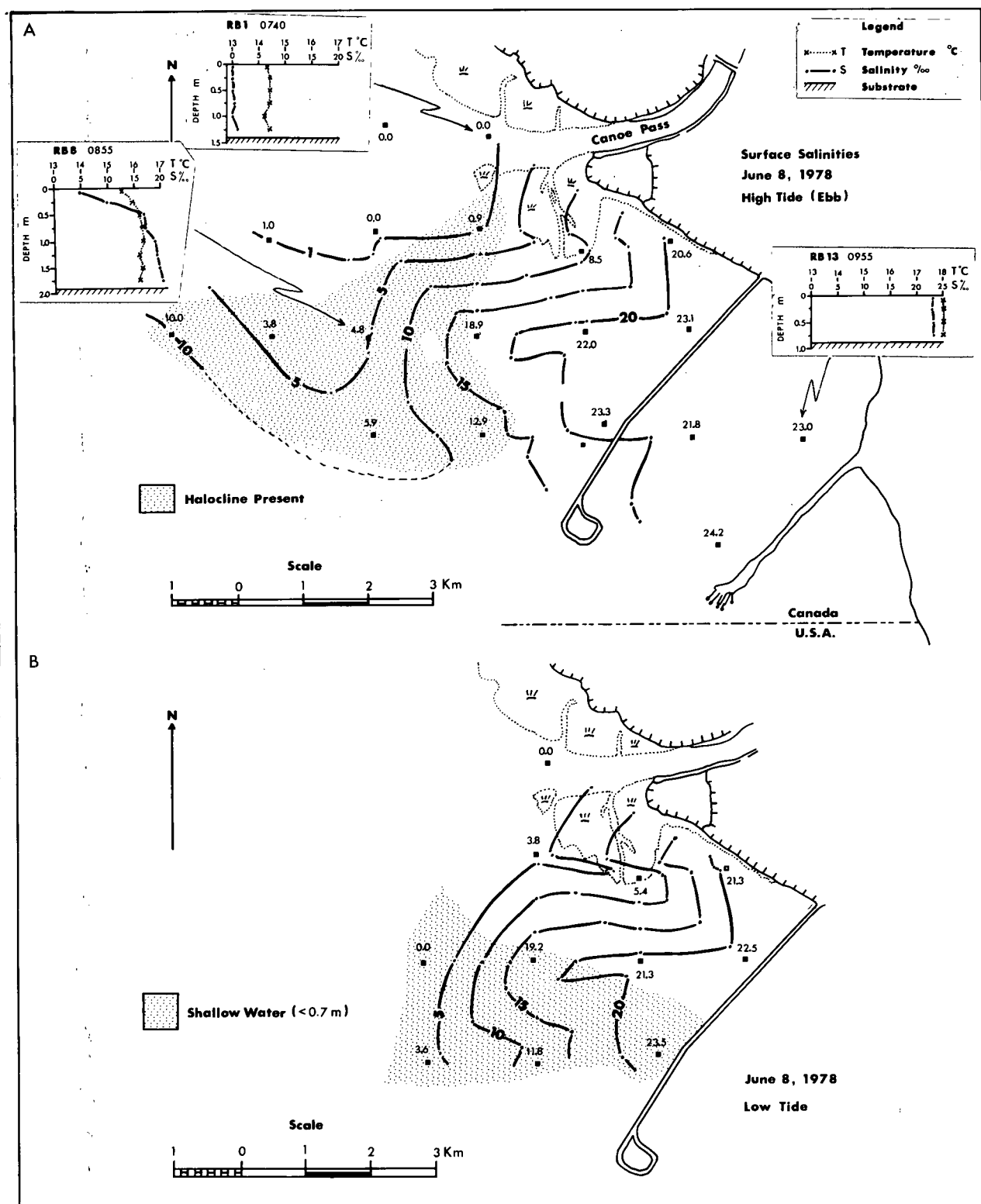


Figure 9. a) Surface-water salinities at high tide on ebb between Canoe Pass and the ferry causeway on June 8, 1978. Stippled area indicates region where a halocline is present in the water column. Mechanical contouring employed. Three representative salinity/temperature profiles included.

b) Surface substrate and shallow water salinities on approaching low tide on June 8, 1978. Mechanical contouring employed.

isohaline (Appendix 8 ) and these waters would almost certainly have the same salinity as the surface substrate waters at low tide, had it been possible to continue sampling until low water). The contours in Figures 9a and b are almost coincident, the only difference being that the two lobes of low salinity water, one from Canoe Pass and the other from the smaller distributary channels of the Brunswick Point marsh, have extended slightly further to the east during the late stages of ebb. Thus, at least in this case, surface substrate salinities at low tide are a very close reflection of surface water salinities at high tide on ebb.

It is not possible on the basis of Figure 8 or 9 to quantitatively define or contour the transition from marine to brackish environments, because the data does not divide naturally into two groups. However, it is possible to precisely define brackish and marine water masses on the basis of the salinity profiles, the boundary between them being defined by the halocline. This lies anywhere between 15 and 20‰ (Fig. 9a; Appendix 8 ). Three different values were tested to define the boundary between the brackish and marine water masses, namely 15‰, 17.5‰ and 20‰. As a measure of 'marine-ness' the percent thickness of the salt wedge at each station was calculated for each of the three boundary definitions (percent thickness rather than actual thickness was calculated to eliminate variation due to variability in water depth across the intertidal zone). The three sets of values were contoured. Figure 10 is the result for 17.5‰. Although the values at individual stations varied depending on which of the three definitions was used, the contours remained very similar in location and pattern (Appendix 8 ), and it does not appear to be important to define the boundary between marine and brackish water masses to within closer than 5‰. Figure 10, of course, only represents one part of one tidal cycle on one day at one particular time of year. However, the data are taken from that part of the tidal cycle which



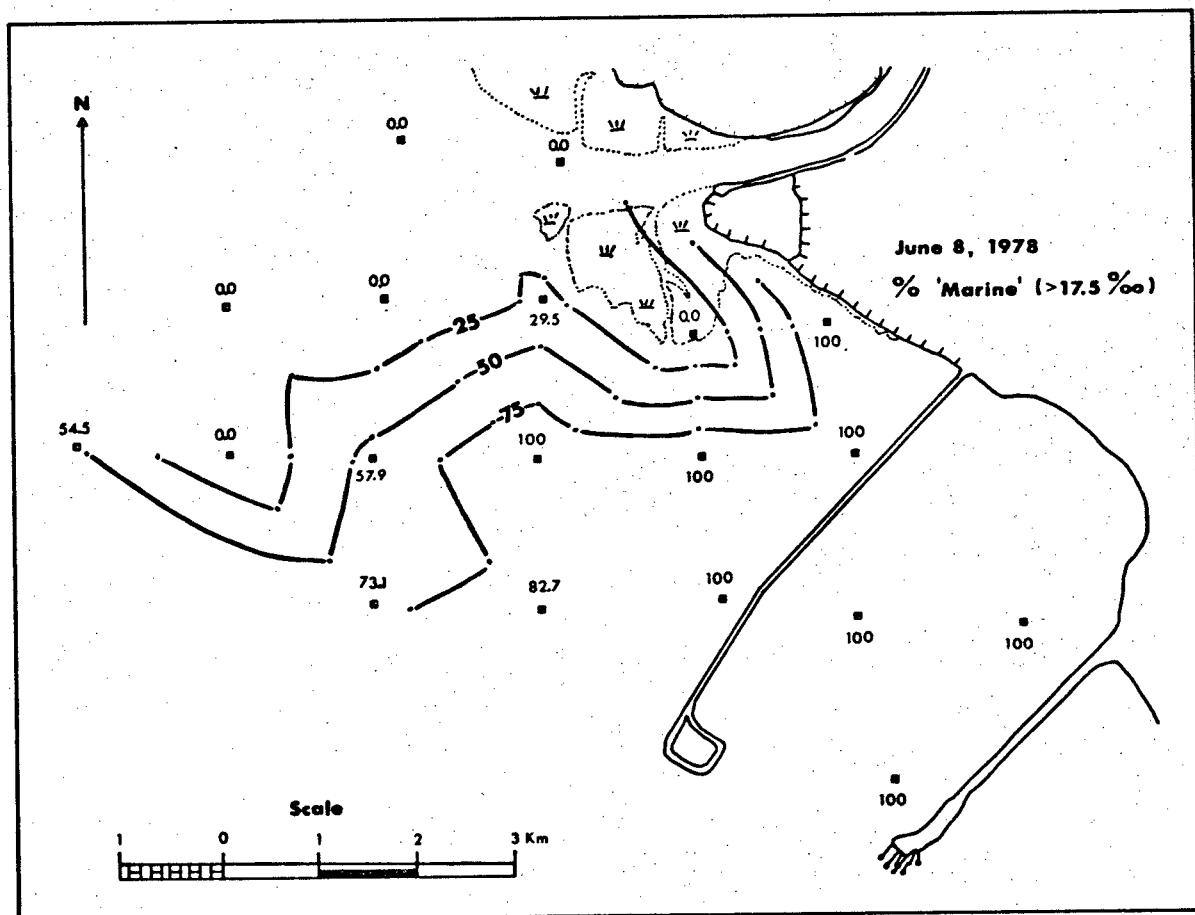


Figure 10. Percent thickness of the salt wedge, for 17.5‰ as the boundary between marine and brackish water masses. Mechanical contouring. Numbers next to stations indicate percent thickness of salt wedge.

determines surface substrate salinities at low tide, which are particularly important to benthic organisms dependent on the surface environment, and it is representative of a fairly critical time of year when the Fraser is at its peak discharge.

#### Discussion of Salinity Regime

Figure 10 illustrates the abrupt transition from a marine to brackish salinity regime between the Coalport causeway and Canoe Pass. The exact point of transition between 'marine' and brackish environments can arbitrarily be defined at the 50% contour in Figure 10. The cause of the abrupt change is thought to be due to the presence of a topographic high between Canoe Pass and the Coalport causeway (Fig. 3) which divides the two environments and prevents low salinity water in Canoe Pass from flooding over towards the causeway at the beginning of flood tide. At the early stages of flood tide, Strait of Georgia water, which is probably of high salinity, floods in around the Coalport from the southeast (Beak-Hinton, 1977) into the topographic depression on the immediate northwest side of the causeway (Fig. 3), establishing a saline wedge in the area before low salinity water can flood over from Canoe Pass. The southeasterly tidal currents on flood would also tend to prevent the low salinity waters of Canoe Pass from reaching this area. However, in the immediate vicinity of the Brunswick Point marsh, distributary channels from Canoe Pass cut through the marsh and discharge low salinity water over this topographic high establishing a low salinity plume in front of the Brunswick Point marsh (Fig. 9, 10). These distributary channels are unusual in that they dry out during low tide, but act as river channels during high tide stages. As the tide floods into Canoe Pass river water is diverted into these distributaries and floods along them to meet the incoming sea.

Strong seaward flowing currents continue during ebb tide as evidenced by the seaward orientation of bedforms (dunes and ripples) at the mouth of the main channel at low tide. At low tide, small streams in the channels drain water back towards Canoe Pass, indicating that the seaward mouths of the channels lie at higher elevations than their entrances at Canoe Pass. Thus, the dominant seaward flow in the channels on both flood and ebb tides must be maintained by a difference in elevation between the water surface in Canoe Pass and sea level over Roberts Bank, that of Canoe Pass being slightly higher. This is a perfectly reasonable suggestion to make as there must be a difference in hydraulic head between Canoe Pass and the sea in order to maintain river flow. These distributary channels are probably essential for the development and maintenance of the brackish marsh at Brunswick Point, as they establish a buffer zone of brackish water between the marsh and the 'marine' area immediately offshore. The recent advance of the marsh at Brunswick Point (Moody, 1978) is not simply a function of elevation, because, if it were, marsh would mantle the entire algal mat zone southeast of this area. The diversion of fresh water flow from Canoe Pass to this area has probably been essential for brackish marsh expansion.

#### DISTRIBUTION OF THALASSINIDEAN SHRIMPS

##### Description

The distribution of thalassinidean burrowing shrimps is presented in Figure 11, based on hovercraft and helicopter sampling surveys in August, 1977, June, 1978, and August, 1978. Stations sampled on foot in September, 1977 and on a transect in September, 1976 (Swinbanks and Murray, 1977) are also included to maximize coverage. Results from the inter-causeway area are included to give a complete picture of shrimp distribution on Roberts Bank. Table III compares Callianassa and Upogebia densities at ten stations sampled

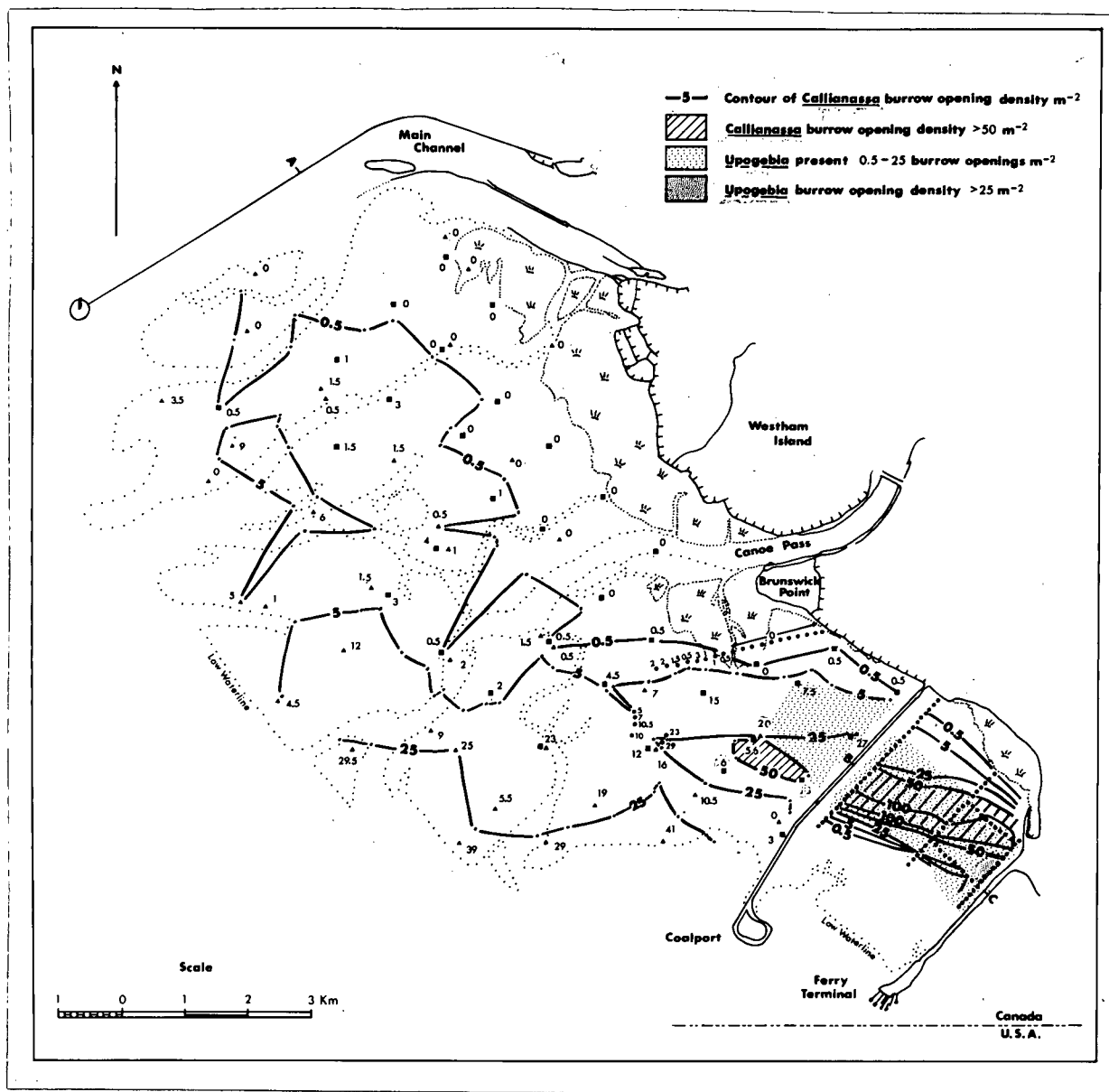


Figure 11. Distribution of thalassinidean shrimp burrow openings on Roberts Bank based on data collected in 1977 and 1978. Where stations sampled in 1977 were reoccupied in 1978 the average density has been used. Data for the inter-causeway area are presented in Part 4A. Mechanical contouring employed.

TABLE III

Comparison of Thalassinidean Shrimp Densities  
at Stations Sampled in 1977 and Reoccupied in 1978

August, 1977			June, 1978			August, 1978		
St.	<u>Callianassa</u>	<u>Upogebia</u>	St.	<u>Callianassa</u>	<u>Upogebia</u>	St.	<u>Callianassa</u>	<u>Upogebia</u>
RA1	0	0	RB1	0	0	-	-	-
RA2	0.5 $\pm$ 0.6	0	RB2	0.5 $\pm$ 0.7	0	-	-	-
RA3	0	0	RB3	0	0	-	-	-
RA4	0.5 $\pm$ 0.7	0	RB4	0.5 $\pm$ 0.7	0	-	-	-
RA5	35.5 $\pm$ 6.4	3.5 $\pm$ 3.5	RB5	20.5 $\pm$ 7.8	12.5 $\pm$ 2.1	RC12	26.0 $\pm$ 10.0	2.0 $\pm$ 2.3
RA7	60.5 $\pm$ 2.1	0	RB6	51.5 $\pm$ 2.1	0	-	-	-
RA8	1.0 $\pm$ 0.8	0	RB7	24.0 $\pm$ 2.8	0	-	-	-
RA9	36.5 $\pm$ 4.9	0	-	-	-	RC9	11.0 $\pm$ 5.1	0
RA10	0	0	-	-	-	RC6	1.0 $\pm$ 1.9	0

Note: Stations in June, 1978 are coincident within 50 m with those occupied in August, 1977.  
Stations occupied in August, 1978 lie within 100 m of those occupied in August, 1977.

in August, 1977 and reoccupied in June, 1978 and/or August, 1978. The agreement between the three sets of data is reasonably close, with the exception of stations RA8 and RB7, where Callianassa densities are markedly different ( $1 \text{ m}^{-2}$  at RA8,  $24 \text{ m}^{-2}$  at RB7). The general similarity between the three sets of data suggests that thalassinidean shrimps maintain fairly stable populations, which might be expected as they are probably long-lived organisms (MacGinitie, 1930 and 1934). There is a pronounced gradient in Callianassa density in the vicinity of station RA8 and RB7 and the discrepancy between these two results may be the result of sampling in slightly different locations.

High densities ( $>50$  burrow openings  $\text{m}^{-2}$ ) of Callianassa are restricted to the marine section of Roberts Bank immediately north of the Coalport causeway and in the inter-causeway area (Fig. 11). The peak in Callianassa distribution shifts to lower intertidal levels as one moves northward from the Coalport, and quite high densities ( $>20$  burrow openings  $\text{m}^{-2}$ ) of Callianassa occur down to the -2.4 m level (Geodetic Datum) - low water mark on August 17 and 18, 1978. As Main Channel is approached Callianassa densities decrease to less than  $0.5 \text{ m}^{-2}$  (burrow openings) at all intertidal levels.

Upogebia were only recorded at two stations on the grid, and they are restricted to the 'marine' area between the Brunswick Point marsh and the causeway.

