

THE EFFECT OF TIDAL TRANSPORT  
ON THE  
ZOOPLANKTON POPULATION  
OF A LOCAL INLET

by

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## ABSTRACT

A series of cruises was made over 14 months to determine the effect of physical transport on the zooplankton of Indian Arm, whose deep water is separated from the marine influence of the Strait of Georgia by a series of shallow sills.

The dominant transport process during the study period was tidal exchange. The topographic features of the inlet, coupled with density stratification found over the year, restricted the exchange of water and plankton to a surface phenomenon.

Four copepod species were sampled using horizontally towed Clarke-Bumpus nets and vertically towed SCOR nets and one meter conical nets. These were analysed to determine the relationship between different life history patterns and tidal exchange, and the effect of this relationship on the populations of these species inside Indian Arm. Corycaeus anglicus is a surface water to mid depth organism found in highest numbers in Vancouver Harbour. The population density reaches a peak in the fall and remains high throughout the winter with transport concomittant with this peak. Euchaeta japonica exhibits ontogenetic depth preferences, nauplii and Stage I copepodites are found mainly in deep water below 200 meters, Stages II-IV are found mainly in shallow water, and Stages V and VI (adults) are found scattered over most of the water column. This species reproduces throughout the year in both Indian Arm and the Strait of Georgia. Euchaeta japonica was transported mainly as the Stage III copepodite and primarily during the

winter months despite the fact that the species is found in surface waters in large numbers at other times of the year, thus producing an isolated population in Indian Arm during the summer. Metridia pacifica is a strong diel migrator found extensively in the upper 50 meters at night, and from 250 meters to 50 meters during the day. Transport of the species across the sill occurs at all times of the year but is significantly greater at night, regardless of the phase of tide. Eucalanus bungi is an ontogenetic migrator, overwintering in deep water (greater than 150 meters), and coming to the surface in the spring to spawn; juvenile stages are found in surface waters during the summer. The data show that this species is transported only during the summer while it is in surface water. Consequently nauplii and younger copepodites are the dispersal stages. The data suggest that the species does not reproduce in Indian Arm and that transport of the species during the summer months can account for the entire overwintering population found in the inlet.

An analysis of the correlation of changes in the zooplankton community with physical parameters varying over the tidal cycle was made. Species known to migrate diel show significant differences in numbers between day and night samples. Relatively few species show differences which can be correlated to the direction of tidal movement. The most significant changes seen in the zooplankton community occur in association with changes in hydrographic properties. Moreover, these changes are manifested not at the species level, but at

the community level as changes in such parameters as diversity and dominance.

The effect of transport on the zooplankton community in Indian Arm varies from species to species. Qualitatively, the effect depends upon the organisms' life cycle including a surface dwelling stage, and/or its ability to survive the surface water transport conditions. Quantitatively, the effect depends on the amount of time spent in surface water, which varies with the depth distribution of the organism, determined by its behavioral characteristics. The overall effect of tidal exchange will be to drive towards equilibrium the population of zooplankton found in Indian Arm and the Strait of Georgia. It is the biology of the individual species which determines the extent of interaction with this transport process and hence the amount of exchange which takes place.

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## INTRODUCTION

### Overview

The spacial distribution of a planktonic organism is, by definition, controlled by the movements of the water in which it occurs. Superimposed on this are the physical, chemical, and biological properties of the water within which the organism must be able to survive. Given the continuity of favorable water properties, the potential exists for organisms separated vertically but at the same geographic location to be transported in different directions by vertically discrete bodies of water moving in different directions.

In coastal waters, transport of organisms by such physical processes as tidal currents and estuarine circulation is well known (e.g. Redfield, 1941; Barlow, 1955; Tyler and Seliger, 1978) and it has been suggested (Stromgren, 1975) that variations in such transport affect the zooplankton communities of fjords. Similarly, it has been shown that physical, chemical, and biological properties of the water encountered by the organisms as they are transported are important (e.g. Evans, 1973; Bary and Regan, 1976). Neritic plankton, however, have an additional limitation placed upon their distribution by the topographic features of the coastline with which they are associated. This limitation is manifested primarily through the influence of these topographic features on the physical

processes involved in transport (e.g. Trinast, 1975; Alldredge and Hamner, 1980).

The general purpose of this study is to examine the effect of physical transport on the zooplankton community of a local inlet. The hypothesis to be tested is that the presence or absence of transport, and changes in its rate, are responsible for the quantitative and qualitative nature of zooplankton populations in an inlet. Specific questions that the study set out to answer were:

- 1) Can the transport of zooplankton be quantitatively measured across an inlet mouth?
- 2) Is the transport affected by different behavior patterns?
- 3) What effect does transport have on the inlet populations?
- 4) Do different transport processes have different effects on the actual transport of zooplankton?
- 5) What numerical changes take place in the zooplankton population being transported across the inlet mouth over the tidal cycle?
- 6) Are these changes associated with measurable variables such as tidal direction, daylight, or hydrographic parameters?

Inherent in such a study is an understanding of two interacting systems: the physical oceanographic processes which are responsible for water movements at the inlet mouth, and the

zooplanktonic biological processes occurring in the water itself.

### Physical Considerations

Geologically, a fjord is a submerged glacial valley forming a deep, narrow, steep sided inlet. The sill frequently found at the mouth is normally a terminal moraine, which is also a result of glaciation and forms a relatively shallow barrier separating the deep water of the fjord from coastal water. Sills are known to markedly influence physical transport processes (Skreslet, 1973; Gade, 1976) and have the overall effect of restricting the exchange between the fjord and adjacent coastal water. This effect is seen most dramatically as an isolation of the fjord deep water (Anderson and Devol, 1973; Siebert et al, 1979; Heggie and Burrell, 1981).

The physical mechanisms responsible for the transport of water into or out of a fjord can be divided into those of a baroclinic nature, driven by horizontal density gradients, and those of a barotropic nature, driven by a horizontal pressure gradient. Estuarine circulation is a semi permanent density current driven by runoff entering the inlet, and primarily affects surface circulation. The seaward flowing surface layer is driven by a down inlet sloping free surface. Vertical entrainment of saline water from below, into this outflowing layer, results in an up inlet compensatory flow in the



subsurface layers (see Dyer, 1973). The magnitudes of up inlet subsurface flow and down inlet surface flow are dependent on the volume of fresh water input, and both are potentially capable of transporting zooplankton.

Replacement of fjord deep water can occur if coastal water above sill depth is of greater density than the resident water of the fjord (Anderson and Devol, 1973; Lafond and Pickard, 1975). The process is set up by vertical diffusive mechanisms within the fjord which gradually reduce the density of the resident inlet deep water (Muench and Heggie, 1978). The intrusion of dense coastal water into the deep basin of a fjord is an intermittent process dependent upon the rate of density decrease in the fjord deep water and the seasonal changes in the density of water at sill depth outside the fjord. An intrusion is most likely to occur at a time when the offshore surface density is at a maximum. The timing of this maximum and thus of the intrusion will vary depending upon local coastal oceanographic processes and runoff patterns (see Gade, 1976).

Over a shallow sill there is a limitation imposed upon the magnitude of a baroclinic flow by the irregular boundaries of the channel. Superimposed on any existent baroclinic flows are transport mechanisms of a barotropic nature driven by a pressure gradient such as those due to tides, local wind fields, and atmospheric pressure changes. No boundary related limitation exists on these flows such that frequently, they can completely override semipermanent or intermittent baroclinic flows. In such a case the baroclinic flow will serve only to diminish or

augment the barotropic flow depending on their relative directions (Gade and Edwards, 1980).

In most shallow-silled fjords therefore, the dominant short term transport process will be that of tidal exchange. Estuarine circulation will be evident only as a net flow varying seasonally with fresh water input and superimposed on the tidal flow. Density driven intrusive flows might be strong enough to override the tidal flow for short periods of time depending on the density gradient established across the sill (Skreslet and Loeng, 1977). While the magnitude of such intrusions is often big enough to replace large volumes of fjord water in a short period of time (Cannon and Ebbesmeyer, 1978), they are of a seasonal nature and often episodic, with many years passing between each renewal (Gade, 1973).