#### Relationship Between Shrimp Density and Substrate Parameters

Stations were grouped into 0.6 m elevation class intervals on the basis of the Swan Wooster (1967) topographic map (Fig. 3), to analyze relationships between Callianassa density and the substrate parameters of percent mud and salinity. Data on Upogebia are insufficient to carry out any statistical

analysis. Mud content data for 1977 and 1978 were pooled, because the general lack of laminated deposits at stations suggests that mud contents do not vary appreciably with time. On the other hand, substrate salinity does show quite drastic temporal variations (Figs. 8, 9; Appendix 8 ), and for this reason the data for August, 1977 were initially treated separately from that for August, 1978. Linear regression analysis reveals no significant correlation between percent mud and Callianassa density (Table IV; Appendix 9 ). Correlation coefficients were less than 0.6, none were significant at the 95% confidence level ( $r$  test), and four out of five were not even significant at the 80% level. Segregating the data into 1977 and 1978 groups did not improve correlations (Table IV). On the other hand, substrate salinity is positively and significantly correlated to Callianassa density. Five out of eight class intervals show positive correlations, which are significant at the 95% confidence level (Fig. 12B, C, F, H and J). Interestingly, the only class interval which showed a negative correlation (Fig. 12G) contains a station from the eelgrass zone next to the Coalport, where salinities are high but Callianassa are absent. Exclusion of this station results in a positive correlation coefficient ( $r=0.383$ ). Unclassed data for 1977 (Fig. 12E), 1978 (Fig. 12K) and 1977/78 (Fig. 12L) also give significant positive correlations. Pooling the classed data for 1977/78 resulted in significantly reduced correlation coefficients (Appendix 9 ) because substrate salinities in August, 1978 were significantly lower than those at comparable stations in August, 1977 (Fig. 9; Appendix 8 ).

In order to further test the hypothesis that Callianassa distribution is correlated to salinity, six stations were located on foot at a fixed tidal level (-1.55 m Geodetic Datum) between Canoe Pass and the Coalport (Fig. 2) in an area showing a pronounced salinity gradient. The grain size of the substrate does not vary appreciably between the stations (Table V), and lies

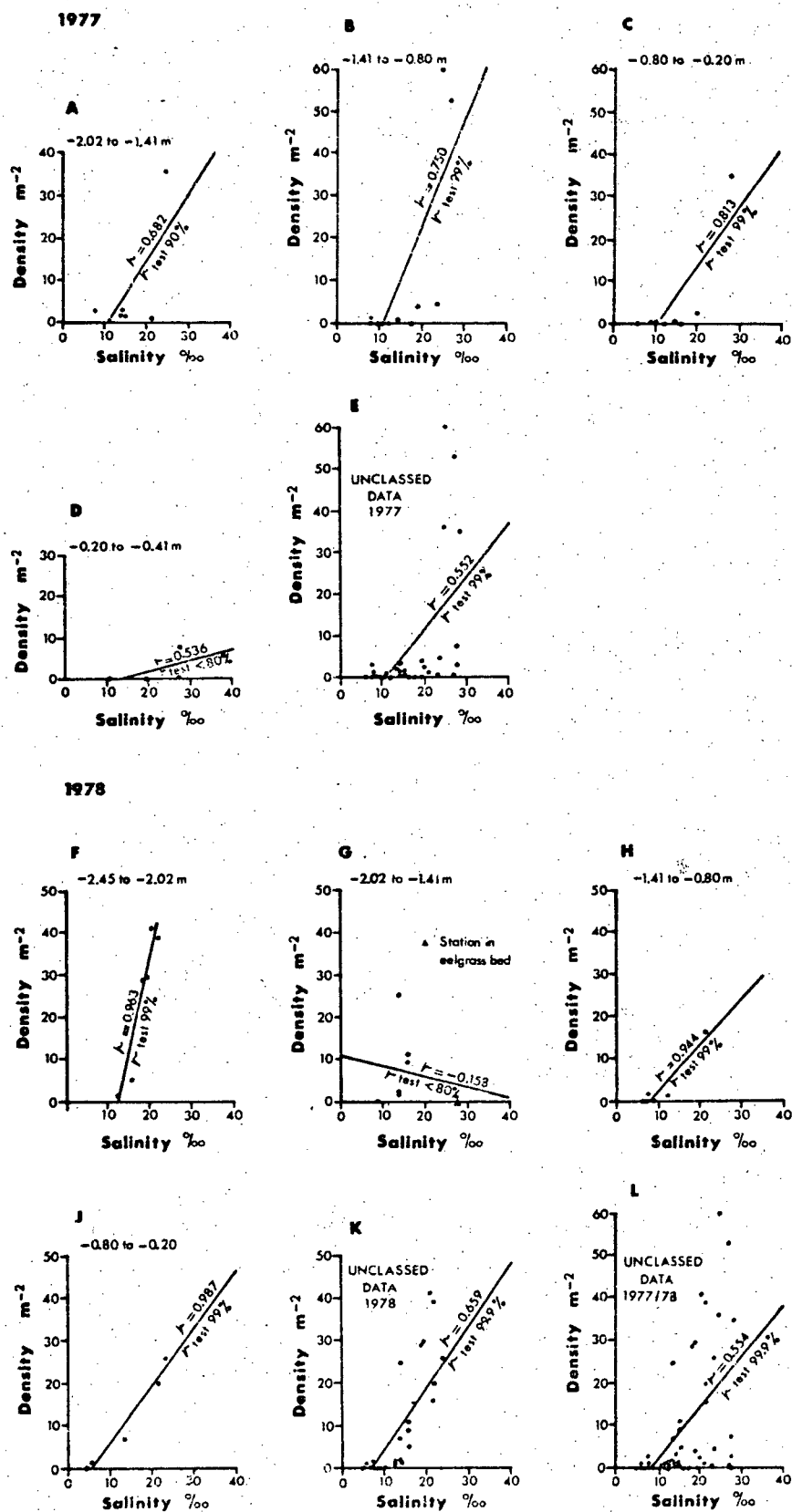


Figure 12. Relationship between *Callianassa* burrow opening density and the salinity of surface substrate waters. Best-fit linear regression lines are drawn along with their correlation coefficients ( $r$ ) and significance level ( $r_{test}$ ).



TABLE IV

Comparison of Correlation Coefficients (r) Between  
Callianassa Burrow Opening Density and Percent  
 Mud Using Pooled and Unpooled Percent Mud Data

Elevation Interval (Geodetic Datum, m)	Pooled Percent Mud Data 1977/78		Unpooled Percent Mud Data			
	r	r test (%)	r	r test (%)	r	r test (%)
-2.45 to -2.02	0.575	80	Insufficient Data (N=2)		0.886	95
-2.02 to -1.41	-0.254	<80	-0.169	<80	-0.481	<80
-1.41 to -0.80	-0.201	<80	-0.201	<80	No Data	
-0.80 to -0.20	-0.199	<80	-0.230	<80	Insufficient Data (N=1)	
-0.20 to +0.41	0.053	<80	0.053	<80	No Data	
Unclassed Data	-0.172	<80	-0.189	<80	-0.322	<80

TABLE V

Relationship Between Surface Substrate Salinity and Callianassa  
Burrow Opening Density at a Fixed Tidal Level at Six Stations  
Midway Between Canoe Pass and the Coalport Causeway (Fig. 2).

Station	Median ( $\emptyset$ )	Mud Content ( $\emptyset$ )	Surface Substrate Salinity (‰)		Density ( $\text{m}^{-2}$ )
			September 10	September 11	
1	2.94	7.39	24.5	21	$23.50 \pm 4.4$
2	2.73	5.41	24.5	21	$19.25 \pm 2.4$
3	2.60	10.48	18.0	19	$10.00 \pm 1.4$
4	2.73	6.09	17.5	19	$10.50 \pm 4.1$
5	2.96	17.94	12.5	9	$6.75 \pm 1.7$
6	3.36	35.93	12.5	9	$5.00 \pm 0.8$

Note: Burrow opening density ( $\text{m}^{-2}$ ) estimated by taking 16 readings with a  $0.25 \text{ m}^{-2}$  quadrat.

well within the range of median grain size and percent mud known to be acceptable to Callianassa in the inter-causeway area (Part 4A). Although the salinity values differed on the two days monitored there was a consistent decrease in salinity from stations 1 to 6 accompanied by a decrease in Callianassa density (Fig. 13a). Salinity profiles, taken with the apparatus described in Appendix 5, revealed that high salinity water (>20‰) is present within 15 cm of the surface, even at stations 5 and 6, where surface salinities are low (Fig. 13b). Thus, adult Callianassa, which live at depths greater than 30 cm on Roberts Bank, encounter these high salinity interstitial waters which are free to enter their unlined burrows (L. Thompson and Pritchard, 1969), and they are not directly exposed to the low salinity surface waters.

#### Discussion of Thalassinidean Shrimp Distribution

The absence of Upogebia from northern Roberts Bank cannot be accounted for in terms of the mud contents of the substrate or tidal elevation. The tidal flats immediately in front of the Westham Island marsh are upper aquazonal to lower amphizonal in exposure and the sediments contain about 50% mud. Under the same conditions of exposure and mud content Upogebia attain densities of 84 burrow openings  $m^{-2}$  in the inter-causeway area (Part 4A), while not one single Upogebia burrow has been observed in front of the Westham Island marsh. Similarly, Callianassa distribution on the brackish tidal flats of Roberts Bank cannot be explained in terms of tidal elevation or grain size. Understandably, Callianassa is absent in the brackish marshes where dense rootlets probably render deposit feeding and burrowing impossible for Callianassa, and, because these marshes extend to much lower elevations than the saltmarshes of Boundary Bay and the inter-causeway area, the upper limit to Callianassa

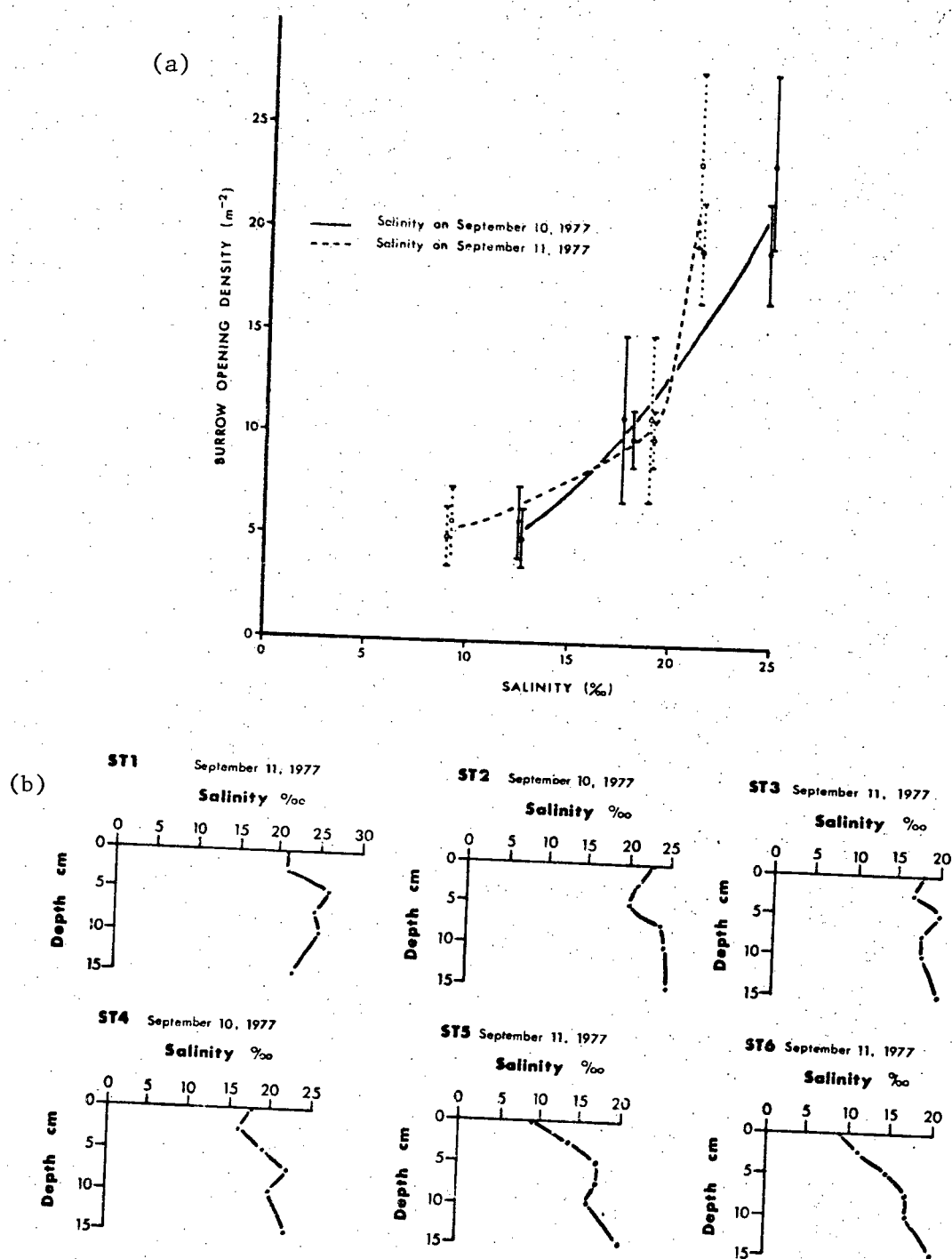


Figure 13. a) Relationship between Callianassa burrow opening density and surface substrate salinity at a fixed tidal level ( $-1.55$  m Geodetic Datum), September 10-11, 1977.  
 b) Substrate salinity profiles at Stations 1-6, September 10-11, 1977.

distribution is inevitably lowered. But Callianassa are also absent or only present in very low densities on the unvegetated tidal flats in front of Westham Island, where tidal elevation and mud contents of the sediment lie well within the ranges known to be acceptable to Callianassa in the inter-causeway area (Part 4A). The positive correlations between Callianassa density and substrate salinity suggest that Callianassa distribution can be explained by substrate salinity. The same is also probably true of Upogebia, although it cannot be demonstrated statistically, because nearly all of the quadrat readings registered zero Upogebia (i.e.,  $<0.5$  burrow openings  $m^{-2}$ ).

Callianassa californiensis can tolerate salinities down to about 10% but does not have any capacity to osmoregulate its blood chloride level in response to reduced salinity (L. Thompson and Pritchard, 1969); salinities lower than about 10% are lethal. Upogebia pugettensis can tolerate salinities down to about 3.5% (L. Thompson and Pritchard, 1969), and shows strong osmoregulatory capacities in salinities below 26‰, maintaining its blood chloride level above that of the surrounding medium (R. Thompson and Pritchard, 1969). Upogebia constructs a mud-lined burrow which opens directly to the surface (R. Thompson and Pritchard, 1969; Swinbanks, 1977). In contrast, Callianassa burrows lack a lining and have constricted apertural necks (R. Thompson and Pritchard, 1969; Swinbanks, 1979). Upogebia circulates water through its burrow for respiratory and feeding purposes (MacGinitie, 1930; Thompson, 1972), and thus the salinity of water within the burrows is similar to that in tidal pools at the surface (L. Thompson and Pritchard, 1969). Callianassa does not require to circulate surface waters through its burrow for the purposes of feeding as it is a deposit feeder (MacGinitie, 1934), nor does Callianassa need to for the purposes of respiration during exposure, because Callianassa can tolerate up to five days of continuous anoxia (R. Thompson and Pritchard, 1969). Thus, because of its mode of life, its

tolerance of anoxia and its unlined burrow, Callianassa can tolerate low salinity surface waters (L. Thompson and Pritchard, 1969). In contrast, Upogebia is dependent on surface waters for suspension feeding and respiration, and its burrow lining is probably impermeable to interstitial waters. Thus, despite being physiologically better adapted to cope with reduced salinity, Upogebia demonstrates lower tolerance of low salinity water in its distribution than Callianassa, as can be seen by comparing Figure 11 with Figures 8, 9 and 10.

Why then do Callianassa densities decrease in areas of reduced surface substrate salinity when salinities at depth remain high? The answer to this probably lies in reproduction. Callianassa has a planktic larval stage (MacGinitie, 1934). Highest shrimp mortality probably occurs in the first few hours after the larvae settle onto the substrate as postlarval shrimps and before they manage to burrow deep into the substrate, because they are then at the mercy of predators and the environment (MacGinitie, 1934). If one can assume that postlarval Callianassa, like the adults, cannot tolerate salinities below 10‰ for any length of time, then one might expect higher postlarval shrimp mortality in areas experiencing low surface substrate salinities, and hence reduced adult populations. However, this assumption may not be entirely justified because Felder (1978) has found limited evidence to suggest that juvenile Callianassa islagrande can tolerate salinities as low as 5‰, whereas adults die in salinities below about 15‰. Despite this, the explanation outlined above may still be valid even if postlarval Callianassa californiensis have a lethal limit lower than 10‰. Postlarval Upogebia form small 'Y' burrows in the surface sediments for suspension feeding (Thompson, 1972). In areas where surface substrate salinity can drop below 3.5‰ mortality among postlarval Upogebia, is probably high, as they must be entirely dependent on surface substrate waters for suspension feeding

and respiration.

The possibly <sup>likely</sup> must be entertained that the correlation between thalassianidean shrimp distribution and substrate salinity is caused by some other factor closely interrelated to salinity, for example turbidity, the concentration of suspended sediments and/or gross sedimentation rates.. Syvitski (1978) has demonstrated that suspended sediment concentration and sedimentation rates are negatively correlated with surface salinity in Howe Sound, B.C. The decrease in Callianassa and Upogebia densities accompanying decreases in salinity could perhaps be caused by increases in any or all three of the factors mentioned above. High turbidity levels might result in low primary productivity due to reduced light availability, resulting directly or indirectly in a reduced food supply for larval shrimps. Or larval or postlarval shrimp mortality might be high in areas where suspended sediment concentrations are excessively high, because, for example, high fluxes of suspended sediments may clog the filtering mechanisms of postlarval Upogebia preventing efficient feeding. Or postlarval shrimp mortality may be high in areas where high gross sedimentation rates may result in juvenile shrimps being smothered to death.

Callianassa are absent from the Z. marina bed adjacent to the Coalport, much as reported for the Z. marina beds in Boundary Bay (Swinbanks, 1979) and the inter-causeway area (Part 4A). This results in an anomalous negative correlation between Callianassa density and substrate salinity in Figure 12G. On the brackish tidal flats, in the absence of eelgrass, Callianassa extend to lower intertidal levels.

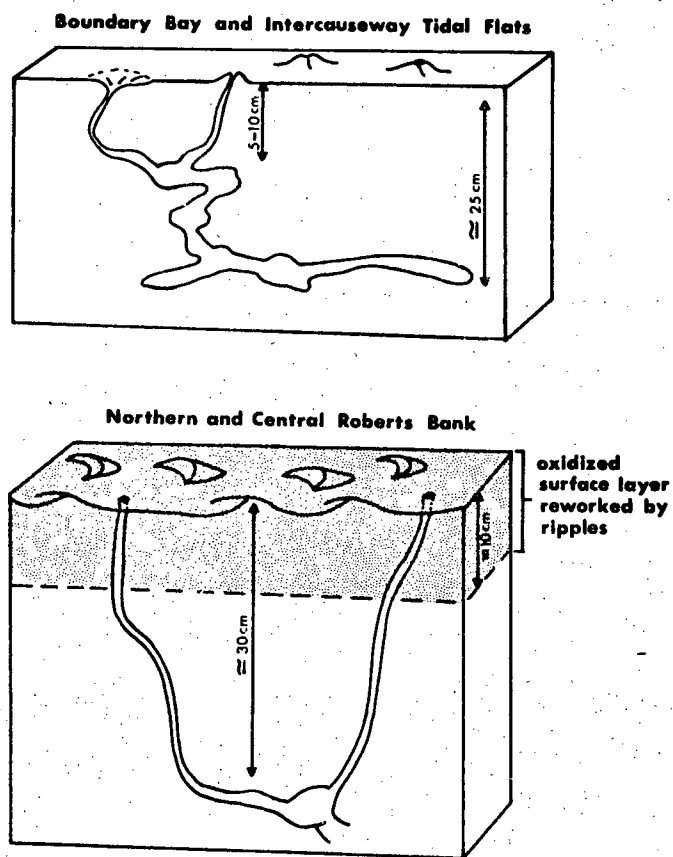
## BURROW GEOMETRY

In Boundary Bay, Callianassa constructs unlined feeding burrows which extend 20 to 30 cm down into the substrate, and then branch horizontally for distances of up to a meter (Swinbanks, 1979; Fig. 14). Each system has two, three or rarely four exits with constricted apertural necks which meet as a bulbous chamber at 5 cm to 10 cm depth. Branching is dichotomous, and there are bulbous turnarounds within the system. The Upogebia burrow is a 'Y' tube extending down to depths of 50 to 60 cm (Swinbanks, 1979; Fig. 14). Thompson (1972) reports burrow depths as great as 90 cm. In contrast to Callianassa burrows, Upogebia burrows are predominantly vertically oriented, do not have constricted entrances, and lack bulbous turnarounds (Fig. 14). The internal walls of the burrow are smooth and lined with mud. Upogebia burrows appear to be permanent dwelling burrows (Thompson, 1972; Swinbanks, 1979). Thompson (1972) has demonstrated that Upogebia secretes mucus from its hind-gut gland to cement the walls of the burrow. However, Thompson surprisingly asserts that "no particular size class of sediment particle is selected by the shrimp to build the burrow," (1972; p.iii) despite the fact that his own grain size data demonstrates that Upogebia burrow linings contain between one and a half to five times as much mud ( $>4.0 \phi$ ) as the surrounding substrate. In addition, the S.E.M. micrographs presented by Thompson (1972) clearly illustrate a high concentration of platy clay minerals in the inner burrow lining, and equant sand grains in the outer lining. The cohesive mud almost certainly aids in wall support. The sand grains form a knobbly exterior to the burrows (Fig. 14), resembling the trace fossil Ophiomorpha (Thompson, 1972).

The value of distinguishing between the trace fossil genera Ophiomorpha and Thalassinoides has recently been questioned (Fürsich, 1973) because there



### Callianassa Burrow



### Upogebia Burrow

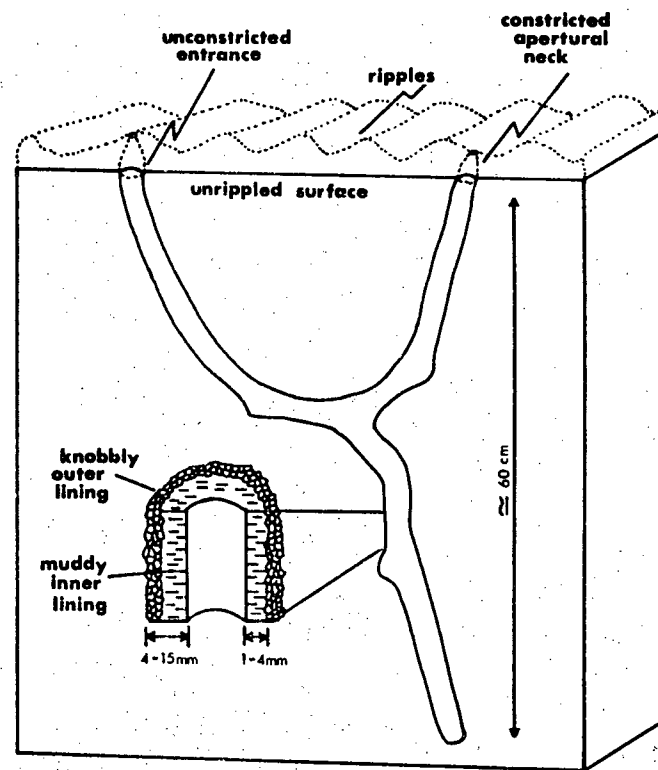
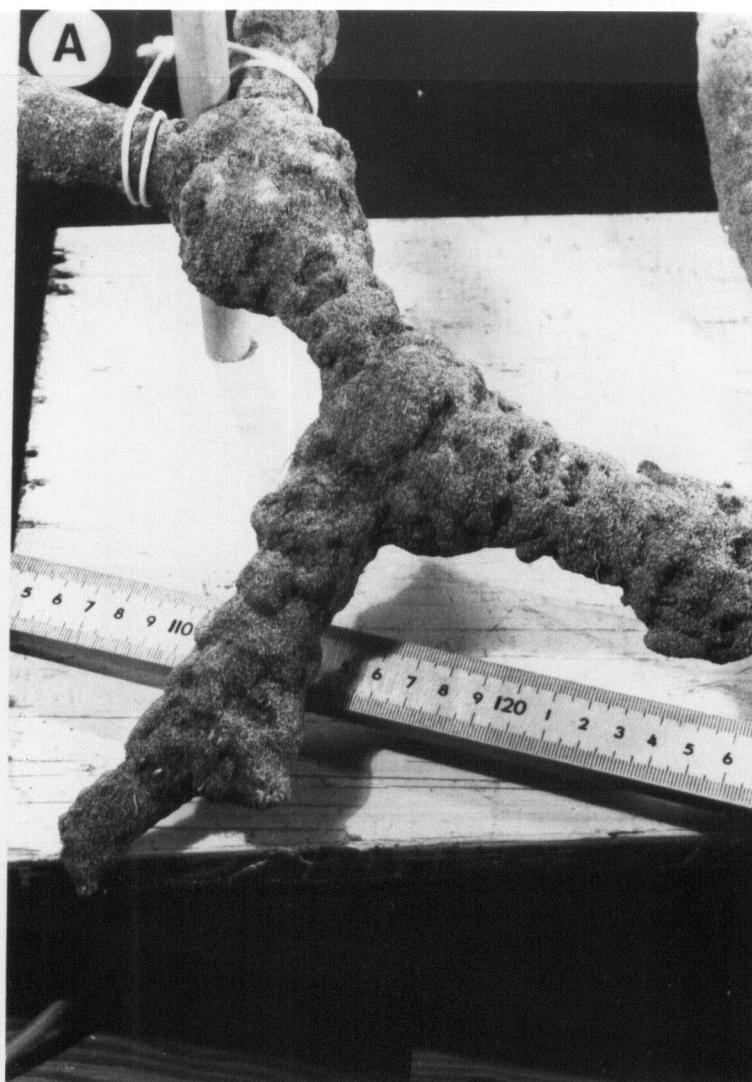


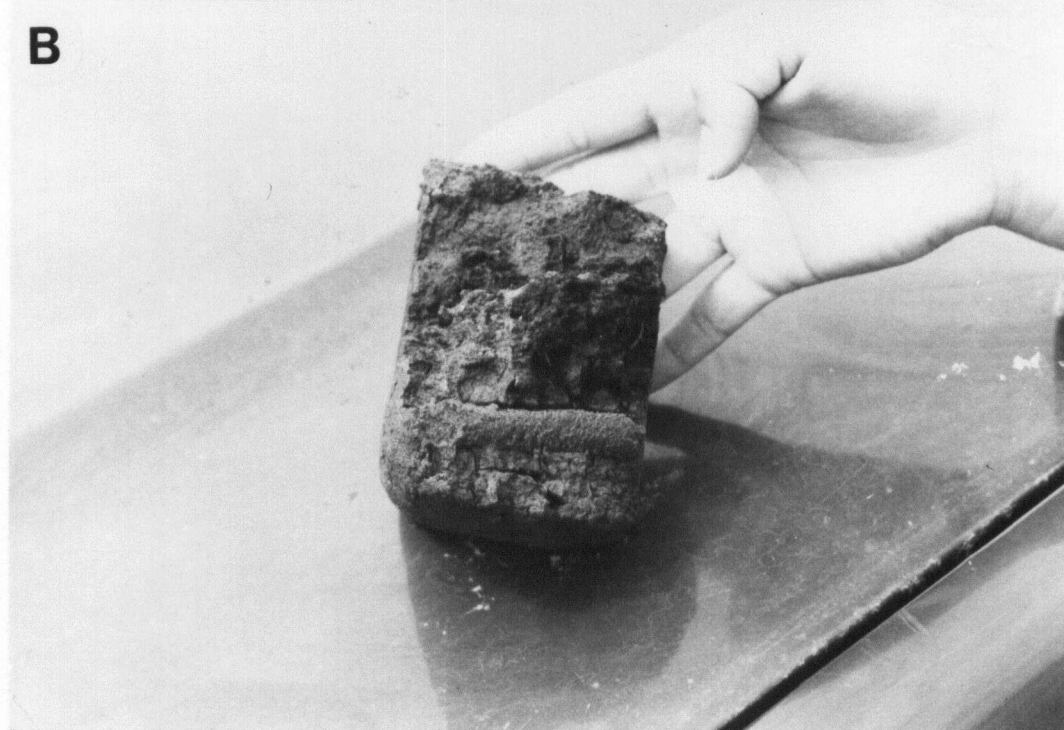
Figure 14. Typical geometry of Callianassa and Upogebia burrows on the Fraser Delta. Dimensions for cross-section of Upogebia burrow lining obtained from Thompson (1972).

is trace fossil evidence that the same organism can produce both Thalassinoides and Ophiomorpha within the same burrow (Kennedy and MacDougall, 1969; Kennedy and Sellwood, 1970). We have found evidence that Callianassa californiensis can produce both. All, but one, of the Callianassa casts retrieved from the Fraser Delta have the characteristic smooth burrow surfaces of Thalassinoides. However, one cast taken with a slower setting resin mixture impregnated the sandy walls of the burrow with resin, and the resulting cast had a thick coating of sand, which has a knobbly surface reminiscent of Ophiomorpha (Fig. 15a). This may be an artifact of resin casting or the resin may have picked out subtle differences in permeability in the burrow walls which could conceivably be highlighted by cementation during diagenesis. On scraping off the sand coating the smooth walls, typical of the other casts, is revealed underneath (Fig. 16a). If one of these burrows were infilled with sediment of a different grain size from that of the walls then the resulting trace fossil would be classified as Thalassinoides. A fossil example was found in a box core from Boundary Bay (Fig. 15b). Here a callianassid burrow enters a mud layer and has been infilled with sand. However, if a burrow such as in Figure 15a was infilled with sand of the same grain size as the burrow walls, the sandy burrow walls with knobbly exterior might form the outline of the trace fossil, and it would be classified as Ophiomorpha. Similarly the burrows of Upogebia could have the appearance of Thalassinoides or Ophiomorpha depending on whether the smooth inner or knobbly outer burrow wall is accentuated by diagenesis. As Bromley and Frey put it "inside every Ophiomorpha there is a Thalassinoides in the guise of a burrow cast" (1974, p. 330). To this we would add that outside every Thalassinoides may lie the ghost of an Ophiomorpha (Fig. 15a). Bromley and Frey (1974), however, still advocate distinguishing the two and in a subsequent paper Frey and Howard (1975) equate Upogebia affinis burrows with Thalassinoides and those of

- Figure 15. a) Resin cast of a Callianassa burrow coated in sand with a knobbly surface reminiscent of Ophiomorpha. Note that at top left the sand lining has been worn away by the string and the inner burrow lining is smooth.
- b) Fossilized Callianassa burrow having the appearance of Thalassinoides. Sand has infilled a burrow in mud.



**B**



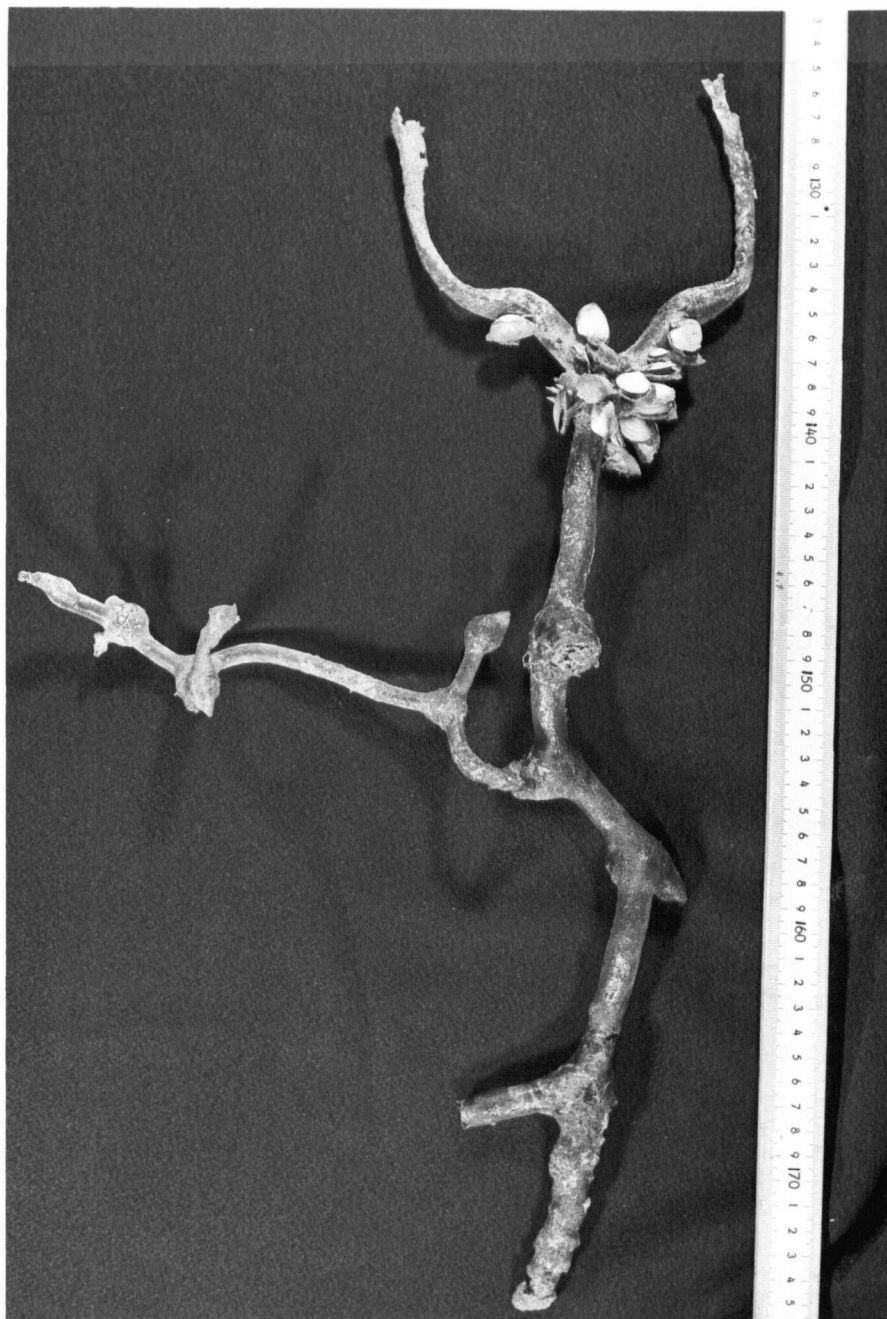


Figure 16. Cast of a Callianassa burrow taken from an area of high burrow density (446 burrow openings  $m^{-2}$ ). Two constricted entrances meet as a bulbous chamber at about 10 cm depth, and a vertical stem extends from this to about 50 cm depth. Cryptomya californica cluster around the bulbous chamber at the junction of the two exits. About thirty of these commensal bivalves are attached to the cast. The burrow is occupied by one shrimp. A burrow system of smaller diameter branches off from this system. It is joined to the main burrow system by a narrow constricted neck and is occupied by a small juvenile shrimp. Scale in centimeters.

U. pugettensis with Ophiomorpha. Apart from lacking knobs the burrows of these two species of Upogebia are very similar. Both have smooth durable burrow linings. We feel that the presence of knobs is not significant. A far more important distinction is that between permanent dwelling burrows with firm impermeable linings and open or short constricted exits used for suspension feeding and respiration, such as those of U. pugettensis and U. affinis, and temporary feeding burrows with permeable linings and constricted entrances, used for deposit feeding, like those of Callianassa californiensis, because, as has been demonstrated, burrow function has a profound bearing on the surface salinity which the organism can tolerate. Upogebia, although physiologically better adapted than Callianassa to tolerate reduced salinities, in fact demonstrates lower tolerance of brackish water because of the function of its burrow as a conduit for suspension feeding and respiration. Such distinctions form the basis of Seilacher's (1964) ethological classification of trace fossils. The continued use an ichnotaxonomic system for trace fossil classification, based on morphology without regard for function, limits the usefulness of trace fossils in paleoenvironmental interpretations.

Farrow (1971) has demonstrated that callianassid burrows exhibit markedly different geometries in the different sedimentary environments of an atoll. Callianassa burrows show significant variability in geometry on different parts of the Fraser Delta. In most areas Callianassa burrows are predominantly horizontally oriented. However, in areas of very high burrow density on the inter-causeway tidal flat Callianassa constructs burrows which are vertically oriented (Fig. 16). This is probably a result of population pressure forcing the shrimps to mine vertically. On central and northern Roberts Bank Callianassa construct burrows with unusually long, constricted apertural necks, which extend about 30 cm down into the substrate (Fig. 14). Beyond

this point box cores have revealed that the burrows appear to have similar geometry to those found in Boundary Bay. However, the long constricted apertural necks have proved to be an insurmountable barrier to resin, and casts have not been obtained from this area. There are a number of possible reasons for the construction of long constricted apertural necks. Callianassa may be avoiding the upper 5-10 cm of the substrate, which is constantly reworked by currents and waves in the relatively high energy environment of this part of Robert's Bank, and/or it may be burrowing deeper to reach regions of stable salinity. The long constricted necks may also reflect a change in feeding behaviour on the part of Callianassa. In the Boundary Bay and inter-causeway areas the bulbous chamber close to the surface may perhaps be used for suspension feeding, at high tide, as a supplement to Callianassa's deposit feeding activities (Swinbanks, 1979). On northern and central Roberts Bank, where the environmental energy is high and the salinity regime unstable, Callianassa probably abandons near surface feeding, and establishes its main burrow complex at greater than 30 cm depth.

Upogebia burrows exhibit similar geometry on all parts of the Fraser Delta (Fig. 14). However, in areas where currents rework the surface of the substrate, Upogebia construct short constricted apertural necks to their burrows. Thompson (1972) reports that Upogebia burrows taper towards the surface. The presence or absence of constriction is probably a function of environmental energy, constrictions being formed when currents rework the surface. The degree of constriction and the length of constricted sections, however, never approaches that of Callianassa burrows, and it seems that when conditions are favourable, Upogebia prefers no constrictions in its burrow.

## REVIEW AND CONCLUSIONS

Figure 17 summarizes all the available data on thalassinidean shrimp distribution by illustrating the stratigraphic succession of thalassinidean burrow density and floral/sedimentological zones to be expected if the Fraser Delta progrades seawards without subsidence. The contours of thalassinidean burrow density in Figure 17, based on living population density, are intended to be used as a qualitative guide to the density of thalassinidean trace fossils to be expected in the geological record.