### Biological Considerations

Although the width of the mouth of a fjord will obviously have a quantitative effect on plankton exchange it will have little qualitative effect. This is because the horizontal distance over which zooplankton species distributions change are usually orders of magnitude larger than the width of inlet mouths. Sill depth, however, will not only have a quantitative effect, but also a qualitative effect on plankton exchange. Vertical gradients in both water properties and zooplankton distributions are of the same scale as sill depths and often

much smaller, especially in coastal regions.

There are two necessary prerequisites for the transport of organisms into or out of an inlet. First, a physical mechanism must be present whereby water is actively being exchanged across the inlet mouth. Obviously this water must be near or above sill depth for such a flow to be possible. Second, the organism must be present in the moving water. Both of these prerequisites are variable and a number of potential possibilities can be proposed.

- 1) Given a constant transport mechanism, the number of organisms exchanged will vary as each species reaches its maximum population density in the water above sill depth at different times of the year. The quantitative nature of the zooplankton transport will thus vary with seasonal cycles in population abundance.

- 2) In contrast, if the population of an organism remains seasonally uniform, variations in transport can only occur with changes in the magnitude of the physical flow.

- 3) If a transport mechanism occurs on a seasonal or episodic basis, such as a density driven intrusion, only those animals present above sill depth during the event will be potentially transportable. Thus, an animal which migrates vertically, either on a diel basis or ontogenetically, will be potentially

transportable only at that time, or developmental stage, when it is in water above sill depth.

Biological variables which must be integrated with the physical variables thus include species specific behavioral and reproductive characteristics.

The species chosen for transport analysis were copepods having different depth distributions and life history patterns. Corycaeus anglicus Lubbock is primarily a surface dwelling species which reproduces in the fall. Cameron (1957) suggests that this is an inshore species which breeds in inlets. Eucalanus bungi (Johnson) migrates ontogenetically, overwintering in deep water (greater than 150 meters) and rising to the surface in the spring to spawn. The younger stages develop in near surface water before migrating to deep water in the fall (Sekiguchi, 1975). This species is a very common member of the North Pacific plankton community (Vinogradov, 1968). Euchaeta japonica Marukawa reproduces throughout the year (Evans, 1973). While Fulton (1968) and Stone (1979) report the adults of this species to be a deep living organism, different life history stages show specific depth preferences (Lewis and Ramnarine, unpublished data). Nauplii and C-I copepodite stages inhabit deep water (over 200 meters), stages C-II to C-IV inhabit near surface water, while C-V and adult stages are found scattered from the surface to deep water. Metridia pacifica Brodskii is found in large numbers in surface water during the day but migrates dielily to below 50 meters at night. This

species breeds in the spring and fall, reaching a population peak in the summer (Stone, 1977).

### The Study Area

The area chosen for study was Indian Arm, a shallow silled fjord connected to the Strait of Georgia through Burrard Inlet (Figure 1). Exchange with the Strait of Georgia is limited by the shallow sills at First Narrows, Second Narrows, and at the entrance to Indian Arm itself (Figure 2).

The physical oceanography of the Indian Arm - Burrard Inlet system has been studied in some detail by Gilmartin (1962), Tabata (1975), and Davidson (1979). Pickard (1961) categorizes British Columbia inlets according to their fresh water input, stating that the distribution of hydrographic properties in a given inlet is largely explained by the nature and volume of its fresh water input. Indian Arm is classified as a medium runoff inlet with little or no contribution from glaciers. Generally, tides are of a semi-diurnal nature and hydrographic properties and circulation follow a regular annual cycle of changes. Major intrusions of deep water are responsible for occasional deviations from this seasonal cycle (Pickard, 1975). Such intrusions take place during the winter on an episodic basis, and are capable of replacing a major portion of the volume of Indian Arm in one month (Davidson, 1979).

General patterns of zooplankton distribution in the Strait

of Georgia area, including Indian Arm, have been studied (Legare, 1957; Gardner, 1977; Mackus et al, 1980, etc.) and patterns of production and seasonal cycles identified (Parsons et al, 1970). The area follows a boreal seasonal cycle, most zooplankton species reaching a population maximum in the summer after the spring phytoplankton bloom. Primary production in the Burrard Inlet - Indian Arm system has been studied by Gilmartin (1964), and more recently by Stockner and Cliff (1979) who consider nitrate limitation and grazing to be the principal factors controlling primary production. Zooplankton studies include those of Shan (1962) on copepods and McHardy and Bary (1965) on ostracods. Shan relates the distribution of four species of copepods to water properties while Woodhouse (1971) and Evans (1971) discuss the distributional ecology of a few select species. Although hypotheses were put forth by these authors, no previous attempt has been made to study mechanisms responsible for the distribution of Indian Arm zooplankton.

#### Summary of Considerations

In general, the qualitative and quantitative nature of the plankton community in a fjord is a function of 1) biological and chemical properties of the water within the inlet, 2) the planktonic community outside the inlet, and 3) the degree of exchange between the two. This degree of exchange is a function of fjord topography, and its interrelation with the barotropic and baroclinic currents present in the area. Seasonal cycles and species specific behavioral patterns will determine the effect

of this interrelation on plankton exchange between Indian Arm and the Strait of Georgia.

## MATERIALS AND METHODS

### Hydrographic Data

#### i) Field Procedures

A series of seven cruises was made over the period January 1980 to November 1981 (see Table I). Ship time for these cruises was provided by the Canadian Hydrographic Service on the Canadian Survey Ships Richardson and Vector. The cruises between February 1980 and March 1981 served as the data collecting series for both biological and hydrographic parameters. The January 1980 cruise was an equipment testing exercise from which no biological data resulted while, during the November 1981 cruise, replicate zooplankton tows were made for statistical application (no hydrographic data being taken).

Figure 1 shows the positions of the six stations occupied during each cruise. They form a transect from the deep water of the Strait of Georgia (stations GEO 1748 and FRA 1) through Burrard Inlet and across the shallow sills (stations VAN 24 and IND 0) into the deep water of Indian Arm (stations IND 1.5 and IND 2.0). The exact location of each station is given in the Department of Oceanography U.B.C. Data Reports 1980 and 1981. (Station GEO 1748 was not occupied during the Feb. 1980 cruise.)

Hydrographic samples at each station were taken from the



surface to close to the bottom. Specific sample depths and the water depth at each station are shown in Table II.

Station IND 0, on the sill at the entrance to Indian Arm, was occupied on each cruise for a period of 25 hours (approximately an entire tidal cycle). Samples from this station were taken at each of four depths every 3 hours over the tidal cycle to provide information on the temporal variability of the hydrographic and biological parameters.

All hydrographic samples were collected with National Institute of Oceanography bottles mounted with Yashino Keike reversing thermometers. Temperature and oxygen were measured at sea, temperature with an accuracy of  $\pm 0.02$  degrees C., and dissolved oxygen content by Winkler titration with the reagent modifications discussed by Carritt and Carpenter (1966), having an accuracy of  $\pm 0.05$  ml/l. Surface temperature and salinity values were collected from bucket samples, the bucket thermometer graduated in tenths of a degree C.

At station IND 0, with the vessel at anchor, a Marine Advisors current meter with deck readout (velocity and direction) was deployed over the stern. Readings were taken at 5 and 20 meters depth as often as conveniently possible but never less than 45 minutes apart.

## ii) Laboratory Procedures and Data Reduction

Salinity was measured using an Auto-lab inductively coupled

salinometer with a reported accuracy of  $\pm 0.003$  ppt. in the salinity range above 28 ppt. and  $\pm 0.02$  ppt. below this value. Density (expressed as  $\sigma_T$ ) was then calculated using Knudsen's formula and applying corrected temperature and salinity values. Final calculation of all hydrographic parameters was carried out using a Department of Oceanography program on a PDP 12 computer.

All current meter readings were first changed from knots to meters per second. The magnitude and direction of each reading was then plotted as a function of time. As the channel at Ind 0 is relatively narrow, with a north-south axis, it was felt that any cross channel component to the flow would be due to eddies and turbulence induced by the highly irregular channel boundaries. These components would be moving along the channel axis incorporated into the mean flow and as such should average to zero over time. The cross channel components to the flow measured by the current meters were thus ignored. A subsequent plot was traced showing only the along channel, north-south, component of flow as a function of time over the sampling period of a tidal cycle.

The north-south components of flow were then averaged over each ebb or flood event to arrive at a mean flow at each of the depths sampled for each tidal phase observed. Since each current meter depth represented an approximately equal portion of the total cross sectional area of the channel at IND 0, the two mean flows were averaged to obtain a single mean flow figure for that phase of the tide. This mean flow was multiplied by the cross

sectional area of the channel at Ind 0 to obtain the average volume transport, and then by the duration of the ebb or flood event to arrive at an estimate of the volume of water transported during that particular tidal phase. This procedure was followed for each phase during which biological samples were taken and for each cruise. The ramifications of boundary friction on this calculation are discussed in the next section.

A second estimate of volume transport was obtained using a numerical model which predicts tidal elevation and average tidal currents across each of a series of transects running through Burrard Inlet and into Indian Arm. The model was written in 1972 by Dr. P.B. Crean of the Department of Oceanography U.B.C. and the Federal Department of Fisheries and Oceans and was further updated in 1977 by M. Foreman. The model was set up to predict the tidal current at section S7, immediately adjacent to the sampling station Ind 0 (see Figure 1). The output gave a prediction of the average current across this section every hour over the entire study period. The hourly current values corresponding to those times during which the station was occupied were then averaged in sequence to obtain an average current velocity for each hour. The velocities for each tidal phase were then summed and multiplied by the cross sectional area of section S7 to obtain the second estimate of volume transport for each phase of the tidal cycle during which data was collected.

Other tidal parameters such as times and elevations were taken from Canadian Tide and Current Tables Vol 5, 1980 and

1981, published by the Canadian Hydrographic Service. Corrections were made to the predictions using Vancouver Harbour as a reference port and applying the differences published for Deep Cove as a secondary port. (Deep Cove is the closest secondary port to the tidal station IND 0, see Figure 1).

### Biological Data

#### i) Field Procedures

Biological samples were taken using Clark-Bumpus nets (Clark and Bumpus, 1950) to obtain vertically discrete samples and either a SCOR net or a conical meter net to obtain vertical hauls. Stations occupied were the same as those used to collect hydrographic data so that each station had a concurrent set of hydrographic and biological samples. The depths sampled are shown in Table II. At station IND 0, samples were taken at three depths every three hours, simultaneously with the hydrographic samples. These samples were used to resolve the temporal changes in the plankton concentration over the tidal cycle.

Each Clark-Bumpus net used had a mouth aperture of 12 cm. and was fitted with a net of Number Two mesh (mesh size: 350 microns). Each net incorporated the modifications recommended by Paquette and Frolander (1957) and contained a calibrated flow

meter which allowed samples to be quantitative (see McHardy, 1961). At stations with a water depth greater than 60 meters two Clark-Bumpus tows were made, each with 3 or 4 nets attached to the wire. The first tow sampled the 3 to 4 shallower depths, the second the remaining deeper depths. All tows were 15 minutes in duration and made with the speed of the towing vessel adjusted to maintain a wire angle of approximately 30 degrees. Depending on sea conditions, vessel speed was usually about 1.5 knots.

At station IND 0 a small fiberglass 150 H.P. inboard/outboard runabout fitted with a derrick and a gas powered winch was used in making the Clark-Bumpus tows. The larger research vessel was anchored on station to complete the hydrographic work and the vertical plankton hauls. This small boat was unavailable for the February 1980 cruise and the larger research vessel was used to make the tows. During this cruise one tow was made every six hours resulting in a single depth series from each tidal phase.

Vertical hauls were taken using either a SCOR net (mesh size: 303 microns) or a Meter net (mesh size 330 microns), from as close to the bottom as possible (see Table II) to the surface. A constant hauling speed of 0.5 meters/second was maintained. At stations deeper than 60 meters, a second haul was made from 50 meters to the surface in an attempt to separate the surface plankton from deeper plankton. The main purpose of the vertical hauls was to provide an integrated sample of the entire water column.

Immediately after sampling, each net was washed down with

sea water. The sample was then transferred into either 4 or 8 ounce labelled glass jars and preserved in a calcium carbonate buffered formalin solution of approximately 5% formalin:seawater.

The purpose of the November 1981 cruise was to take replicate zooplankton tows in order to establish statistical confidence limits applicable to copepod densities calculated from previous cruises. A series of six replicate Clark-Bumpus tows were made, each with three nets on the wire. All tows were made with the vessel starting at the same location (IND 2.0) and moving in the same direction along a fixed course. Each tow lasted 15 minutes and all were made during the same tidal phase (a small ebb) to minimize the variability in the samples caused by tidal effects (see Sameoto, 1975). The sampling depths chosen (see Table IV) were designed to increase the probability of consistently catching each of the copepod study species at at least one depth. In addition, four replicate vertical hauls were made at station IND 0 using the SCOR net. All hauls were of identical length, used a constant hauling speed and were made during the same tidal phase. Samples from all the biological replicates were treated and preserved in the usual manner.

#### ii) Laboratory Procedures and Data Reduction

Zooplankton were sorted and counted using a Wild M5 dissecting microscope. All samples were completely examined for

the relevant species and no splitting of hauls was attempted. The laboratory procedures therefore contributed no sampling error or bias to the data beyond any counting errors.

The taxonomic level to which the zooplankton were sorted varied with each taxonomic group (see Table III). For the analysis of changes in the whole zooplankton community over the tidal cycle at IND 0 it was felt that identification to species would be important only for taxonomic groups which contained numerous local species. This procedure will not greatly affect the validity of the parameters used to describe changes in the zooplankton community over the tidal cycle as each was used only to compare samples treated in a similar fashion. Some bias will be introduced by the lumping of taxa. However, this effect will be minimized due to the few specimens found in each group, and also the limited number of species actually lumped together. (Where the number of species included in a group is known, it is given in the table.)

Copepods more mature than the first copepodite stage were identified to species but not sorted by age or sex. Medusae, ostracods, amphipods and cladocerans were identified to genus while groups with low taxonomic diversity or very few individuals were identified only as specifically as was needed to delineate separate groups (see Table III). No satisfactory key exists for identifying naupliar stages and they were classified as a separate group. Copepods used in the transport study were sorted to species and those exhibiting a known ontogenetic depth preference, Euchaeta japonica (Evans, 1973;

Lewis and Ramnarine, unpublished data) and Eucalanus bungi (Krause and Lewis, 1979), were sexed and aged to the first copepodite stage.

Copepods were sorted using Brodskii (1950) and Fulton (1968) as keys. Other groups of zooplankton were sorted using Fulton (1968). Serious doubt regarding the correct taxonomic name for two of the study species remains in the published and unpublished literature. Evans (1973) states that Euchaeta japonica should correctly be called Pareuchaeta elongata. Thorpe (1980) claims to have found significant differences in the Metridia specimens found in Indian Arm and those found in the North Pacific which have been described as Metridia pacifica by Brodskii (1950). As the taxonomic status of these species is still unresolved, and such work is beyond the scope of this ecological study, the names used correspond to those found in the keys most commonly used for British Columbia zooplankton.

Following identification and counting, the data were transformed into density values using the volume of water filtered by each net as measured by the calibrated flow meter associated with that net. All zooplankton densities are expressed in number per cubic meter of water and all transport calculations were done using these values.

The sampling depths chosen for Cruise 81/33, to establish confidence limits, resulted in a data table which could be used to calculate statistical parameters for all of the copepod study species. Eucalanus bungi was consistently caught by the 200m net while Euchaeta japonica and Metridia pacifica were both



consistently caught at 100m. Corycaeus anglicus was caught at all three depths but most consistently at 100m and 20m (see Table IV).

The statistical procedure to establish confidence limits was that recommended by Cassie (1962), using a  $\log_{10}(x+1)$  transformation as in Stone (1977) to log normalize the plankton distribution (see Cassie, 1968). The transformed replicate data were used to calculate a log standard deviation for each species (see Table V). This log standard deviation was then applied to similarly transformed data from previous cruises and, using the  $t$  value associated with the original five degrees of freedom established from the 6 replicate tows, was used to establish 95% confidence limits for each density value. These transformed confidence limits were then changed to their original form of animals per cubic meter. Mathematically expressed, the procedure followed was:

$$95\% \text{ LIMITS} = (\log r \pm \log sd \ t) \text{ antilog} - 1$$

where  $r$  is the number of animals per cubic meter of a particular species;  $\log \text{ sd}$  is the logarithmic standard deviation of the species as estimated from the replicates, and  $t$  is the  $t$  value associated with 5 degrees of freedom.