The distribution of floral/sedimentological zones is critical to thalassinidean shrimp distribution. In terms of both Geodetic elevation and tidal elevation (as defined by exposure zones) the algal mat and eelgrass zones on the 'marine' tidal flats of Roberts Bank lie at lower elevations than their equivalents in Boundary Bay. This is probably due to differences in the nature of tidal channel drainage and substrate in the two areas. On the Boundary Bay tidal flats the substrate consists entirely of sand and the main tidal channel system is confined to the region below mean sea level, extending into subtidal regions. The upper reaches of the channels are broad and shallow, producing depressions in which submergence duration is enhanced and in which Z. marina beds can attain higher tidal elevations than on Roberts Bank (Swinbanks, 1979). On Roberts Bank the main tidal channel system occurs above mean sea level as a dendritic system of small channels draining water from the muds of the upper tidal flats. Plateaus between the drainage channels experience enhanced exposure favourable to the development of blue-green algal mats and, probably as a result, the algal mat zone extends to lower intertidal levels. On Roberts Bank the saltmarsh zone sets the upper limit to Callianassa distribution, and dense Z. marina growth appears to limit their population at low intertidal levels, while the highest densities of Callianassa occur in the non-vegetated sandflat and causeway zones. In Boundary Bay Upogebia



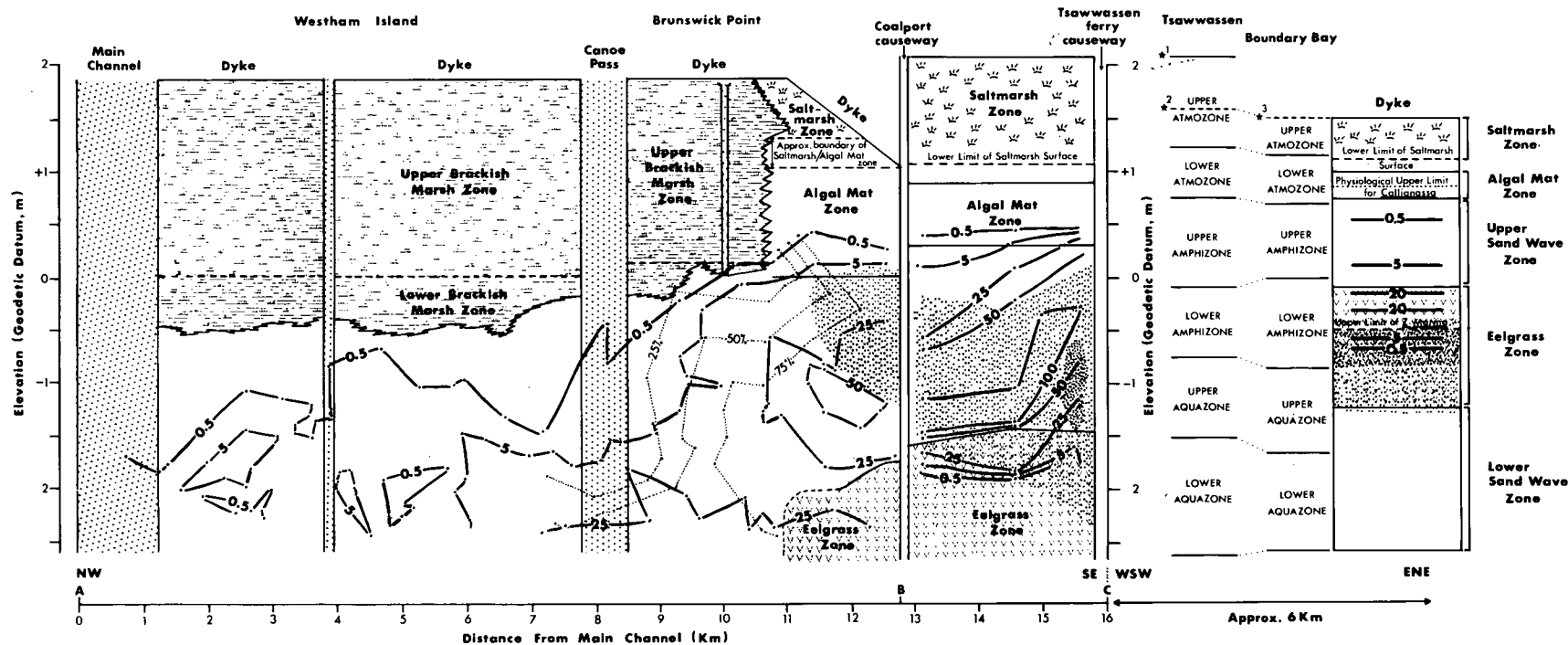
Figure 17. Summary of the distribution of thalassinidean burrows and floral/sedimentological zones on all the tidal flats of the Fraser Delta south of Main Channel, in the form a stratigraphic succession, constructed by projecting all the density data in Figure 11 onto a vertical plane passing through points A, B and C in Figure 11. The data on percent thickness of the salt wedge in Figure 10 have also been included to demonstrate the relationship between thalassinidean shrimp distribution and salinity regime. No data on the salt wedge are available NW of Canoe Pass. Data from Boundary Bay are based on Transect A alone (Swinbanks, 1979). Exposure zones allow cross correlation between Roberts Bank and Boundary Bay. Winter tidal data are not available for Boundary Bay and as a result the upper limit of the atmozone cannot be defined, but the spring tidal levels for June indicated allow cross correlation in the uppermost intertidal regions.

# NORTHERN AND CENTRAL ROBERTS BANK

## INTERCAUSEWAY TIDAL FLAT

## EXPOSURE ZONES

## BOUNDARY BAY



*Upogebia* present 0.5-25 burrow openings  $m^{-2}$   
*Upogebia* burrow opening density  $>25 m^{-2}$

Channel fill  
 -5- Contour of *Callianassa* burrow opening density  $m^{-2}$

--- 25% --- Percent thickness of the salt wedge ( $>17.5\%$ )

$\star^1$  Level of Spring Higher High Water in December at Tsawwassen  
 $\star^2$  Level of Spring Higher High Water in June at Tsawwassen

$\star^3$  Level of Spring Higher High Water in June at Boundary Bay  
 No winter Tidal Data available for Boundary Bay

are restricted to the beds of dense Z. marina growth where the mud contents of the sediments are sufficiently high (greater than about 2% mud). On Roberts Bank where mud contents of the sediments are an order of magnitude higher Upogebia span a wider elevation range extending up to the base of the upper amphizone, a level above which the maximum duration of anoxia due to exposure probably exceeds the lethal limit for postmolt Upogebia. In Boundary Bay where the upper limit of the algal mat zone extends to a slightly higher elevation than on Roberts Bank, Callianassa attains its physiological limit in elevation by extending up to, but not beyond, elevations experiencing a maximum of about five days of continuous anoxia due to exposure.

Between the Coalport and Canoe Pass on Roberts Bank a major transition in floral/sedimentological zonation occurs as a result of an abrupt transition from a 'marine' to brackish salinity regime. The algal mat zone is replaced by the lower part of the upper brackish marsh, while the lower brackish marsh, which consists predominantly of Scirpus americanus, becomes the lateral equivalent of the upper half of the sandflat zone. The eelgrass zone is replaced by a sandflat/mudflat zone, which is devoid of floral cover and crosscut by river channels, both active and relict. In response to these changes, the peak in Callianassa distribution moves to lower intertidal levels, because of the presence of low salinity water at higher tidal levels and because of the disappearance of eelgrass in lower intertidal regions. The lower limit of the brackish marsh forms the upper limit to Callianassa distribution. In close proximity to the major channels of the Fraser River, Callianassa are absent.

Upogebia is apparently more sensitive to the environmental factors of grain size and salinity than Callianassa. Upogebia shows a distinct preference for muddier substrates and cannot tolerate low salinity, surface substrate waters. The presence of sufficient mud in the substrate is probably

essential to Upogebia for the construction of its mud-lined burrow, and the circulation of surface waters through its impermeable mud-lined burrow for suspension feeding and respiration makes Upogebia more sensitive than Callianassa to changes in salinity regime, despite the fact that Upogebia is physiologically better adapted to cope with fluctuating salinities.

The positive correlation between Callianassa density and surface substrate salinity, and the distribution patterns of Callianassa and Upogebia suggest that the density of fossil burrows of both shrimps in the geological record could be used as a qualitative indication of paleosalinity, Upogebia burrows being a more sensitive indicator than those of Callianassa. The two types of burrow, used in conjunction, should form a powerful tool in paleoenvironmental reconstructions. In this regard it is considered very significant to distinguish between mud-lined, impermeable, permanent dwelling burrows with open entrances used for suspension feeding (e.g., Upogebia burrows) and unlined, permeable, temporary feeding burrows with long constricted entrances, used primarily for deposit-feeding (e.g., Callianassa burrows), because these factors determine whether the occupant shrimp is exposed to oxygenated surface waters susceptible to fresh water incursion, or whether it is exposed to hypoxic, high salinity interstitial waters. The distinction between Thalassinoides and Ophiomorpha, on the other hand, is considered to be of little significance from a paleoenvironmental point of view, as both Upogebia and Callianassa can probably produce both trace fossils under the right circumstances, and the distinction may simply reflect the grain size of the burrow filling sediment and/or the mode of diagenetic enhancement of the fossil burrow. On northern and central Roberts Bank Callianassa constructs burrows with longer, more constricted apertural necks than in the inter-causeway or Boundary Bay areas. This is thought to reflect a change in feeding mode, with Callianassa abandoning near surface feeding, because of

the instability of the surface, which is reworked by currents and exposed to fluctuating salinities.

#### ACKNOWLEDGEMENTS

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## SUMMARY AND CONCLUSION

The subdivision of the intertidal region into exposure zones at extreme critical tidal levels is advocated because 1) it allows cross correlation between different tidal regions experiencing different types of astronomically controlled tide 2) The critical tidal levels on which it is based may be causally related to intertidal zonation.

Boundary Bay tidal flats are unusual because they demonstrate very limited variability in substrate grain size. As a result a clear floral/faunal zonation is developed, controlled primarily by elevation and exposure. There are five floral/sedimentological zones on the tidal flats characterized by distinctive macrofaunal assemblages. These are from the shoreline seaward: the saltmarsh, algal mat, upper sand wave, eelgrass and lower sand wave zones. Topography of small and large scale of both physical and biogenic origin creates lateral heterogeneity within the biofacies of each zone. Abarenicola pacifica is abundant in the upper sand wave zone and this polychaete annually reworks about  $10^6 \text{ m}^3$  of sand. Abarenicola has the capacity to size-sort a sand/clay mixture by floating the clay out in the head shaft irrigation current.

The marine tidal flats of southeastern Roberts Bank have comparable floral zones to those of Boundary Bay, but only four major floral/sedimentological zones are present: saltmarsh, algal mat, sandflat and eelgrass zones. The lower limit of the saltmarsh lies at the same elevation as in Boundary Bay; just below the lower limit of the upper atmozone. However, compared with Boundary Bay, the algal mat zone extends to lower intertidal levels while the Zostera marina beds do not attain such high elevations. This is attributed to differences in the style of tidal channel drainage in the two areas, which in turn is a function of the grain size of the substrate.

On the inter-causeway tidal flat lateral variations in grain size are pronounced and greatly influence thalassinidean shrimp distribution.

Thalassinidean shrimps attain their highest densities on these tidal flats and there is some evidence of a negative interaction between Callianassa and Upogebia which may be a form of trophic group ammensalism. In the area of their peak density (446 burrow openings  $m^{-2}$ ) Callianassa rework the substrate they live in to a depth of 50 cm in about five months.

On central and northern Roberts Bank the tidal flats of the Fraser Delta undergo a major transition from a marine to a brackish environment due to the influx of freshwater from the Fraser River. The floral/sedimentological zones of the tidal flats are completely restructured. A brackish marsh zone laterally replaces the saltmarsh zone, the algal mat zone and the upper half of the sandflat zone while a sandflat/mudflat zone cross-cut by both active and relic channels displaces the eelgrass zone and the lower half of the sandflat zone. The brackish marsh extends well below mean sea level to about the upper limit of the aquazone. In response to these changes the peak in Callianassa distribution shifts to lower intertidal levels and Upogebia disappear altogether.

Upogebia constructs a mud-lined permanent dwelling burrow for suspension feeding and respiration purposes, whereas Callianassa builds an unlined temporary feeding burrow for deposit feeding. Upogebia is much more sensitive to the environmental factors of grain size, exposure and salinity than Callianassa due largely to the nature and function of its burrow. Upogebia shows a distinct preference for muddy substrates. It probably requires mud for constructing its burrow. Upogebia does not extend above the upper limit of the lower amphizone because immediately above this level the maximum duration of exposure probably results in a duration of anoxia lethal to postmolt Upogebia. In contrast Callianassa extends up to lower atmazonal

elevations, because of its greater capacity to tolerate anoxia. Anoxia tolerance is an adaption probably essential for life in an unlined burrow. Upogebia although physiologically better adapted to cope with reduced salinity in fact demonstrates lower tolerance of low salinity water in its distribution than Callianassa, probably because the function of its burrow as a conduit for respiration and feeding subjects the shrimp to low salinity surface waters, whereas Callianassa in its unlined burrow used for deposit feeding is protected from low salinity surface waters by high salinity interstitial waters which are free to enter its unlined burrow. These two types of burrow with their differing sensitivity to the environmental factors of exposure duration and salinity should form a powerful tool in paleoenvironmental reconstructions when used in conjunction. Tables I and II summarize the factors limiting and influencing thalassinidean shrimp distribution on Fraser Delta tidal flats.

Table III summarizes all nine floral and faunal distributional limits on the Fraser Delta tidal flats which have been found to lie within 15 cm or less of an exposure zone boundary or any other extreme critical tidal level. It is only possible to offer a convincing argument for their being a causal relationship between these faunal/floral limits and extreme critical tidal levels in the case of Callianassa and Upogebia because pertinent physiological data are only available for these organisms. However, the fact that so many different floral and faunal limits in different environments of the delta coincide with extreme critical tidal levels should at least warrant reconsideration of the tide factor hypothesis.

TABLE I

SUMMARY OF ENVIRONMENTAL FACTORS LIMITING THALASSINIDEAN SHRIMP DISTRIBUTION ON FRASER DELTA TIDAL FLATS

LIMIT	BOUNDARY BAY			INTER-CAUSEWAY AREA AND AREA S.E. OF BRUNSWICK PT.			NORTHERN AND CENTRAL ROBERTS BANK		
	ELEVATION (Geodetic Datum, m)	EXPOSURE ZONE	LIMITING FACTOR	ELEVATION (Geodetic Datum, m)	EXPOSURE ZONE	LIMITING FACTOR	ELEVATION (Geodetic Datum, m)	EXPOSURE ZONE	LIMITING FACTOR(S)
Upper limit of <u>Callianassa</u>	+0.9	Near upper limit of Lower Atmozone	>5 days anoxia due to exposure	+0.9	Lower Atmozone	Presence of saltmarsh	-0.2 to -0.5	Lower Amphizone	Brackish marsh and low salinity water
Lower limit of <u>Callianassa</u>	-0.6	Lower half of Lower Amphizone	Dense <u>Z. marina</u>	-1.8 to -1.9	Near upper limit of Lower Aquazone	Dense <u>Z. marina</u>	<-2.4	Near base of Lower Aquazone	Limit unknown
Upper limit of <u>Upogebia</u>	-0.5	Lower Amphizone	Insufficient mud*	0.0	Upper limit of Lower Amphizone	Anoxia due to Level 2 Exposure	NOT PRESENT DUE TO PRESENCE OF LOW SALINITY WATER		
Lower limit of <u>Upogebia</u>	-1.3	Upper Aquazone	Insufficient mud	<-2.2	Lower Aquazone	Limit unknown			

\* Upogebia restricted to beds of dense Z. marina where mud contents of sediment are higher (>2%).

TABLE II

SUMMARY OF EFFECTS OF VARIOUS ENVIRONMENTAL FACTORS ON THALASSINIDEAN SHRIMP DENSITY

	↑ <u>Callianassa</u>	↑ <u>Upogebia</u>	↑ % Mud	↑ Salinity**
<u>Callianassa</u>	-	↓	↑	↑
<u>Upogebia</u>	↓	-	↑↑	↑↑

\*\* Salinity in the range of 0 to 30‰

↑ Positive correlation      ↓ Negative correlation

↑ Weak positive correlation

↑↑ Strong positive correlation

TABLE III

Schematic Summary of All Floral and Faunal Distributional Limits on Fraser Delta Tidal Flats Which Lie Within 15 cm Or Less of an Exposure Zone Boundary Or Other Extreme Critical Tidal Level

	<u>MARINE TIDAL FLATS</u>		<u>BRACKISH TIDAL FLATS</u>
	Boundary Bay	Inter-causeway Area	Northern & Central Roberts Bank
UPPER			
ATMOZONE			
	<u>Lower Limit of Saltmarsh Zone</u>	<u>Lower Limit of Saltmarsh Zone</u>	
LOWER			
ATMOZONE	<u>Upper Limit of Callianassa**</u>		
	<u>Algal Mat Zone Lower Limit</u>		
	<u>Abarenicola Upper Limit</u>		
UPPER			
AMPHIZONE			
M.S.L.*			<u>Lower Limit of Upper Brackish Marsh</u>
	<u>Upper Limit of Z. Americana</u>	<u>Upper Limit of Upogebia</u>	
LOWER			
AMPHIZONE			
UPPER			
AQUAZONE			
		<u>Upper Limit of Z. marina</u>	
LOWER			
AQUAZONE			

\* M.S.L = Mean Sea Level

\*\* Upper limit of Callianassa lies at level at which the maximum duration of continuous exposure jumps from 4 to 9 days.

APPENDIX 1 -- SURVEY DATA FOR BOUNDARY BAY (PART 2)

## Survey Data for Transect A Boundary Bay

### Location of Starting Point

The starting point (T1) is located approximately where 72nd Avenue meets the dyke. The starting point lies on the dirt track entrance to the gate into the field on the west side of 72nd Avenue. Its precise location is on the axis of the ditch, which parallels the west side of 72nd Avenue, 6.49 m from the bench mark (marked by a metal sign with B.M. written in yellow on a red background), which lies at the corner of the fence facing the dyke.

### Orientation of Transect

The transect runs north/south (i.e., a continuation of 72nd Avenue). Station A1 lies at the edge of the saltmarsh and is 513.6 m ( $\pm 0.7$  m) south of the starting point (T1). Stations A1 to A22 were spaced at 91.4 m (300 ft) intervals by taping with a 30.5 m (100 ft) tape. The spacings of stations T1 to T6 were determined by stadia surveying and are as follows:

T1/T2    85.03 m  $\pm$  0.30 m

T2/T4    155.74 m  $\pm$  0.43 m

T4/T5    65.55 m  $\pm$  0.30 m

T5/T6    99.36 m  $\pm$  0.30 m

T6/A1    107.89 m  $\pm$  0.30 m

### Accuracy

Elevation differences were measured using an alidade which can measure the sine of the angle of elevation directly to  $\pm 0.5 \times 10^{-4}$ . At every station a foresight to next the station and backsight to the previous station were .

taken. If the instrument was perfectly leveled and no errors were made, then the foresight at a given station would exactly equal the backsight from the next. If the alidade was not in perfect adjustment, such that when it was leveled it was in fact tilted, then this would introduce a constant systematic error between foresight and backsight readings. Such an error was detected. There was a constant discrepancy between foresight and backsight readings of about  $12 \times 10^{-4}$ . Positive readings (i.e., elevation increasing towards observed station) always exceeded negative readings by this constant amount, indicating that when the instrument registered level it was in fact tilted downwards at about  $0.03^\circ$ . To overcome this problem the discrepancy between foresight and backsight readings was halved to obtain an estimate of true zero and the foresight reading used in calculations of elevation corrected using this estimated zero. By averaging all the estimated zeros for transects A and B (67 stations) a better estimate of true zero was obtained and this was determined to be when instrument registered an elevation with sine  $+5.9 \pm 0.7 \times 10^{-4}$ . This assumes that the true zero of the instrument did not vary with time and that deviations of estimated zeros from this value were due to accidental errors. Carrying this assumption one step further an estimate of accidental errors in surveying could be made by determining the average deviation of the estimated zeros from true zero, i.e.,

$$\text{average error of sine value} = \frac{\sum |\text{True zero} - \text{estimated zero}|}{N}$$

where  $N = 67$ .

This error was determined to be  $\pm 0.6 \times 10^{-4}$ , which over the station to station to station distance of 91.4 m is equivalent to an error of  $\pm 5.5$  mm.

Another possible source of error is in the measurement of distance between stations. The effects of this error are very small unless the error is



systematic (e.g., tape was not exactly 30.5 m long). Assuming the worst and estimating a systematic error of 0.3 m in the measurement of distance between each station, then this introduces an average elevation error of  $\pm 0.35$  mm for the average slope of transect A. This error is cumulative. For stations T1 to A1 slope distances were determined by stadia surveying, introducing an accidental error of  $\pm 0.3$  m in slope distance.

The errors estimated in the table are the sum of both systematic and accidental errors. By the theory of Least Squares accidental errors increase in proportion to the square root of the number of observations. Systematic errors are cumulative. In combining systematic and accidental errors to arrive at an overall estimate of error the worst was assumed, namely that the two sources of error are cumulative.