The coefficient of variation (CV) is a measure of plankton patchiness and can be used to compare the relative variability of replicates. It is useful when one can assume a log normal distribution of animals which, for plankton, is acceptable in most cases. CV is calculated by expressing the sample standard deviation as a percentage of the sample mean. Cassie (1962)

states that the coefficient for plankton usually has a value between 22 and 44% and that much higher values are not rare. The CV values calculated for Euchaeta japonica and Metridia pacifica at 100m are both within this range and the values for Eucalanus bungi at 200m and Corycaeus anglicus at 100m and 20m are only slightly larger. (see Table V).

Higher values of CV are due to low mean values of plankton counts. In these cases the assumption of a log normal distribution becomes less tenable and the distribution actually approaches a Poisson distribution. As the mean of replicate counts gets smaller the log normal distribution results in a less satisfactory representation of the data (Cassie, 1962). Low densities of copepods in the samples are thus the probable cause of the high values of CV seen in Table V.

The logarithmic coefficient of variation (CV') is also useful in comparing the variability of replicates as the variability within samples resulting from an interaction of biological and physical processes is more likely to be multiplicative than additive (Cassie, 1968). CV' values calculated for the study species (see Table V) are all within the range found by Stone (1977) for similar coastal zooplankton samples.

Artificially low values are generated by very low mean values in the replicates. The  $\log(x+1)$  transformation, which will have little effect on larger values, will overcorrect smaller values. This may be closer to the Poisson distribution discussed above than to the log normal distribution.

Statistical procedures used in analysing the data were carried out on the University of British Columbia MTS system and programs found in the Institute of Animal Resource Ecology Data Center. Population parameters used in analysing zooplankton differences over the tidal cycle were calculated using Zoology 403 statistical programs written by Dr. C.J. Krebs of the Department of Zoology at the University of British Columbia.

The calculation of animals transported across the sill during a tidal event involved averaging depth specific samples to arrive at mean animal densities for each sampling time. The cross sectional area of the channel at IND 0 is approximately 30,445 meters<sup>2</sup>. At each sampling time, each of the three nets used was assumed to have obtained a zooplankton sample representative of that portion of the water column to which it was closest. The 5 meter net represents the depth interval 0-7.5 meters, the 10 meter net from 7.5-15 meters, and the 20 meter net from 15-bottom. From the depth profile published on Chart 3434 of the Canadian Hydrographic Service it was calculated that the cross sectional area enclosed by each of these depth intervals is approximately equal ( $\pm 4\%$ ). The animal densities from each net could thus be averaged to obtain the mean animal density for each sampling time across the IND 0 cross section.

As the sampling interval was every three hours and the duration of a tidal event was about six hours, there were often two and sometimes three such mean animal density values calculated for each tidal phase. The final animal density which can be multiplied by the volume transport figures was obtained

by averaging all density values taken during a tidal phase.

## RESULTS AND DISCUSSION

### Hydrographic Data

#### i) Deep water Intrusions

The shallow sill present at the entrance to Indian Arm restricts the exchange of water with the Strait of Georgia and thus the horizontal continuity of water properties across the study area. For a deep water intrusion to occur, water above sill depth (approximately 20 meters) in the Strait of Georgia must be more dense than resident fjord deep water. In the Strait of Georgia, surface water density reaches a maximum in winter due to the reduced flow of the Fraser River (Waldichuck, 1957). An Indian Arm deep water intrusion is therefore primarily a winter phenomenon.

Figure 3 shows the density structure with depth along a longitudinal axis through the study area in January, 1981. Water of sufficient density to replace Indian Arm bottom water is present above sill depth at stations GEO 1748 and FRA 1. At First Narrows however, vertical mixing is such that surface densities are severely reduced by the outflowing brackish water from Vancouver Harbour. Further mixing at Second Narrows and the Indian Arm sill reduced the density of water passing Station IND 0 to a value equivalent to that at approximately 40 meters in Indian Arm. The density of water at the actual entrance to

Indian Arm was thus dynamically incapable of penetrating below about 40 meters and bottom water in Indian Arm remained undisturbed. A similar density structure was present during the winter of 1980 (see Figure 4).

A very distinct indicator of bottom water replacement is the oxygen concentration in deep water (Davidson, 1979). Due to biological and chemical oxygen demand, relatively stagnant water in the fjord basin will have a low oxygen concentration, the amount depending on diffusion within the fjord and primarily on the length of time since the last renewal. Intruding water, originating in the upper water column of the Strait of Georgia will have a much higher concentration. Figure 5 shows the effect of this intruding oxygenated water on the oxygen concentration at Station IND 2.0 from 150 meters to the bottom from August 1970 to April 1981. (Data was obtained from the Department of Oceanography University of British Columbia, Data Reports 1970 - 1981). The negative slope following an intrusion reflects the balance between biological respiration, chemical oxygen demand and diffusion. Immediately obvious is the lack of any apparent oxygen increase during the study period, January 1980 - April 1981. The resident deep water of Indian Arm remained undisturbed by any major physical event and the oxygen concentration steadily decreased reflecting the net oxygen demand.

During the study period, no major deep water intrusion took place and transport of deep water zooplankton across the sill such as that reported by Stone (1977), was not possible. Water exchange between Indian Arm and the Strait of Georgia was due to

tidal action and estuarine circulation and the potential existed for the exchange of shallow dwelling organisms only.

## ii) Estuarine Circulation

The pattern of estuarine circulation in Indian Arm has two distinct features. First, there is a bimodal seasonal cycle with a mid summer maximum due to snow melt in the mountainous drainage basin and a second maximum in the late fall-early winter months (October, November, December), in response to a local peak in precipitation (Davidson, 1979). Second, the circulation is complicated by intense vertical mixing at the sills. This decreases the density of water moving into the inlet in deeper layers by mixing brackish outward moving surface water down into the incoming water. Similarly, there is an increase in density of near surface water by vertical mixing with the inward moving dense water in the deeper layers. An example of this phenomenon can be seen in Figures 3 and 4. This strong vertical mixing at the sills greatly reduces the transport potential of this mechanism. Large quantities of the outward moving surface layer are returned into the inlet by being mixed down into the lower layer (Gade, 1976). Organisms in the upper layer are thus partially returned to the inlet. Likewise, organisms in the denser water outside which might otherwise have been transported into the inlet, are mixed up into the seaward flowing surface water. This trapping of water and its associated properties within a fjord by mixing over a sill is a well known phenomenon (e.g. Gade, 1976).

A second ramification of this vertical mixing and its reduction of the incoming water density is the maintenance of the estuarine circulation as a system associated with the upper water column. Water which was potentially capable of penetrating into deep water and involving a large part of the water column in the circulation, is now maintained in the upper layers. Estuarine circulation in Indian Arm is thus restricted to the upper water column.

A crude estimation of the magnitude of the transport by estuarine circulation in Indian Arm can be obtained as follows:

Total volume of freshwater entering Indian Arm = 41 cu. m/sec.

(Davidson, 1979) =  $1.29 \times 10^9$  cu. m/year = R

Salinity of upper layer at IND 0 (averaged over all cruises) = 21.1ppt = S

Salinity of lower layer at IND 0 (averaged over all cruises) = 26.0ppt = S'

Assuming a constant volume of Indian Arm and conservation of salt in the inlet, using Knudsen's equations (from Saalen, 1967), the volume of water, V', entering the inlet is;

$$V' = R S / S' - S = 5.55 \times 10^9 \text{ cu. m/year}$$

The volume of Indian Arm (D. Dunbar, Pers. Comm.) is approximately  $2.25 \times 10^9$  cu. meters. Estuarine circulation is potentially capable of replacing the total volume of the inlet



about twice per year. The volume of water brought into the inlet by flood tides (see next section) is approximately  $4.2 \times 10^{10}$  cu. m/year. Averaged over a year, estuarine circulation is responsible for about 13% of the water entering Indian Arm. The estuarine circulation makes up a small part of the total transport at the sill. At times of maximum fresh water input the percentage brought into the inlet via this mechanism would increase.