Table of Survey Data Transect A

Station	Sine of Elevation Angle ( $\times 10^{-4}$ )	Estimated Zero for Sine ( $\times 10^{-4}$ )	Corrected Sine for foresight ( $\times 10^{-4}$ )	Elevation Difference (m)	Geodetic Elevation (m)
B.M.					B.M. 1.524
T1	T1/B.M. -266.0	5.25	-271.25	-0.177	T1 1.701 $\pm$ 0.005
T2	T1/T2 120.5* -110.0**	5.25	115.25	0.978	T2 2.679 $\pm$ 0.011
T4	T2/T4 - 68.0 79.0	5.50	- 73.50	-1.143	T4 1.536 $\pm$ 0.020
T5	T4/T5 76.5 - 61.0	7.75	68.75	0.451	T5 1.987 $\pm$ 0.022
T6	T5/T6 - 80.0 88.5	4.25	- 84.25	-0.838	T6 1.149 $\pm$ 0.025
A1	T6/A1 - 10.0 21.0	5.50	- 15.50	-0.168	A1 0.981 $\pm$ 0.026
A2	A1/A2 3.5 11.5	7.50	- 4.00	-0.037	A2 0.945 $\pm$ 0.028
A3	A2/A3 - 3.5 17.0	6.75	- 10.25	-0.094	A3 0.850 $\pm$ 0.030
A4	A3/A4 8.0 4.0	6.00	2.00	0.018	A4 0.869 $\pm$ 0.031
A5	A4/A5 - 6.5 19.0	6.25	- 12.75	-0.116	A5 0.753 $\pm$ 0.031
A6	A5/A6 5.5 5.0	5.25	0.25	0.003	A6 0.756 $\pm$ 0.033
A7	A6/A7 - 8.0 21.0	6.50	- 14.50	-0.131	A7 0.625 $\pm$ 0.034
A8	A7/A8 - 3.0 14.0	5.50	- 8.50	-0.076	A8 0.549 $\pm$ 0.035
A9	A8/A9 - 4.0 15.0	5.50	- 9.50	-0.085	A9 0.463 $\pm$ 0.037
A9 1/3	A9/A9 1/3 - 18.0	(6.75)	- 24.75	-0.076	A9 1/3 0.387 $\pm$ 0.037
A9 1/3	A10/A9 1/3 27.0	(6.75)	20.25	0.125	A9 1/3 0.390 $\pm$ 0.037
A10	A9/A10 - 14.5 28.0	6.75	- 21.25	-0.195	A10 0.268 $\pm$ 0.037
A11	A10/A11 - 6.0 19.0	6.50	- 12.50	-0.113	A11 0.155 $\pm$ 0.039

\* foresight

\*\* backsight

Station	Sine of Elevation Angle ( $\times 10^{-4}$ )	Estimated Zero for Sine ( $\times 10^{-4}$ )	Corrected Sine for foresight ( $\times 10^{-4}$ )	Elevation Difference (m)	Geodetic Elevation (m)
A12	A11/A12 -17.0* 31.0**	7.00	-24.00	-0.219	A12 -0.064 $\pm$ 0.040
A13	A12/A13 2.5 10.0	6.25	- 3.75	-0.034	A13 -0.098 $\pm$ 0.040
A14	A13/A14 - 0.5 11.5	5.50	- 6.00	-0.055	A14 -0.152 $\pm$ 0.042
A15	A14/A15 - 4.5 17.5	6.50	-11.00	-0.101	A15 -0.253 $\pm$ 0.043
A16	A15/A16 - 7.0 17.5	5.25	-12.25	-0.113	A16 -0.366 $\pm$ 0.043
A17	A16/A17 - 8.0 18.0	5.00	-13.00	-0.119	A17 -0.485 $\pm$ 0.045
A18	A17/A18 - 9.5 22.5	6.50	-16.00	-0.146	A18 -0.631 $\pm$ 0.045
A19	A18/A19 -14.0 25.0	5.25	-19.75	-0.180	A19 -0.811 $\pm$ 0.046
A20	A19/A20 -14.0 26.0	6.00	-20.00	-0.183	A20 -0.994 $\pm$ 0.048
A21	A20/A21 2.0 19.5	10.75	- 8.75	-0.079	A21 -1.073 $\pm$ 0.048
A22	A21/A22 - 9.0	(10.75)	-19.75	-0.180	A22 -1.253 $\pm$ 0.049

\* foresight  
\*\* backsight

## Survey Data for Transect B Boundary Bay

### Location of Starting Point

The starting point (1) is located on the south side of the dyke where 96th Avenue meets the dyke. Its exact location is on the north/south line which parallels the western side of 96th Avenue, and passes through the western metal dyke gatepost at the end of 96th Avenue. It is on this line 25.41 m (uncorrected for elevation difference) from the bench mark at the end of 96th Avenue. The bench mark is located just outside the S.E. corner of the garden of the house on the western side of the end of 96th Avenue.

### Orientation of Transect

The transect runs north/south (i.e., a continuation of 96th Avenue). Station B1 lies at the southern edge of the saltmarsh. Stations B1 to B38 are spaced at 91.4 m (300 ft) intervals. Survey station 2 is 28.37 m (uncorrected for elevation difference) south of 1, and 48.21 m north of B1. These distances were taped.

### Accuracy

The average accidental error in elevation between successive stations at 91.4 m intervals is  $\pm 5.5$  mm, as in the case of transect A. The average systematic error assuming a distance error of 0.3 m between successive stations is slightly lower than transect A at  $\pm 0.21$  mm, because the average slope of transect B is less than that of transect A. The errors in the table are the sum of systematic and accidental errors.

Table of Survey Data Transect B

Station	Sine of Angle	Elevation ( $\times 10^{-4}$ )	Estimated Zero for Sine ( $\times 10^{-4}$ )	Corrected Sine for foresight ( $\times 10^{-4}$ )	Elevation Difference (m)	Geodetic Elevation (m)
B.M.	-----	-----	-----	-----	-----	B.M. 1.521
1	B.M./1	794* -784**	5.00	789.00	2.002	1 3.523 $\pm$ 0.005
2	1/2	-846 860	7.00	-853.00	-2.420	2 1.103 $\pm$ 0.010
B1	2/B1	- 8 17	4.50	- 12.50	-0.061	B1 1.042 $\pm$ 0.012
B2	B1/B2	- 2.0 14.0	6.00	- 8.00	-0.073	B2 0.969 $\pm$ 0.014
B3	B2/B3	0.0 13.0	6.50	- 6.50	-0.058	B3 0.011 $\pm$ 0.016
B4	B3/B4	- 2.0 15.5	6.75	- 8.75	-0.079	B4 0.832 $\pm$ 0.018
B5	B4/B5	- 8.0 22.0	7.00	- 15.00	-0.137	B5 0.695 $\pm$ 0.020
B6	B5/B6	- 2.0 13.5	5.74	- 7.75	-0.070	B6 0.625 $\pm$ 0.021
B7	B6/B7	- 2.5 15.5	6.50	- 9.00	-0.082	B7 0.543 $\pm$ 0.023
B8	B7/B8	- 5.0 17.0	6.00	- 11.00	-0.101	B8 0.442 $\pm$ 0.024
B9	B8/B9	- 7.0 20.5	6.75	- 13.75	-0.125	B9 0.317 $\pm$ 0.025
B10	B9/B10	- 1.5 13.5	6.00	- 7.50	-0.070	B10 0.247 $\pm$ 0.026
B11	B10/B11	- 7.0 18.5	5.75	- 12.75	-0.116	B11 0.131 $\pm$ 0.028
B12	B11/B12	- 8.0 20.0	6.00	- 14.00	-0.128	B12 0.003 $\pm$ 0.029
B13	B12/B13	- 29.0 41.5	6.25	- 35.25	-0.323	B13 -0.320 $\pm$ 0.030
B14	B13/B14	8.5 4.0	6.25	2.25	0.021	B14 -0.299 $\pm$ 0.031
B15	B14/B15	- 4.5 13.5	4.50	- 9.00	-0.082	B15 -0.381 $\pm$ 0.032
B16	B15/B16	- 10.0 19.0	4.50	- 14.50	-0.131	B16 -0.512 $\pm$ 0.033
B17	B16/B17	- 6.5 16.0	4.75	- 11.25	-0.104	B17 -0.616 $\pm$ 0.033

\* foresight

\*\* backsight

Station	Sine of Elevation Angle ( $\times 10^{-4}$ )	Estimated Zero for Sine ( $\times 10^{-4}$ )	Corrected Sine for foresight ( $\times 10^{-4}$ )	Elevation Difference (m)	Geodetic Elevation (m)
B18	B17/B18 - 1.0* 12.0**	5.50	- 6.50	-0.058	B18 -0.674 $\pm$ 0.034
B19	B18/B19 - 8.5 19.0	5.25	-13.75	-0.125	B19 -0.799 $\pm$ 0.035
B20	B19/B20 1.5 11.5	6.50	- 5.00	-0.046	B20 -0.844 $\pm$ 0.036
B21	B20/B21 - 7.5 20.0	6.25	-13.75	-0.125	B21 -0.969 $\pm$ 0.037
B22	B21/B22 11.5 0.5	6.00	5.50	0.049	B22 -0.920 $\pm$ 0.038
B23	B22/B23 5.5 5.0	5.25	0.25	0.003	B23 -0.017 $\pm$ 0.039
B24	B23/B24 9.5 3.0	6.25	3.25	0.030	B24 -0.887 $\pm$ 0.039
B25	B24/B25 13.0 - 1.5	5.75	7.25	0.067	B25 -0.820 $\pm$ 0.041
B26	B25/B26 13.5 - 1.5	6.00	7.50	0.067	B26 -0.753 $\pm$ 0.041
B27	B26/B27 - 3.5 14.5	5.50	- 9.00	-0.082	B27 -0.835 $\pm$ 0.042
B28	B27/B28 0.0 11.0	5.50	- 5.50	-0.049	B28 -0.884 $\pm$ 0.042
B29	B28/B29 3.5 11.0	7.25	- 3.75	-0.034	B29 -0.917 $\pm$ 0.043
B30	B29/B30 1.0 10.0	5.50	- 4.50	-0.040	B30 -0.057 $\pm$ 0.044
B31	B30/B31 8.0 4.0	6.00	2.00	0.018	B31 -0.939 $\pm$ 0.045
B32	B31/B32 - 7.5 18.5	5.50	-13.00	-0.119	B32 -1.058 $\pm$ 0.045
B33	B32/B33 4.5 8.5	6.50	- 2.00	-0.018	B33 -1.076 $\pm$ 0.046
B34	B33/B34 5.0 6.5	5.75	- 0.75	-0.006	B34 -1.082 $\pm$ 0.047
B35	B34/B35 0.0 10.0	5.00	- 5.00	-0.046	B35 -1.128 $\pm$ 0.047
B36	B35/B36 - 3.0 14.0	5.50	- 8.50	-0.076	B36 -1.204 $\pm$ 0.048
B37	B36/B37 1.0 10.0	5.50	- 4.50	-0.040	B37 -1.244 $\pm$ 0.049
B38	B37/B38 - 7.0 19.5	6.25	-13.25	-0.122	B38 -1.365 $\pm$ 0.049

\* foresight

\*\* backsight

APPENDIX 2 -- FAUNAL DENSITIES AND GRAIN SIZE DATA ON  
TRANSECTS A AND B, BOUNDARY BAY (PART 2)

Transect A

Station	<u>Batillaria</u>	<u>Nassarius</u>	<u>Callianassa</u> &/or <u>Upogebia</u>	<u>Mya</u>	<u>Abarenicola</u>	<u>Praxillela</u>	<u>Spio</u>
A1	P	0	0	0	0	0	7000
A2	16	0	p	P	0	0	4400
A3	25	0	p	P	0	0	4400
A4	31	0	p	P	0	0	4400
A5	32	0	p	P	19	0	600
A6	48	0	p	P	25	0	2500
A7	40	0	p	P	134	0	1200
A8	28	0	0.5 (C)	P	28	0	600
A9	12	0	P	P	25	0	600
A9 1/3	51	0	P	P	133	0	<600
A10	28	0	1 (C)	1	65	0	1900
A11	16	0	4 (C)	0.5	36	0	1900
A12	18	0	7 (C)	3.5	20	0	36000
A13	36	0	14 (C)	2.5	24	0	22000
A14	17	0	22 (C)	0	24	0	33000
A15	6	1	24 (C)	0	9	40	48000
A16	5	1.5	10 (C/U)	0	13	110	27000
A17	2	4.5	10 (C/U)	0	1	110	37000
A18	p	1	44 (C/U)	0	P	260	20000
A19	0	1	28 (U)	0	P	410	12000
A20	0	1	18 (U)	0	P	650	4000
A21	0	1	10 (U)	0	P	320	7000
A22	0	1	6 (U)	0	P	390	<600

P = present ( $<0.5 \text{ m}^{-2}$ )

(C) = Callianassa only

(C/U) = Callianassa and Upogebia

(U) = Upogebia only

N.B.: all densities in numbers per square meter.  
Spio densities rounded to nearest hundred.

(Cont'd....)



<u>Transect B</u>						
<u>Station</u>	<u>Batillaria</u>	<u>Nassarius</u>	<u>Callianassa</u>	<u>Abarenicola</u>	<u>Praxillela</u>	<u>Spio</u>
B1	1.5	0	0	0	0	12500
B2	6	0	0	0	0	12500
B3	7	0	0	0	0	5000
B4	28	0	P	0	0	7500
B5	29	0	P	20	0	2500
B6	57	0	3	5	0	2500
B7	18	0	4	18	0	<600
B8	21	0	1	15	0	<600
B9	13	0	7	42	0	600
B10	4.5	0	6	51	0	600
B11	7	0	14	61	0	<600
B12	5	0	15	23	0	600
B13	2.5	0	5	5	0	600
B14	1.5	0	7	31	0	<600
B15	1.5	0	12	14	0	<600
B16	1	P	0	6	0	1200
B17	0	P	0	3	3.5	P.N.D.
B18	0	0.5	0	4.5	4.5	P.N.D.
B19	2	P	0	0.5	56	P.N.D.
B20	4	1	0	0.5	91	P.N.D.
B21	13	2	0	0.5	73	P.N.D.
B22	26	5	0	P	54	P.N.D.
B23	32	0.5	0	0.5	44	P.N.D.
B24	8	P	0	0	12	25000
B25	0	P	0	1	0	8100
B26	0	0.5	0	3.5	0	7500
B27	0	1	0	1.5	0	4400
B28	0	P	0	5	0	5000
B29	0	P	0	4.5	0	2500
B30	0	P	0	P	0	3800
B31	0	P	0	P	10	3800
B32	0	P	0	1.5	10	1200
B33	0	5	0	P	10	1200
B34	0	1	0	P	10	3100
B35	0	0.5	0	5	100	600
B36	0	0.5	0	P	100	<600
B37	0	0	0	P	150	<600
B38	0	0	0	P	100	<600

P = present ( $<0.5 \text{ m}^{-2}$ )

P.N.D.: present but not determined.

N.B.: all densities in numbers per square meter.

## Grain Size Data Transects A and B Boundary Bay

Station	Graphic Mean ( $\phi$ )	Incl. Graphic Std. Dev. ( $\phi$ )	% Mud	Station	Graphic Mean ( $\phi$ )	Incl. Graphic Std. Dev. ( $\phi$ )	% Mud
A1	3.21	0.41	4.20	B24	2.60	0.33	0.25
A2	3.15	0.40	4.88	B25	2.59	0.31	0.56
A3	3.22	0.43	5.98	B26	2.50	0.31	0.26
A4	3.31	0.44	4.70	B27	2.55	0.33	0.63
A5	3.26	0.36	3.99	B28	2.53	0.32	0.31
A6	3.14	0.36	4.14	B29	2.52	0.32	0.44
A7	2.99	0.34	1.97	B30	2.48	0.31	0.26
A8	2.90	0.33	1.14	B31	2.43	0.32	0.28
A9	2.85	0.32	1.24	B32	2.42	0.33	0.25
A9 1/3	2.88	0.35	0.92	B33	2.41	0.29	0.21
A10	2.78	0.36	0.81	B34	2.38	0.32	0.14
A11	2.78	0.38	2.09	B35	--	--	--
A12	2.70	0.39	1.32	B36	2.47	0.32	0.31
A13	2.75	0.39	1.23				
A14	2.63	0.40	0.95				
A15	2.69	0.42	1.49				
A16	2.69	0.39	0.82				
A17	2.75	0.43	2.51				
A18	2.77	0.52	2.65				
A19	2.88	0.60	7.00				
A20	2.97	0.55	6.07				
A21	2.97	0.53	5.70				
A22	2.77	0.45	2.78				
B1	2.87	0.50	3.56				
B2	3.07	0.43	3.86				
B3	3.20	0.45	8.03				
B4	3.15	0.40	4.53				
B5	3.09	0.37	3.84				
B6	3.10	0.38	2.81				
B7	2.98	0.33	1.71				
B8	2.94	0.32	0.87				
B9	2.87	0.35	0.95				
B10	2.80	0.34	0.56				
B11	2.80	0.33	0.78				
B12	2.67	0.33	0.36				
B13	2.81	0.37	1.36				
B14	2.76	0.33	0.45				
B15	2.71	0.34	0.72				
B16	2.73	0.34	0.41				
B17	2.71	0.35	0.46				
B18	2.71	0.34	0.59				
B19	2.70	0.33	0.51				
B20	2.74	0.34	0.79				
B21	2.73	0.36	1.77				
B22	2.65	0.36	0.62				
B23	2.65	0.34	0.37				

APPENDIX 3 -- SURVEY DATA FOR STATIONS  
ON THE INTER-CAUSEWAY TIDAL FLAT (PART 4A)

## Survey Data for Transects A, B, C and D on the Inter-Causeway Tidal Flat

### Transect A

Transect A parallels the Tsawwassen ferry terminal causeway and lies  $150 \pm 1$  m from the raised concrete edge of Highway 17. Station A1 lies on the sandflat about 10 m from the edge of the cobbles on the shore. Stations were taped at 100 m intervals. Station numbers increase seawards.

Methods-- Elevations were determined by leveling from bench mark 'A' (Fig. 2 in back cover) with a T2 transit. The instrument was set up at every fourth station. At each set-up a backsight was taken to the preceding two stations and a foresight to the following two stations (i.e., maximum sighting distance 200 m). The stadia rod was mounted on a 0.5 m wooden spike, and pushed into the substrate at each station until its base was flush with the substrate, and held vertical by the rodman. This eliminated errors due to the rod sinking into the substrate while being held, and by simply rotating it on its axis the stadia rod could be tied in to the next set-up of the transit, by backsighting. The intersection of the cross hair on the stadia rod could be read to an accuracy of  $\pm 5$  mm over the 200 m sighting distance employed. Readings were constantly double checked by flipping the telescope through  $180^\circ$ . This eliminates the possibility of introducing an error due to incorrect leveling. The estimated error, therefore, is an accidental error of  $\pm 5$  mm. By the theory of least squares this error increases in proportion to the square root of the number of observations and this is how the errors were estimated in the following tables of data. The same surveying techniques were used from transects B, C and D.

### Transect B

Transect B starts from the promontory immediately southeast of the breach in the dyke. It parallels transect A at a distance of 1 km ( $\pm 3$  m). Station B1 lies 57 m from the edge of the marsh, which forms a cliff about 70 cm high. Station numbers increase seawards.

### Transect C

Transect C is located 258 m from the southeastern edge of the causeway road, and parallels the causeway. Station C1 is located 100 m from the base of the dyke. Station numbers increase seawards.

### Transect D

Transect D starts at A2 and ends at B7. D1 is adjacent to A2 and D9 is adjacent to B7.

### Transect E

Transect E starts at A11 and ends at B16. E1 is adjacent to A11 and E9 is adjacent to B16.

### Elevation of Algal Mat Zone/Saltmarsh Zone Boundary

The elevation of the upper limit of the algal mat zone was determined at seven points along the perimeter of the marsh between transects C and B. Station 1 lies next to B.M. 'C' and stations were consecutively numbered going towards transect B. The elevation of the upper limit of the algal mat zone was determined on the tidal flat immediately adjacent to the edge of the marsh. The elevation of the lower limit of the saltmarsh surface was determined on the tops of saltmarsh clumps at the edge of the saltmarsh at stations 1 and 7.