The significant feature of this mechanism is its effect on the surface layers of water in Indian Arm. Although the flow is superimposed on the dominant tidal exchange, estuarine circulation establishes a net seaward movement in the upper layer of the water column. Over many tidal cycles this net movement would be an effective mechanism for the transport of zooplankton species living in the near surface water of the inlet.

### iii) Tidal Exchange

During the study period, tides were the dominant transport mechanism at the Indian Arm sill. The volume of water transported during a tidal phase was estimated both by current meter and by tidal model.

The current meter deployed at Indian 0 during each cruise met with varying success. The meter failed to work satisfactorily during Cruise 80/2 and the directional indicator failed to operate during Cruise 80/12 resulting in no current meter estimate of volume transport over these cruises. An

example of the current meter data collected is shown in Figure 6 (from Cruise 81/6). Figure 7 shows the data generated by ignoring the cross channel components of flow. In Figure 6 the flow at both 20 meters and 5 meters is shown to be predominantly north-south or along the channel; cross channel components, however, are evident. The north-south component of flow was always in the direction of tidal flow at 5 meters. At 20 meters the flow is both smaller in magnitude and more varied in its response to tidal direction. The general trend, however, is for the flow at both depths to be in the same direction as the tidal flow. Table VI shows the calculated volumes of water transported across the sill during each of the tidal phases over which currents were measured. In all cases the calculated volume of water transported across the sill was in the same direction as tidal flow, which is to be expected.

The residual, or net flow, at the end of a complete tidal cycle should be close to zero excluding the freshwater outflow (about 13% of tidal flow, see previous section). For the current meter data the net transport (summed over the tidal cycle) is the same order of magnitude as the transport during an entire tidal phase, and is often larger (see Table VI). Moreover, the calculated net flow is often up inlet, precisely opposite to the predicted down inlet net flow caused by the freshwater. These are indicators of the error involved in the calculation of volume transport with the sampling techniques used. There are a number of possible explanations for these errors. Calculation of the Reynolds Number at Ind 0 showed that the flow would be fully

turbulent at any current velocity above approximately 0.01 meters/second. This indicates that the flow is turbulent at any time other than slack water. For a fully turbulent flow in a channel there is a cross channel current shear such that the flow is at a maximum near the surface in the center of the channel and falls to a minimum near the boundaries due to frictional effects. This effect is greatly intensified in a channel of such highly irregular boundaries as those found on the Indian Arm sill. The current meter at 5 meters in the center of the channel therefore measured a maximum flow, and the 20 meter current readings reflect a decrease in flow of unknown magnitude presumably due to bottom friction. The current meter readings give no estimate of the reduced current velocities near the lateral boundaries. Multiplying by the cross section of the channel therefore results in an overestimation of volume transport. In addition, because readings were taken on the order of once every half hour, small eddies induced in the highly turbulent flow resulted in cross channel components which were treated as major components to the flow in the channel during the calculations. Sampling at a much higher frequency might have eliminated these cross channel components of eddies by averaging. The sampling frequency did not enable these high frequency events to be averaged out of the main flow. Other errors which could not be avoided with the sampling gear available were induced by movements of the ship while at anchor. Although these were minimized as much as possible by eliminating readings taken during large ship movements, smaller or slower

movements were not always detectable, especially at night.

For the above reasons, volume transport values obtained from current meter readings were not used in the calculation of zooplankton transport. The current meter values were used only for comparison and as an indicator of the general validity of volume transport calculated from the tidal model predictions of velocity. Table VI and Table VII show the volume transport calculated from the two series of data.

Upon summation over the single complete tidal cycles associated with the cruise times, it was found that volume transport calculated from the tidal model also yielded very large net flows. Unlike the current meter data, however, the tidal model was able to provide transport values for tides immediately prior to and immediately after the sampled tide. Assuming that the total volume of Indian Arm was not in flux, and that the net flow should be small, (equal to the freshwater outflow), the volumes of water transported over tidal phases of similar vertical change, regardless of direction, could be averaged. The result was an average volume transport associated with any large or small tidal change which was applicable to the zooplankton data from the cruise to which the volumes correspond (see Table VII). It was felt that these average values would yield a more reliable estimate of longer term transport trends.

The applicability of model derived data to the real environment must always be questioned. Any model is obviously a simplification and the tidal model is no exception. Velocities predicted are those due to tidal action only and no account of

freshwater outflow or other physical transport mechanism is taken. The model is based on the volumes of water needed to meet tidal height requirements across transects through the inlet. Volume transport across the Ind 0 cross section is therefore based on the volume of water which must pass this plane to account for empirically predicted tidal heights in Indian Arm. Unlike the current meter derived velocity data, the model velocities are derived from a volume consideration and are therefore averaged over the entire cross section. It is at the sill that the model will be the least accurate (Dr. S. Pond, Pers. Comm.), although this inaccuracy is primarily in the time scale of predictions rather than its magnitude. It was felt that the model would yield sufficiently reliable data to enable calculation of general trends over the study period. The inaccuracy in the times of predicted flows would be relatively unimportant as the precise timing of individual tidal events will not affect estimates of tidal volume transport over long periods of time which was the objective of the study.

### Transport of the Study Species

#### i) *Corycaeus anglicus*

The density of *C. anglicus* at each depth sampled over the five cruises in the study area is shown in Table VIII. A number of general trends are immediately obvious. The species is never found in great numbers in the Strait of Georgia and is most numerous in Vancouver Harbour (Station VAN 24) and at IND 0.

While it is more numerous in Indian Arm than in the Strait of Georgia, in general it seems not to be present in large numbers in deep water areas. C. anglicus is found over most of the water column at the deeper stations but is most numerous at the surface and mid depths. Maximum population densities were recorded at the time of the fall cruise (October), in agreement with Legare (1957).

Seasonal trends in the magnitude of C. anglicus transport across the Indian Arm sill are concomitant with the fall population peak (see Figure 8). Due to its presence throughout the year in near surface water one would expect transport over the sill on a continuous basis. Figure 8 supports this. A crude estimate of the total transport of C. anglicus between each cruise can be obtained by assuming that values calculated for each cruise can be applied to all the tidal cycles occurring in the time interval. Values for adjacent cruises were applied to half the tidal cycles to estimate the transport between cruises. Table IX shows that the transport of C. anglicus between cruises approximates (within an order of magnitude) the population of the species in Indian Arm calculated at the time of the second cruise.

The total population of a species in an area should be a function of transport (immigration and emigration), mortality and natality within the area. The transport values show that the total population in Indian Arm can be accounted for by exchange over the sill. Moreover, population variations such as the decrease between January 1981 (cruise 81/1) and March 1981

(cruise 81/6) are accounted for by transportation out of the inlet as seen during the January cruise. Figure 9 shows the average concentration of C. anglicus in the upper 50 meters during its breeding season in October. The large population at VAN 24 is an obvious feature and suggests a preferred breeding site and a major source of this species. Although no counts of juveniles or egg clusters were made for this species and no conclusive evidence can be presented regarding the ability of C. anglicus to reproduce in Indian Arm, the transport data suggest that mortality and natality play a minor role in determining the population density of this species in Indian Arm. It is thus suggested that the inlet population is primarily a result of transport across the sill from Vancouver Harbour.

ii) Euchaeta japonica

The depth distribution of E. japonica during the five cruises at each station is shown in Table X. The species is present in the Strait of Georgia and in Indian Arm at all times of the year but is absent from Vancouver Harbour and the Indian Arm sill from March until January. Exchange of this species across the sill was therefore observed only during the winter months.

The species is found in large numbers above sill depth in the Strait of Georgia and in Indian Arm in October. Tidal exchange of water and plankton are known to occur at this time, yet the population in Indian Arm appears to be unaffected. Transport was observed during Cruises 80/2 and 81/1 only and

calculation of the exchange of E. japonica during the winter months was carried out using figures derived from only these two cruises. Transport was assumed to commence sometime between the October cruise and the January cruise and was assumed to have terminated sometime after February as it was not observed in March. The numbers of E. japonica exchanged over the winter period of November, December, and January are given in Table XI. Transport of E. japonica seems to have little correlation with the density of the species in Indian Arm as shown in the same table. A net transport into the inlet is calculated for the winter months yet available measurements of post winter (or transport) conditions (Cruises 80/12 and 81/6) show a decrease in the population. Cruise 80/18, an example of pre winter conditions, shows a larger population in Indian Arm than both during and after the period of exchange. This implies that transport has a relatively small effect on the population and that other factors such as mortality and natality are the dominant factors controlling population density of the species in Indian Arm.