### Bench Marks

The elevations and locations of bench marks were obtained from the

municipal engineer of Delta Municipality. The bench marks were established for dyking purposes. Bench mark 'A' has reference number 66. It is a concrete block with a metal plate set on top with 'Legal Survey British Columbia' stamped on it. It marks the corner of a District Lot and lies between Highway 17 and the gravel road parallelling the causeway about 100 m southwest of the fence of the B.C. Hydro station. Bench mark 'B' has reference number 70. It is an iron pin, and lies about 0.3 m from the edge of the marsh next to a wooden post. It lies about 100 m southeast of a major breach in the dyke. Bench mark 'C' has reference number 74. It is a nail driven horizontally into the base of a telegraph pole about 0.5 m above ground level. It is marked with flagging tape. The telegraph pole is the twelfth pole encountered walking southeast from the dyke gate at the Coalport causeway. The nail is on the seaward side of the pole.

#### Independent Check of Survey Data

The survey data was independently checked by comparing observed tidal heights for ten low waters at the Tsawwassen ferry terminal tidal gauge with the observed height of the waterline on each transect at the time of low tide. The location of the waterline between surveyed stations was estimated to the nearest 10 m and its elevation determined by linear interpolation between the known elevations of the stations. The table of comparisons follows the tables of survey data.

Table of Station Elevations on the Inter-Causeway Tidal Flat

Transect A Station Elevation (Geodetic Datum, m)		Transect B Station Elevation (Geodetic Datum, m)		Transect C Station Elevation (Geodetic Datum, m)	
B.M.	2.728	B.M.	1.594	B.M.	3.266
A1	0.140 ± 0.005	B1	0.433 ± 0.002	C1	0.536 ± 0.006
A2	-0.062 ± 0.005	B2	0.396 ± 0.005	C2	0.416 ± 0.007
A3	-0.277 ± 0.005	B3	0.256 ± 0.005	C3	0.426 ± 0.008
A4	-0.492 ± 0.007	B4	0.081 ± 0.006	C4	0.376 ± 0.009
A5	-0.722 ± 0.008	B5	-0.059 ± 0.007	C5	0.371 ± 0.009
A6	-0.902 ± 0.009	B6	-0.224 ± 0.008	C6	0.251 ± 0.010
A7	-1.032 ± 0.009	B7	-0.389 ± 0.009	C7	0.096 ± 0.010
A8	-1.192 ± 0.010	B8	-0.519 ± 0.009	C8	-0.009 ± 0.011
A9	-1.322 ± 0.010	B9	-0.669 ± 0.010	C9	-0.089 ± 0.011
A10	-1.452 ± 0.011	B10	-0.839 ± 0.010	C10	-0.189 ± 0.012
A11	-1.597 ± 0.011	B11	-0.954 ± 0.010	C11	-0.294 ± 0.012
A12	-1.732 ± 0.012	B12	-1.024 ± 0.011	C12	-0.404 ± 0.013
A13	-1.807 ± 0.012	B13	-1.149 ± 0.012	C13	-0.469 ± 0.013
A14	-1.907 ± 0.013	B14	-1.264 ± 0.012	C14	-0.514 ± 0.014
A15	-2.047 ± 0.013	B15	-1.379 ± 0.013	C15	-0.579 ± 0.014
A16	-2.182 ± 0.014	B16	-1.469 ± 0.013	C16	-0.689 ± 0.015
		B17	-1.544 ± 0.014	C17	-0.774 ± 0.015
		B18	-1.719 ± 0.014	C18	-0.889 ± 0.016
		B19	-1.874 ± 0.015	C19	-0.974 ± 0.016
		B20	-1.889 ± 0.015	C20	-1.074 ± 0.017
		B21	-2.004 ± 0.016	C21	-1.189 ± 0.017
				C22	-1.294 ± 0.017
				C23	-1.409 ± 0.017
				C24	-1.499 ± 0.018
				C25	-1.559 ± 0.018
				C26	-1.759 ± 0.019
				C27	-1.782 ± 0.019
				C28	-1.892 ± 0.019
				C29	-1.987 ± 0.019
Transect D Station Elevation (Geodetic Datum, m)		Upper Limit of Algal Mat Zone Station Elevation (Geodetic Datum, m)		Lower Limit of Saltmarsh Surface Station Elevation (Geodetic Datum, m)	
D2	-0.266 ± 0.011	1	0.916 ± 0.005	1	1.066 ± 0.005
D4	-0.376 ± 0.010	2	0.893 ± 0.007	7	1.071 ± 0.009
D6	-0.364 ± 0.009	3	0.823 ± 0.007		
D8	-0.364 ± 0.007	4	0.893 ± 0.007		
		5	0.926 ± 0.007		
		6	0.926 ± 0.009		
		7	0.826 ± 0.009		

Comparison of Survey Data with Observed Tidal Data  
at the Tsawwassen Ferry Terminal Tidal Gauge

<u>Date</u>	<u>Time (P.S.T.)</u>	<u>Observed Low Water *Chart Datum (m)</u>	<u>Position of Waterline</u>	<u>Surveyed Elevation *Chart Datum (m)</u>	<u>Discrepancy (cm)</u>
Sept. 22/77	0655	1.42 (LLW)	A11.0	1.358	- 6.2
"	"	1.42 ( " )	C24.5	1.425	+ 0.5
Sept. 24/77	0856	1.56 ( " )	A10.0	1.503	- 5.7
"	"	1.56 ( " )	B16.25	1.466	- 9.4
"	"	1.56 ( " )	C23.75	1.477	- 8.3
Sept. 26/77	1036	1.78 ( " )	A 8.2	1.737	- 4.3
"	"	1.78 ( " )	C20.9	1.776	- 0.4
Oct. 2/77	1451	2.90 (HLW)	C 8.0	2.945	+ 4.5
Oct. 31/77	1456	3.24 ( " )	C 5.3	3.289	+ 4.9
Jul. 24/78	1413	1.55 (LLW)	A 9.5	1.568	+ 1.8
"	"	1.55 ( " )	B15.25	1.552	+ 0.2
"	"	1.55 ( " )	C23.5	1.500	- 5.0
Jul. 25/78	1501	2.03 ( " )	A 6.5	1.988	- 4.2
"	"	2.03 ( " )	B11.7	1.951	- 7.9
"	"	2.03 ( " )	C18.6	2.014	- 1.6
Jul. 28/78	1800	3.19 (HLW)	B 3.0	3.210	+ 2.0
"	"	3.19 ( " )	C 5.5	3.265	+ 7.5
Aug. 6/78	1248	1.26 (LLW)	B17.5	1.322	+ 6.2
Aug. 7/78	1311	1.44 ( " )	C24.5	1.425	- 1.5
Average Discrepancy					<u>± 4.3</u>

\* Tsawwassen Chart Datum = - 2.954 m Geodetic Datum

P.S.T. = Pacific Standard Time

Note: The waterline was observed for one hour around the time of low water and its lowest position recorded. Wave action was negligible at the time of low tide.



APPENDIX 4 -- GRAIN SIZE AND THALASSINIDEAN SHRIMP DENSITY DATA  
FOR STATIONS ON THE INTER-CAUSEWAY TIDAL FLAT (PART 4A)

Grain size and thalassinidean shrimp density data for  
Stations on Inter-Causeway Tidal Flat

Station	Median ( $\phi$ )	% Mud	<u>Upogebia</u> (burrow openings $m^{-2}$ )		<u>Callianassa</u> (burrow openings $m^{-2}$ )	
A1	3.18	20.43	0	0	70	90
A2	3.61	38.95	15	3	38	36
A3	3.80	43.33	28	11	95	113
A4	3.94	47.17	4	29	56	57
A5	3.81	44.19	82	44	35	76
A6	3.99	49.51	29	80	59	17
A7	4.04	50.95	81	67	30	24
A8	4.02	50.23	60	26	18	30
A9	4.06	51.71	114	55	15	22
A10	4.15	53.53	32	34	10	12
A11	3.85	47.27	8	14	21	15
A12	4.06	51.12	9	9	24	15
A13	3.65	43.33	0	14	10	24
A14	3.36	33.16	1	4	31	51
A15	3.59	44.13	10	3	7	8
A16	3.26	23.74	0	2	9	14
B1	3.88	44.80	0	0	1	0
B2	3.75	38.98	0	0	1	1
B3	3.45	12.31	0	0	10	14
B4	3.34	11.78	0	0	20	30
B5	3.30	9.93	0	0	32	12
B6	3.30	10.53	0	0	55	45
B7	3.30	13.83	5	0	49	53
B8	3.24	10.99	4	3	36	46
B9	3.24	10.58	10	4	53	60
B10	3.23	10.16	5	8	45	42
B11	3.26	12.49	0	0	51	49
B12	3.08	6.64	6	22	83	115
B13	2.98	6.14	1	6	82	128
B14	3.02	9.90	0	7	112	111
B15	3.17	13.81	7	9	97	106
B16	3.19	7.47	0	8	12	18
B17	3.17	17.07	4	0	108	72
B18	3.07	6.96	2	4	116	120
B19	3.05	8.32	0	1	67	74
B20	3.03	12.82	2	6	0	2
B21	3.02	12.10	0	0	0	0
C1	>>4.00	91.84	0	0	0	0
C2	>>4.00	88.09	0	0	0	0
C3	>4.00	65.49	0	0	0	0
C4	3.40	19.18	0	0	2	0
C5	3.38	18.27	0	0	0	0
C6	3.28	9.39	0	0	2	2
C7	3.25	11.58	0	0	5	7
C8	3.17	8.83	0	0	5	6
C9	3.15	8.79	0	0	4	10
C10	3.07	7.62	3	0	5	6

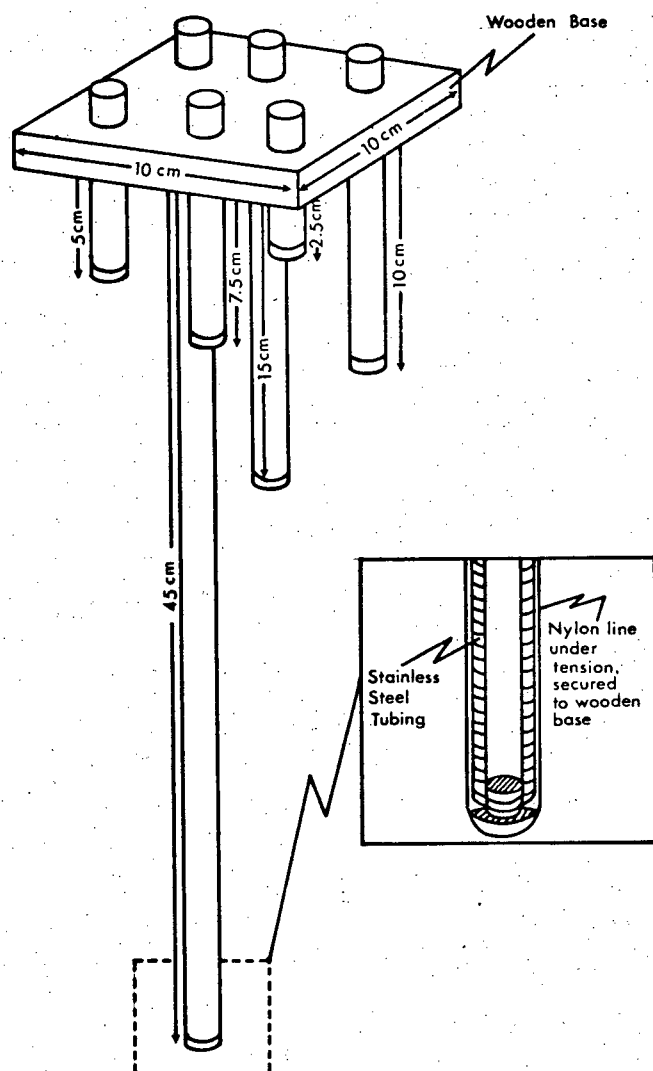
Station	Median ( $\phi$ )	% Mud	Upogebia (burrow openings $m^{-2}$ )		Callianassa (burrow openings $m^{-2}$ )	
C11	3.02	7.51	8	7	9	12
C12	2.98	7.03	13	7	8	18
C13	2.92	5.90	2	3	16	23
C14	2.90	6.27	10	12	6	14
C15	2.94	11.05	6	10	23	26
C16	2.89	8.22	0	4	43	62
C17	2.92	9.24	4	7	63	70
C18	2.90	8.75	7	6	68	87
C19	2.88	8.65	6	4	84	100
C20	2.90	9.86	7	2	86	101
C21	2.88	8.65	9	24	123	84
C22	2.82	8.90	0	5	96	107
C23	2.85	12.76	1	4	133	125
C24	2.88	10.99	8	0	95	82
C25	2.75	7.32	0	0	22	55
C26	2.76	8.66	0	0	13	11
C27	2.91	20.74	0	0	2	0
C28	2.86	15.78	0	0	0	0
C29	2.93	25.78	0	0	0	0
D1	3.46	29.74	2	2	180	164
D2	3.46	27.16	16	4	142	144
D3	3.44	25.94	22	18	92	120
D4	3.41	22.16	8	18	62	38
D5	3.36	15.41	0	0	104	94
D6	3.27	10.29	0	0	106	96
D7	3.32	13.34	0	0	64	102
D8	3.26	8.67	0	0	62	50
D9	3.26	8.78	0	0	42	76
E1	4.05	51.07	22	20	8	20
E2	3.75	46.06	6	12	6	4
E3	3.37	30.41	18	12	20	22
E4	3.38	29.56	26	10	22	30
E5	3.34	25.30	10	6	48	28
E6	3.30	20.40	2	10	44	44
E7	3.25	19.18	18	4	28	20
E8	3.13	11.21	4	8	44	42
E9	3.10	10.64	4	0	32	46
*CP12	2.48	7.79	0		10	
*CP18	2.57	4.55	0		83	
*CP24	2.82	8.40	0		172	
**FT4	3.41	38.19	0		70	
**FT8	2.65	10.48	2.5		446	
**FT11	2.92	13.13	3		354	

\* CP12 is in 'causeway zone' next to Coalport causeway adjacent to C12.  
 CP18 is in 'causeway zone' next to Coalport causeway adjacent to C18.  
 CP24 is in 'causeway zone' next to Coalport causeway adjacent to C24.

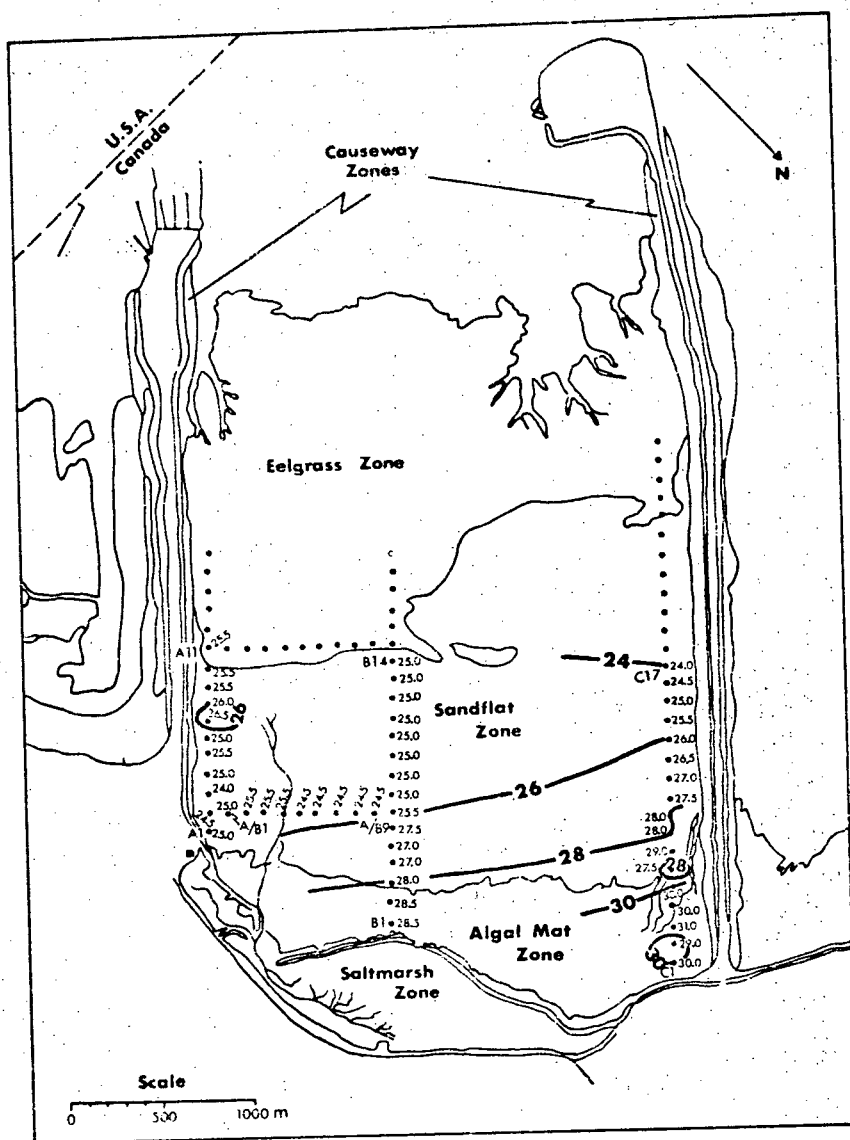
\*\* FT4 is in 'causeway zone' next to ferry causeway adjacent to A4.  
 FT8 is in 'causeway zone' next to ferry causeway adjacent to A8.  
 FT11 is in 'causeway zone' next to ferry causeway adjacent to A11.

Note: There are two thalassinidean burrow density readings for each station.  
 Every 4 of the 8 quadrats ( $0.25 m^2$ ) taken at each station were summed  
 at the time of data collection.

APPENDIX 5 -- SUPPLEMENTAL INFORMATION REGARDING  
SURFACE SUBSTRATE SALINITY AND SUBSTRATE SALINITY PROFILES  
ON INTER-CAUSEWAY TIDAL FLAT, ROBERTS BANK (PART 4A)



Apparatus used to take salinity profiles of the sediment column. A metal plug at the end of each tube, held in position by nylon line under tension, prevents water from entering the sampling tubes as the apparatus is pushed into the substrate. A metal rod is then pushed into each tube to release the plug and allow interstitial waters to flow in at the required sampling depth. Water samples were drawn off with a glass tube and salinity determined directly with a refractometer.



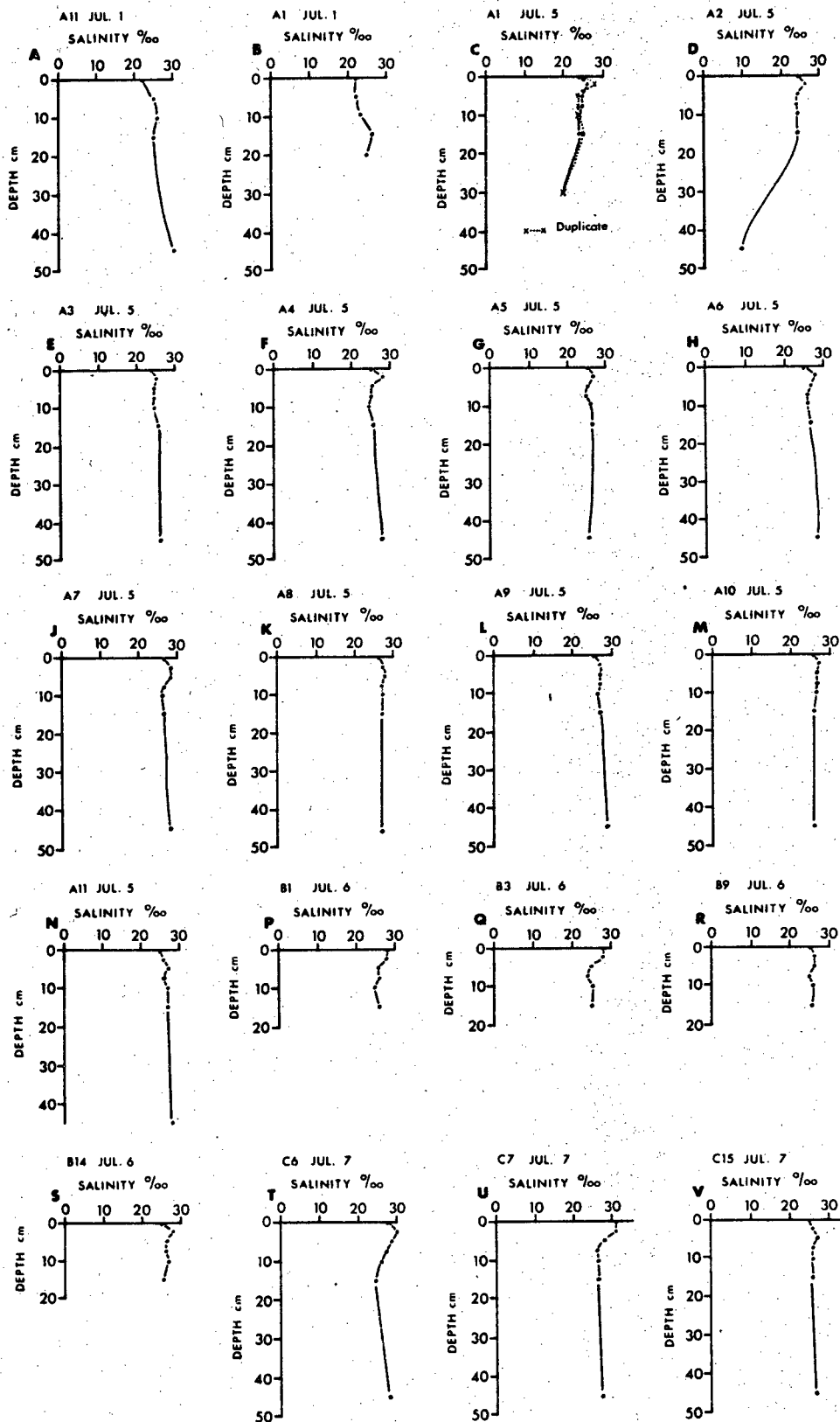
## Legend

- 28— Contour of substrate salinity ‰  
 •260 Transect station with substrate salinity indicated ‰

## Sampling Dates

- A1 - A11 JULY 5, 1977  
 A/B1 - A/B9 JULY 6, 1977  
 B1 - B14 JULY 6, 1977  
 C1 - C17 JULY 7, 1977

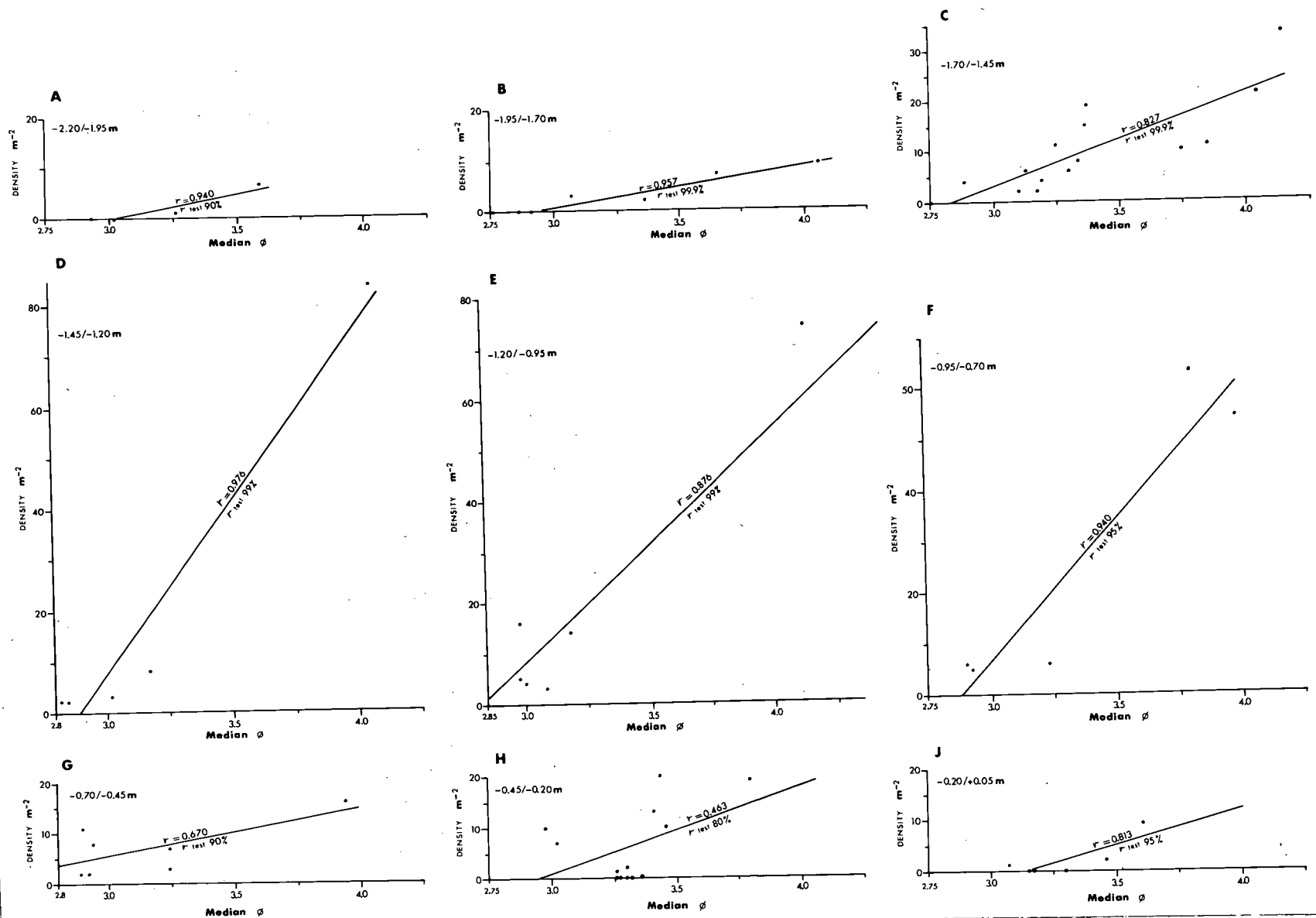
Surface substrate salinities at low tide as measured over the period July 5-7, 1977. Trend of contours between transects determined by mechanical contouring.



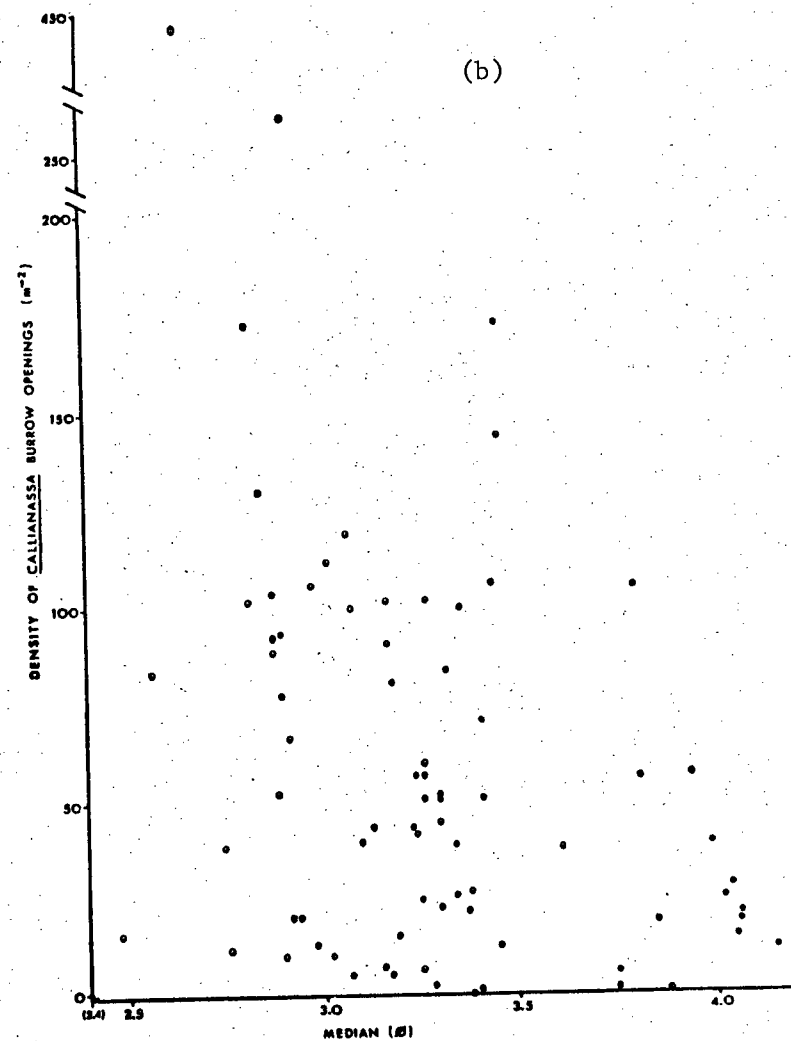
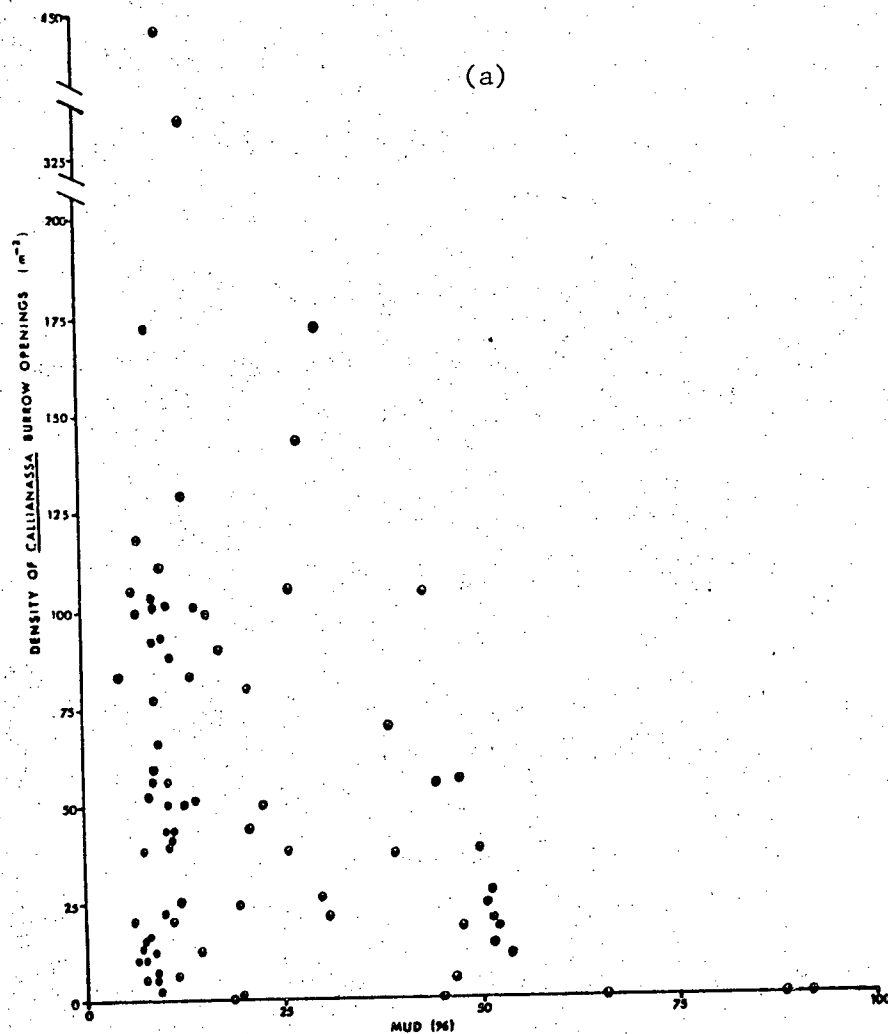
Substrate salinity profiles of the sediment column at low tide on transects A, B and C. taken over the period July 1-7, 1977.

APPENDIX 6 -- SUPPLEMENTAL DATA ON CORRELATIONS  
BETWEEN THALASSINIDEAN SHRIMP DENSITIES AND GRAIN SIZE  
ON THE INTER-CAUSEWAY TIDAL FLAT (PART 4A)

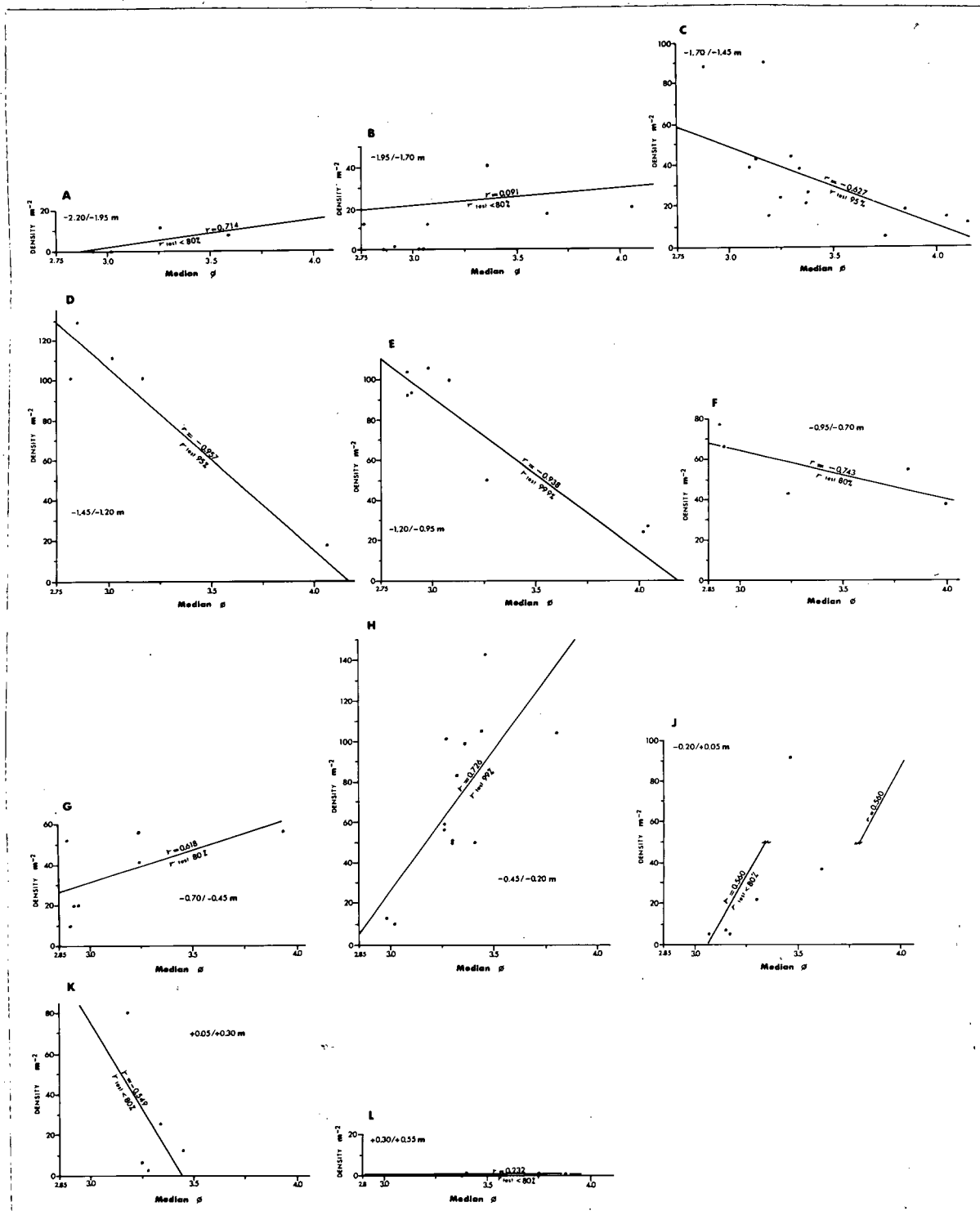




Relationship between median grain size ( $\phi$ ) and *Upogebia* burrow opening density, with data grouped into 0.25 m elevation class intervals. Best-fit linear regression lines are indicated, along with their correlation coefficients ( $r$ ) and confidence levels ( $r$  test). Elevation (Geodetic Datum) of increases from Ato J.



- (a) Density of Callianassa burrow openings vs median grain size ( $\phi$ ), regardless of elevation.
- (b) Density of Callianassa burrow openings vs mud content (%), regardless of elevation.



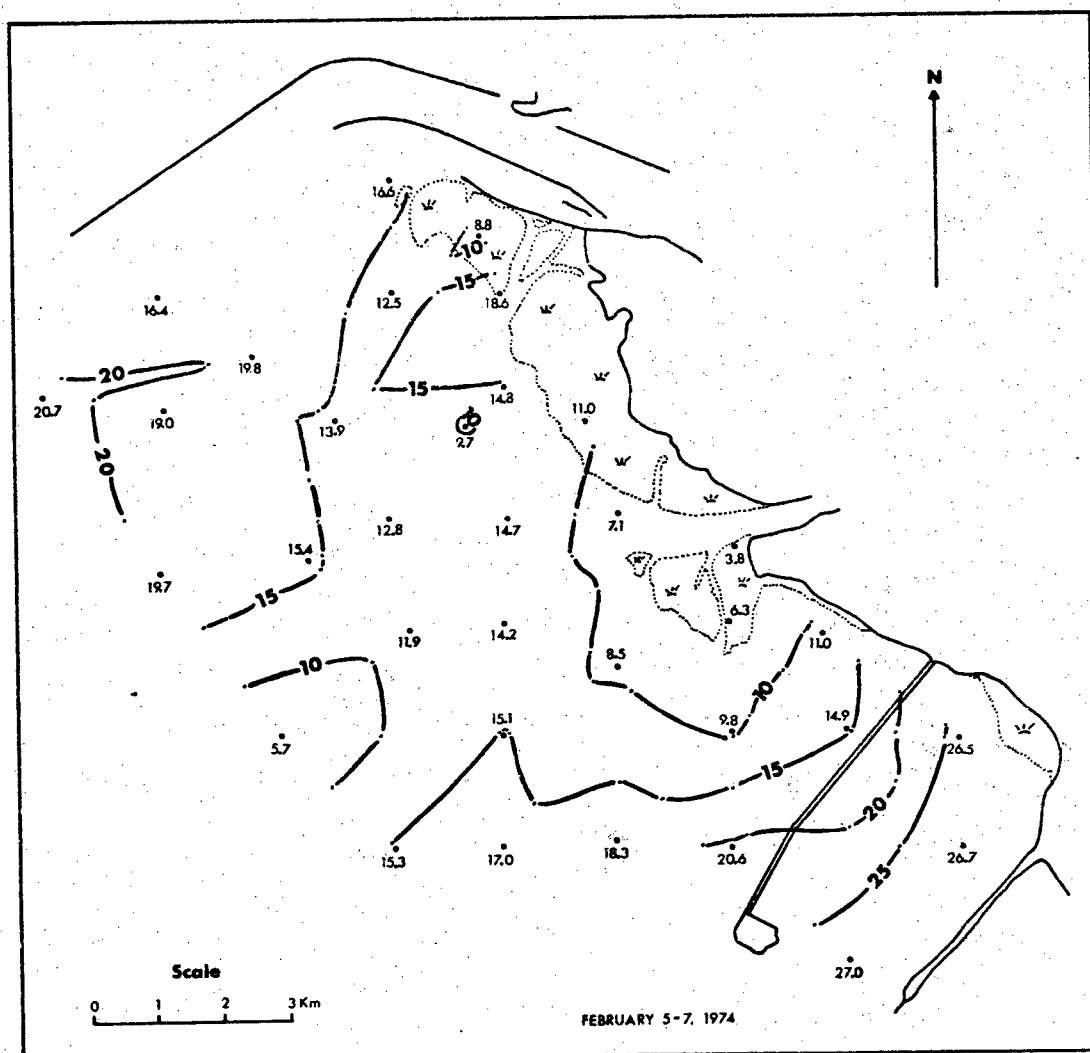
Relationship between median grain size ( $\phi$ ) and *Callianassa* burrow opening density, with data grouped into 0.25 m elevation class intervals. Best-fit linear regression lines are indicated, along with their correlation coefficients ( $r$ ) and confidence levels ( $r$  test). Elevation (Geodetic Datum) increases A to L.