Table XII shows that E. japonica is present in water transported across the sill primarily as a Stage III copepodite. The table shows that the high density of Stage III's at the sill is not simply a result of higher concentrations of this stage in potentially exchangeable water. Figure 10 shows that sill water exchanged over the tidal cycle during the January 1981 cruise was most similar in temperature and salinity properties (and presumably in other biologically important properties as well,



e.g. Bary, 1963) to water from the upper 10 meters of Vancouver Harbour and water from the upper 30 meters of Indian Arm. The percentage of Stage III E. japonica in this water is considerably less than that found in tidally exchanged water above the sill. It is interesting to note, however, that in the Strait of Georgia, water which is above sill depth, or hydrographically similar to that which is, (see Figure 10), has a similar percent composition of Stage III copepodites to water found over the sill. The high percentage of Stage III copepodites in the Strait of Georgia is not the reason for winter transport per se. Potentially exchangeable water in October (Cruise 80/18, see Figure 18) shows a similar high percentage of this stage (see Table XIII) and similar densities to those found in January yet transport does not occur.

Reasons for the lack of transport during the summer can only be speculated upon as the data obtained during this study do not explain the anomaly. A breeding population of E. japonica exists in both the Strait of Georgia and Indian Arm at this time. The presence of juvenile stages (copepodite Stages I, II, and III) is evidence of this (see Table XIV). In spite of 1) observed exchange of water between the two areas, 2) evidence of the exchange of other species, and 3) the presence of E. japonica in potentially exchangeable water, the populations are isolated for much of the year. It is possible that summer exchange occurs via naupliar stages which were not identified or counted. E. japonica spends approximately 20 days (Evans, 1971) as a nauplius larva, which is enough time for it to be

transported from the Strait of Georgia into Indian Arm or vice versa. The complete absence of Stage I and II copepodites from both Vancouver Harbour and Ind 0, however, reduces the likelihood of such an occurrence. Furthermore, Evans (1971), states that the naupliar stages are seldom observed above 100 meters in the study area. Their exchange across the 20 meter sills thus appears unlikely. A possible explanation for the lack of summer transport is the presence of biologically inadequate conditions in the waters of Vancouver Harbour and the Indian Arm sill.

### iii) Metridia pacifica

The density of M. pacifica in the study area at each station on each cruise is shown in Table XV. The species is common at every depth sampled and is found throughout the year. Transport across the sill at IND 0 was observed on each cruise.

M. pacifica is known to exhibit a strong diel migration (Stone, 1977) and evidence of this is shown in Figure 11. Station FRA 1 was sampled during daylight on Cruise 80/12 and at night on Cruise 81/1. The daytime sample shows the majority of animals at mid depth, centered around 100 meters, while at night the population was concentrated near the surface. At Station IND 0, evidence of the diel migration was seen over a single cruise. Table XVI shows the densities of M. pacifica at each depth over the tidal cycle during the day and during the night in October (Cruise 80/18). Results of a t-test to determine differences between day and night densities show that the concentration of

M. pacifica was significantly higher at night regardless of the direction of tidal movement. However, a similar test for all data from Cruises 80/12 and 81/6 found no significant difference between the two sets of samples. Cruise 81/6 data from only 20 meters, however, shows a highly significant increase at night (Table XVI).

Transport of M. pacifica across the sill during each cruise is shown in Table XVII. While transport occurs throughout the year, the direction of net transport seems to have little correlation with season and shows no clear trends over the study period. The total number of animals estimated to have been transported between each cruise was calculated by averaging values from adjacent cruises over the number of tidal cycles which took place in the time interval between the cruises. There was little correlation between transport and the total population of M. pacifica in Indian Arm at the time of the second cruise. The population seemed to remain relatively constant (within confidence limits) over the first four cruises yet transport over this time period varied both in magnitude and direction. The population decrease between Cruise 81/1 and 81/6 is supported by the direction of net transport at this time, but only accounts for approximately 15% of the change. These data indicate that transport has a minor effect on the population densities of the species in Indian Arm and that factors such as seasonal breeding cycles and mortality probably play a more dominant role. The lack of correlation between net transport and seasonal breeding cycles could also be an artifact of the

sampling procedure. The species occurs in high densities in the upper portion of the water column and it is not unreasonable to assume that the distribution is patchy. The advection of patches of this species across the sill by tidal currents would produce variability in the density of the species which could have been missed by the sampling interval used. The coefficient of variation (CV), calculated for M. pacifica (see Table V), however, does not indicate high degrees of patchiness. (Samples from which the CV calculation were made were all taken from the same location over a short period of time.)

Where depth permits, the diel migration of M. pacifica will take the animal below sill depth and out of potentially exchangeable water. In shallower water, such as over the sill, the animal may migrate to a position very near the sediment-water interface, depths which could not be sampled with the equipment available. The diel migration of zooplankton is thought to be made in response to changes (or rates of change) in light intensity such that daylight causes a downward migration to a depth of suitably low light. In shallow water this depth may be unattainable but a very close association with the sediment-water interface or even an immersion into the sediment (Lewis, Pers. Comm.), might produce the necessary light conditions. If such is the case, animals carried into shallow water by tidal currents will have a greatly reduced or negligible transport during the day by currents in the water column above them. At night, as they move away from the sediment-water interface, they again become susceptible not only

to the current in the water column but also the sampling equipment.

Transport of M. pacifica is affected in a quantitative manner by the diel migration such that exchange of the species occurs mainly at night. The effect of this migration may at first appear to have an effect on distribution, however, because the migration occurs throughout the year and the species is in potentially exchangeable water each time it nears the surface, there will be no effect on the overall exchange. The long term effect of this situation is to allow continual exchange of the populations in the Strait of Georgia and in Indian Arm. This suggests that they can be considered a single population, exposed to different environmental factors depending upon their location.

iv) Eucalanus bungi

E. bungi was the least abundant of the copepods chosen for study. Its density at each station over the study period at each depth is shown in Table XVIII. Immediately obvious is the ontogenetic vertical migration exhibited by this species in the Strait of Georgia. The overwintering population is seen to occupy deep water (below 150 meters). During the summer they are scattered over much of the water column and present in near surface water in large numbers. By fall (Cruise 80/18), they are again scarce in the upper water column and found mainly in deep

water. A further characteristic to be noted from this table is the complete absence of this species from the upper 100 meters of Indian Arm. This is in accordance with the distribution seen by Krause and Lewis (1979).

Figure 12 shows that the ontogenetic migration has severe ramifications on the exchange of E. bungi between Indian Arm and the Strait of Georgia. From the data, transport over the sill appears to occur only during the summer when the species is present in surface water in the Strait of Georgia. This species is not present in the potentially exchangeable water of Indian Arm (Figure 13, Table XVIII). The data indicate that specimens found in Vancouver Harbour and at IND 0 had their origin in the Strait of Georgia and that transport is primarily unidirectional.

An estimate of the total seasonal transport of E. bungi across the sill is shown in Table XIX. Transport values calculated from the data collected during Cruise 80/12 were multiplied by the total number of tidal cycles in which E. bungi occupies near surface (potentially exchangeable) water in the Strait of Georgia. Krause and Lewis (1979), found that peak populations in these waters occurred in June and July, dropping sharply in August. Transport was estimated to have occurred over a two and a half month period and Table XIX shows that such a period of transport can account for the entire overwintering population in Indian Arm. The transport data suggests that natality within the inlet has little influence on the population and that the dominant process governing population density is

exchange across the sill. This suggestion is supported by the distribution of younger copepodite stages (Stages I, II, and III; Table XX) during the breeding season (Cruise 80/12). While the presence of these stages in near surface water of the Strait of Georgia indicates a reproducing population they are never observed in Indian Arm. Lack of a breeding population in Indian Arm is supported by similar data from Krause and Lewis (1979).

E. bungi appears to be transported across the sill primarily as younger copepodite stages, in spite of the fact that these stages are never seen in Indian Arm (see also Krause and Lewis, 1979). Data from IND 0 (Table XX) show that the transported organisms are all younger than Stage IV and that, similar to Euchaeta japonica, the primary dispersive stages of E. bungi seem to be the young copepodites.

The data suggest that there is no breeding population of E. bungi in Indian Arm and that animals observed in the inlet are solely a result of summer transport. The fate of these animals the following spring when they migrate into surface water to spawn is unknown. No data on the horizontal or vertical distribution of E. bungi in the vicinity of Indian Arm at the time of the onset of the upward migration is available. However, two possibilities exist, first, that the organisms might migrate into near surface water as they do in the Strait of Georgia, but be carried out of the inlet by the seaward flowing upper layer. The magnitude of this flow would be at its seasonal peak as a result of spring run off. Such a situation would remove all E. bungi from Indian Arm except those which failed to migrate; no

juvenile stages would be observed, and no animals would be found in near surface water following the migration. A similar situation has been observed in Knight Inlet (Stone, 1979) where surface dwelling plankton are completely advected from the headwaters of the inlet under conditions of high run off. Second, E. bungi might fail to migrate into surface water in Indian Arm and be unable to complete its life cycle. Vinogradov (1968) states that migration of this species might be triggered by variations in water temperature. Such seasonal changes would have to occur at depths below 200 meters to affect the overwintering population. In open ocean situations, such deep seasonal changes are small or nonexistent. Penner (1978) suggests that a more plausible trigger to the spring migration is the increase in sinking detrital material caused by the onset of the spring phytoplankton bloom. Figure 14 shows that changes in the temperature of Indian Arm bottom water are quite small and have no seasonal pattern but show a continuous warming trend over the entire study period. Seasonal temperature changes do occur in the deep water of the Strait of Georgia (Pickard, 1975) although Penner (1978) found that the upward migration of E. bungi had started before any such change had occurred. In Indian Arm the timing of the bloom varies but is a dominant feature of the seasonal cycle of primary production (Gilmartin, 1964) and could provide the necessary cue. The timing of the upward migration in relation to the onset of the spring phytoplankton bloom has not been studied in sufficient detail to allow deductions regarding its cause. However, any appreciable



advection of phytoplankton detritus out of the inlet by estuarine circulation could reduce the stimulatory effect.

#### Zooplankton Community Changes at IND 0 Over a Tidal Cycle

Data analysis on the four copepod species chosen for the transport study, centered on seasonal trends, the interaction of depth distribution and life history patterns with transport processes, and the effects of transport on the population in Indian Arm. Corequisite to this was an analysis of changes and patterns in the zooplankton community and hydrographic properties which were manifested over the much shorter time period of a single tidal cycle. Unlike a river fed estuary, the sill provides a location which, over a tidal cycle will be subjected to marine influence on both flood and ebb tides. As water is exchanged across the sill by tidal currents one might expect the zooplankton community and hydrographic properties to change depending upon the source of the water and the degree of mixing it has undergone. Both of these variables can be investigated using temperature and salinity characteristics as conservative tracers.

Figure 15 shows the tidal cycle and the sampling times of Cruise 80/18 (sample numbering is in a code related to Cruise 80/18 and has no meaning apart from the samples being consecutive). The semidiurnal nature of the tide is obvious. Large fluctuations in both temperature and salinity take place in the surface water (see Figures 16 and 17) due to the strong influence of local precipitation, runoff, and other weather

patterns. Such fluctuations decrease sharply with depth.

Figure 18 shows the temperature and salinity characteristics of water at each station in the study area at the time of the cruise. Although the coldest temperatures are found in Indian Arm deep water, stratification is such that near surface water (potentially exchangeable across the sill) is considerably warmer, and water resident in Vancouver Harbour is both cooler and more saline. Water found over the sill during a tidal cycle will be a mixture of these latter two types of water, its characteristics dependent upon the relative amounts of each present at any given time.

Surface water at hour 14 (sample 14) shows the largest change in both temperature and salinity (see Figures 16 and 17). Its correlation with the tidal cycle and the reason it should be so different from adjacent samples is difficult to explain. Figure 19 shows the time progressive T/S plot for water at 0 meters. Two characteristics bear noting; the extent of the difference of the water from sample 14 and the similarity of the water from samples 16, 17, and 18, all of which were taken during the same flood tide. This similarity is probably due to intense vertical mixing of the water as it moves through Second Narrows and over the Indian Arm sill creating a more homogeneous body of water.

The zooplankton community at the sill is more likely to be influenced by changes in the characteristics of water below 5 meters which accounts for approximately 90% of the water column. Changes in the hydrographic properties of this water take place

over the tidal cycle. Furthermore, these changes can be correlated with the direction of tidal movement and the source of the water. Figure 20 shows the time progressive T/S plot from each sample time averaged over the deeper part of the water column (5, 10 and 20 meters). Correlations between characteristics of the deeper water and the tidal cycle are more obvious. The coldest and most saline water occurs towards the end of, and immediately after, a large flood tide (samples 11, 18 and 19), labelled Type A. Figure 18 confirms that this is to be expected from water originating in Vancouver Harbour. Samples 12 and 13, labelled Type B, appear to be very similar to each other and although warmer and fresher than the previous group, are still more saline than other water sampled over the tidal cycle. Samples 12 and 13 probably reflect a slight mixing of Indian Arm water with the water brought into the sill vicinity during the large flood previously discussed. Water from samples 14, 15, 16, and 17, labelled Type C, are the least saline water found over the tidal cycle and occur during and immediately after a large ebb. Figure 18 confirms that water advected out of Indian Arm will have these characteristics.

The eight most abundant copepod species were plotted against the tidal cycle and analysed using a Spearman Rank Correlation Coefficient for changes in the density which could be correlated with tidal height. Figure 21 shows the four most abundant copepods and the tidal cycle. Oithona helgolandica was the only species which showed a significant correlation, greater densities being found at times of high water. Figure 22 shows

the second four most abundant copepods, two of which showed a significant correlation. Corycaeus anglicus was found to be in greater densities at times of high water, and Calanus pacificus at times of low water.

Two indices of diversity were calculated, Simpson's (Simpson, 1949) which is sensitive to changes in common species, and the Shannon-Weiner (logs taken to base 2; Patten, 1962) which is sensitive to changes in rarer species. These indices and percent dominance (McNaughton, 1967) were calculated for the community as a whole, for copepods only, for all other invertebrates, and for all other invertebrates minus larvaceans and siphonophores (which make up 85% of the numbers of other invertebrates). These data were plotted against the tidal cycle and analysed using Spearman Rank Correlation Coefficient for changes which seemed to be in phase with tidal height (see Figures 23, 24, 25, and 26).

The inverse relationship between percent dominance of copepods and tidal height was statistically significant, increasing on an ebb tide and decreasing with the flood (Figure 24). Simpson's index of diversity for copepods was positively correlated with tidal height and both this and the Shannon-Weiner index showed distinct minima reached at times of low tide, most notably for Simpson's index (more common species). These characteristics could be due to a fjord copepod community, dominated by only a few copepod species, which is moved towards the sill during the ebb tide.

The diversity and dominance of other invertebrates (Figure

25) does not show a consistent relationship to tidal height and no significant correlation was found. Maximum diversity for both indices is reached during the large ebb tide and minimum diversity occurs at the end of the major flood tide. These data points are due largely to changes in the densities of larvaceans and siphonophores. When these two very dominant groups are removed (Figure 26), these maxima disappear. The remainder of the invertebrates did not show significant correlation with tidal height. Diversity and dominance for the total zooplankton community ( Figure 23) probably strongly reflect the overwhelming influence of the large numbers of larvaceans and siphonophores.

An analysis of variance using a randomized complete block design for one replicate was calculated for the total density at each sampling time. The results show a significant difference ( $p=0.05$ ) in the numbers of copepods caught at each sampling time, indicating that significant changes in copepod densities do occur over the tidal cycle. The question then to be asked is do these changes occur in relation to any identifiable physical parameter?

Three different parameter relationships were statistically tested to answer this question:

- 1) The community might show a variation in relation to the direction of tidal flow which could not be resolved from the graphs previously analysed.
- 2) If the population has a significant number of

diurnal vertical migrators, the community might show variations between samples taken at night and during the day.

3) Based on hydrographic data, the water moving over the sill could be grouped into three categories based on similar temperature and salinity characteristics (see Figure 20). The zooplankton community might vary between these water types.