# APPENDIX 7

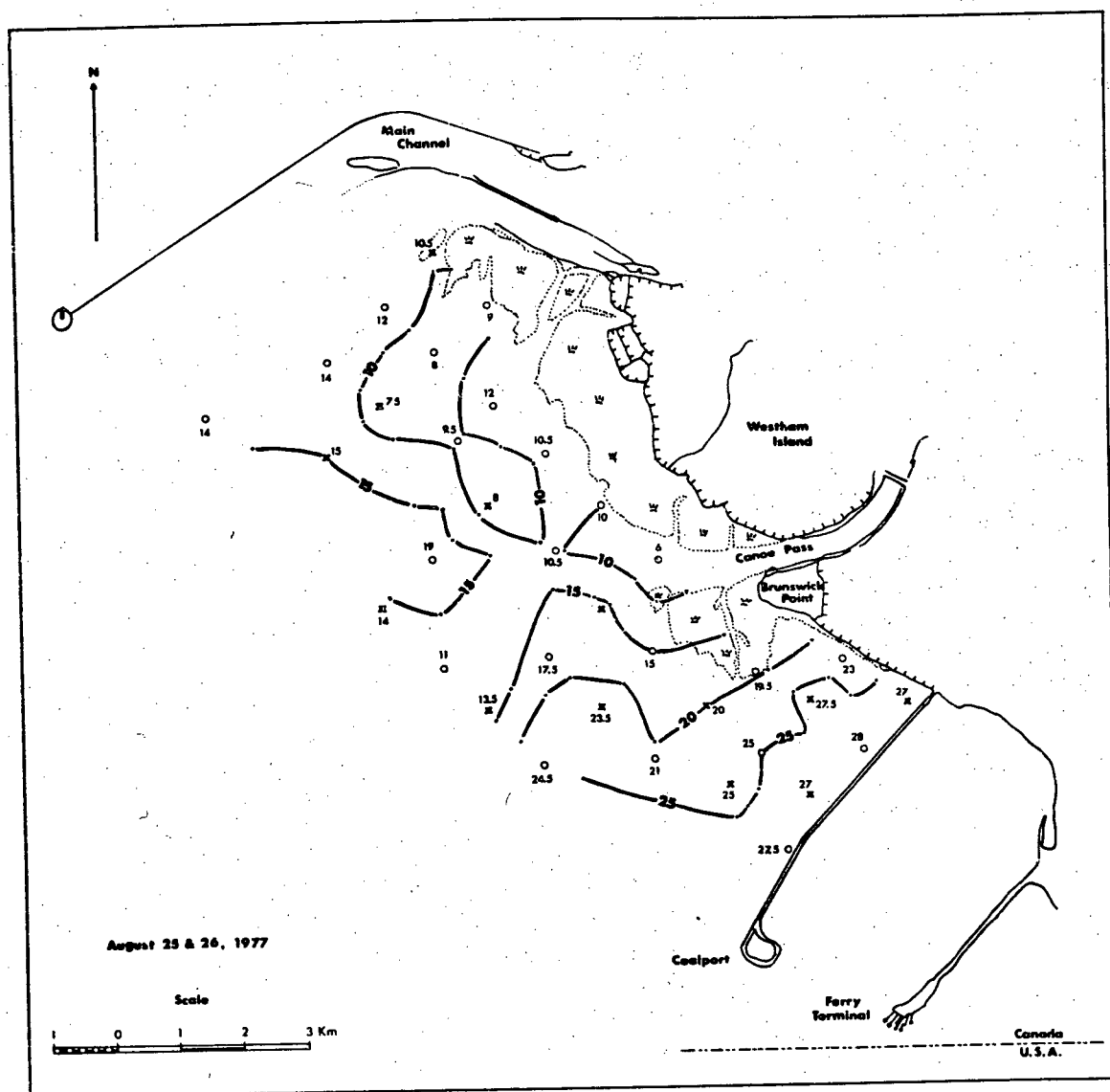
## Characteristics of the Stations Used to Determine Reworking Rates by Thalassinidean Shrimps

Station	Burrow Openings m <sup>-2</sup>		Median ( $\emptyset$ )	Mud Content (%)	Geodetic Elevation (m)	Exposure Zone
	<u>Callianassa</u>	<u>Upogebia</u>				
C23	129	2	2.85	13	-1.41	Upper Aquazone
C21	103	16	2.88	9	-1.19	Upper Aquazone
C17	66	5	2.92	9	-0.77	Upper Aquazone
C15	20	8	2.94	11	-0.58	Lower Amphizone
C12	13	10	2.98	7	-0.40	Lower Amphizone
A7	27	74	4.04	51	-1.03	Upper Aquazone

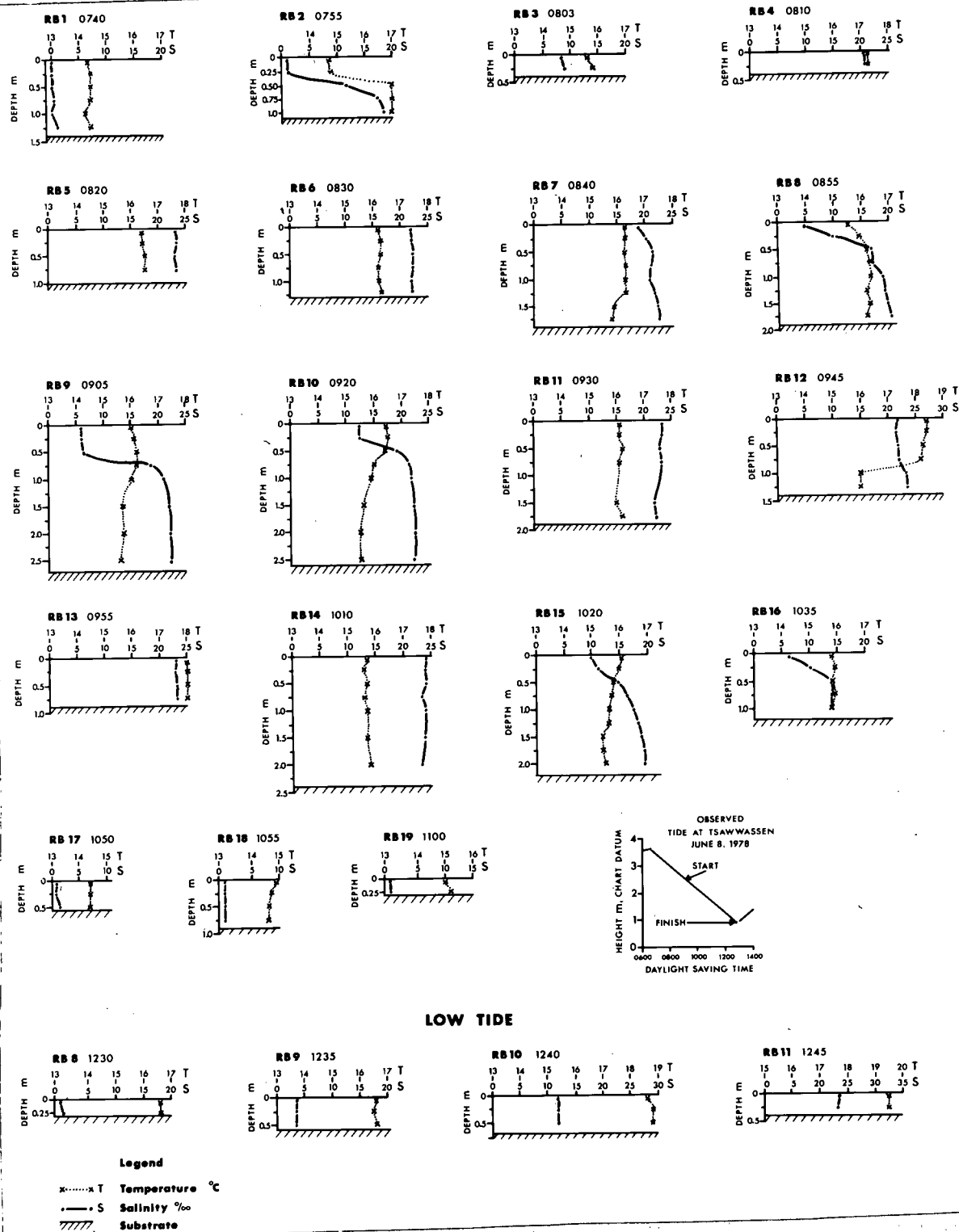
APPENDIX 8 -- SUPPLEMENTAL DATA ON SALINITY  
FOR NORTHERN AND CENTRAL ROBERTS BANK (PART 4B)



Surface substrate salinities on Roberts Bank at low tide on February 5-7, 1974. Data from Levings and Coustalin (1975), recontoured by mechanical contouring.

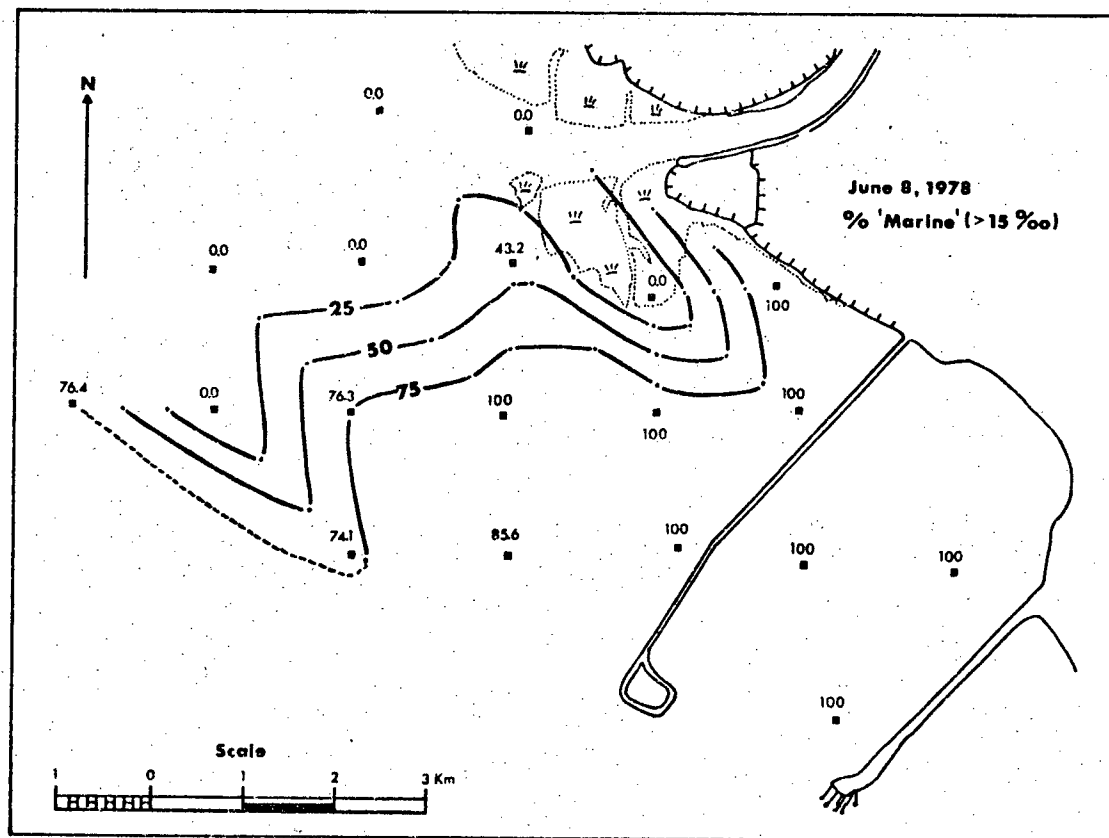


Surface substrate salinities on Roberts Bank at low tide on August 25 and 26, 1977. Mechanical contouring employed.

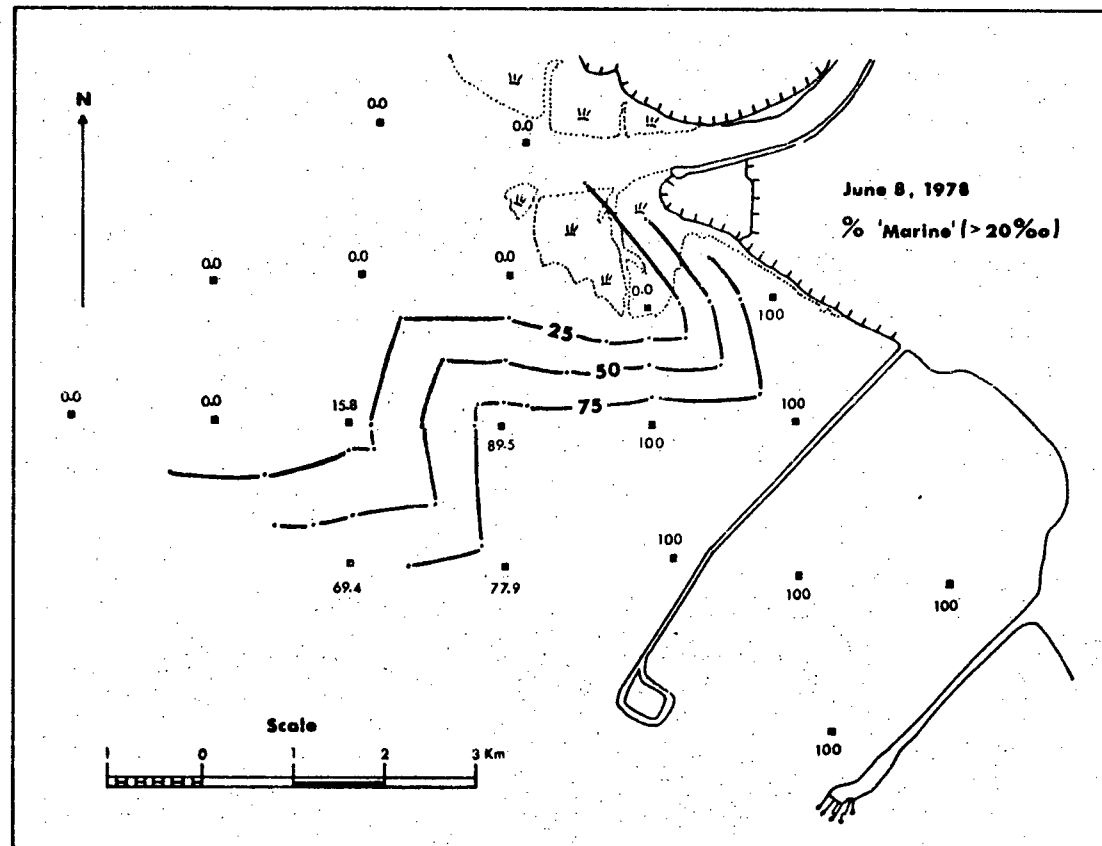


Salinity and temperature profiles of the water column taken on June 8, 1978 at high tide on ebb, between Canoe Pass and the Tsawwassen ferry terminal. Four profiles were also taken in the lower intertidal regions on approaching low tide. Refer to Figure 2 for station locations.



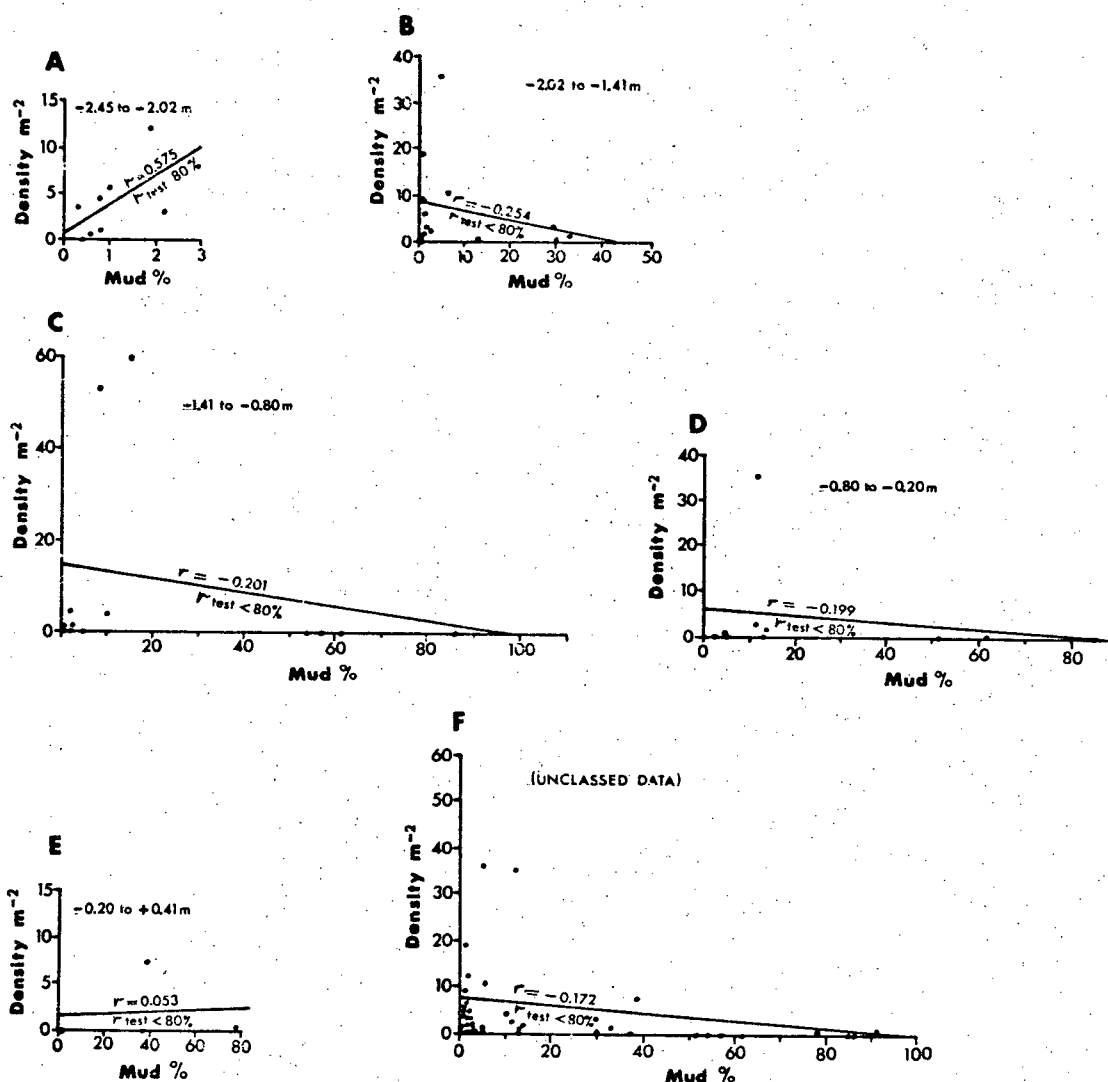


Percent thickness of the salt wedge, for 15%, as the boundary between marine and brackish water masses.  
Mechanical contouring.



Percent thickness of the salt wedge, for 20% as the boundary between marine and brackish water masses. Mechanical contouring.

APPENDIX 9 -- SUPPLEMENTAL DATA ON CORRELATIONS  
BETWEEN CALLIANASSA DENSITY AND SUBSTRATE PARAMETERS  
FOR NORTHERN AND CENTRAL ROBERTS BANK (PART 4B)



Relationship between *Callianassa* burrow opening density and the mud content of the substrate. Best-fit linear regression lines are drawn along with their correlation coefficients ( $r$ ) and significance level ( $r$  test).

# APPENDIX

Comparison of Correlation Coefficients (r) Between  
Callianassa Burrow Opening Density and Substrate  
 Salinity Using Pooled and Unpooled Salinity Data

Elevation Interval (Geodetic Datum, m)	Pooled Salinity Data 1977/78		Unpooled Salinity Data			
			1977		1978	
	r	r test (%)	r	r test (%)	r	r test (%)
-2.45 to -2.02	0.341	<80.0	Insufficient Data (N=2)		0.963	99
-2.02 to -1.41	0.333	<80.0	0.682	90	-0.158	<80
-1.41 to -0.80	0.106	<80.0	0.750	99	0.944	99
-0.80 to -0.20	0.904	99.9	0.812	99	0.981	99
-0.20 to +0.41	0.619	80.0	0.577	<80	Insufficient Data (N=2)	