Samples were divided into those taken on an ebb tide (Numbers 11, 14, 15, and 19) and those taken during a flood tide (Numbers 12, 13, 16, 17, and 18, see Figure 15) and a U-test used to test a number of different parameters and species densities for significant differences between the two. There is a significant increase ( $p = 0.05$ ) in the numbers of siphonophores during ebb tides, suggesting a larger population of these animals in Indian Arm than in Vancouver Harbour. Both the Simpson's and Shannon-Wiener index indicate a higher diversity of other invertebrates during ebb tides ( $p = 0.05$ ). This could be due to a more diverse community of invertebrates in Indian Arm than in the shallower region of Vancouver Harbour. The reason for parameters having a correlation with tidal height yet showing no difference between ebb and flood tidal phases might be the strict division of samples between ebb and flood based on sampling time. Hydrographically, it is difficult to decide in which tide a sample taken within an hour of slack water should be placed. Evidence of this can be seen more

clearly in Figure 20 showing the changes in the hydrographic properties. A comparison with Figure 15 shows that water characteristics do not fluctuate strictly in unison with tidal direction.

Samples were then divided into those taken during the day (Numbers 11, 12, 13, 18, and 19) and those taken at night (Numbers 14, 15, 16, and 17). A U-test was run on a number of different species densities and other community parameters to test for significant differences between the groups, results of which are shown in Table XXI. Two of the tested parameters showed significant differences. Corycaeus anglicus had higher densities during the day, a trend which is opposite to that expected if there was a diel migration. The data were thus not interpreted as evidence of migration. Euphausiids, however, are known to be strong diel migrators (Bary, 1967) and we see significantly higher densities at night than during the day ( $p = 0.5$ ). Two factors might contribute to this increase:

- 1) Euphausiids in Indian Arm which during the day have migrated into deeper water and are therefore unexchangeable, might move into near surface water at night and be carried over the sill by either tidal currents or the seaward flowing surface component of the estuarine circulation.
- 2) Euphausiids which might permanently inhabit the shallow areas in the vicinity of the sill might migrate to depths in such close proximity

to the sediment-water interface so as to be unavailable to the sampling equipment used. During the night, their upward movement would increase their catchability.

It is interesting to compare these vertical haul data to those derived from the Clarke-Bumpus nets used in the transport study. A significant difference (t-test,  $p = 0.05$ ) was found in the density of Metridia pacifica (a known diel migrator), between day and night samples using Clarke-Bumpus nets (see Table XVI), yet the vertical hauls failed to show this for samples taken at the same location at the same time (see Table XXI). This discrepancy could be due to the previously discussed patchy nature of the distribution of this species, and the failure of a single vertical haul to adequately sample the community. The Clarke-Bumpus nets, which integrate over a larger horizontal distance, might quantitatively sample a patchy species more effectively.

The final hypothesis to be tested was that there were different community parameters or groups of zooplankton carried over the sill that were associated with the hydrographically discernable water types characterized by temperature and salinity shown in Figure 20. Such an association has been noted in the open ocean in space (e.g. Bary, 1963) but in the literature few examples exist of variations over time at a single station. A notable exception is Stone (1977), who documented water type and copepod associations on a seasonal basis in Knight Inlet. Data presented by Stromgren (1975),



indicate that copepod diversity could be a function of the circulation of the fjord, specifically of the transport in the upper part of the water column.

The water characteristics were divided into the three groups discussed earlier (see Figure 20); type A composed of samples 18, 19 and 11, type B of samples 12 and 13, and type C of samples 14, 15, 16, and 17. The only stipulation imposed on these groupings was that samples within them should be chronologically consecutive, a logical restriction when looking for trends or patterns within a continuum. Sample 11 can be considered as occurring both before sample 12, and after sample 19 as the tide at this point had completed an entire cycle.

The relationship of the above hydrographic groupings to the copepod data was tested by calculating Kendall's coefficient of concordance of copepod densities for pairs of consecutive samples over the tidal cycle, ( Figure 27). The three highest levels of concordance each support the groupings made based on hydrographic data. Similarly, samples at the beginning or end of any group show a higher concordance with the adjacent sample within their group than with the adjacent sample outside their group in each case. This is most obvious between samples 17 and 18. The decision to place samples 11 and 19 in the same group is strongly supported by the concordance data.

A Kruskal-Wallis one way analysis of variance was used to test for differences between the three water types in a number of community parameters, the results of which are presented in Table XXII. There were significant differences in the Shannon-

Weiner and Simpson's diversity index for copepods. The community in water type A, at the end of the major flood tide, had a higher diversity than that of the other water types found at different times over the sill. This pattern is opposite to that found by Stromgren (1975) in two Norwegian fjords where an increased exposure to coastal water led to a decreased diversity. A possible explanation for this discrepancy might be differences in fresh water influence. The Norwegian data were obtained at a time of low run off, but in Indian Arm, the fresh water input of October might be expected to result in a higher diversity of marine plankton in water originating in coastal regions due to the increasing estuarine conditions encountered towards the head of the inlet. The only tested copepod which showed a significant change in density associated with the water types was C. anglicus which was found to be in higher numbers in water type A. This supports the data presented in the transport chapter on this species which indicated a Vancouver Harbour origin of this species. No significance could be found in the association of changes in other parameters with water type.

The most distinct changes in the copepod community are manifested over the tidal cycle not in relation to the direction of tidal flow directly, but rather in relation to hydrographically discernable bodies of water advected over the sill by tidal currents. This suggests that turbulence and mixing induced by the boundary conditions of the harbour system are such that water properties become temporally dissociated from tidal direction. The source of the water, however, can be traced

through hydrographic properties. Water associated with the end of a large flood tide was shown to be the most unique in terms of community parameters. Wooldridge and Erasmus (1980) have shown that certain zooplankton species utilize the tidal currents via behavioral patterns to maintain themselves within an estuary. If such were the case at the fjord mouth, one would expect to see significant changes in species densities in relation to tidal direction, which the data did not show. The importance of maintaining position within a fjord might not be so critical to the survival of a zooplankton as it is in an estuary where water conditions are drastically different from coastal water.

Community changes associated with the types of water were more prevalent in copepods than other invertebrates. Moreover, these changes were found at the community level rather than at the species level. The reason for this could be due to the influence of rarer species of copepods on the diversity indices. The changes occurring in the density of these species over the tidal cycle could not be distinguished with the techniques used in this study. More numerous species did not show changes over the tidal cycle. An exception to this generality was found for C. anglicus which had a source in close proximity to one side of the sill. During the summer, a similar response might be expected for E. bungi as it also has a source on only one side of the sill.

## CONCLUSIONS

The effect of physical transport on the zooplankton community of Indian Arm was investigated through a detailed study of a series of key copepod species. The data indicated that a general statement on the effect of physical transport, encompassing the whole zooplankton community, was not possible due to the unique nature of each species. Species specific differences, occurring primarily as a result of different behavioral patterns, resulted in differing transport characteristics among the study species.

The data showed that a quantitative estimate of zooplankton transport across the inlet mouth was possible. The accuracy of the estimate depended upon the resolution of spatial and temporal changes in the zooplankton community as it crossed the sill, and on the accuracy of the volume transport calculation. The variability of the data revealed distinct limitations in the ability of the technique to resolve smaller changes. This variability seemed greatest for more abundant species such as Metridia pacifica. The reasons for this were probably due to the patchy nature of the species distribution. In such a case, estimates of transport over short periods of time such as a single tidal cycle were least reliable. Extrapolated over a season, however, general trends could be shown. For less abundant species, such as Eucalanus bungi, the results were less variable and transport estimates over a single tidal cycle seemed more reliable. These data could also be extrapolated over

an entire season and showed close correlation with observed population trends in Indian Arm. Because of the time interval between them, the cruises yielded data which could only be used to describe general seasonal trends in the transport of the species studied. These seasonal trends indicated the varying degrees to which transport affected the resident population of the studied species in Indian Arm.

The study showed that the variability in the transport of different species was primarily a result of biological processes within the water rather than changes in the magnitude of physical transport. Changes in species abundance in potentially transportable water were orders of magnitude larger than changes in the volume exchanged across the sill. This generalization is true, however, only under the physical transport regimes studied. For example, a density driven intrusion which could not be studied, would result in very large changes in volume transport, possibly of the same order of magnitude as the biological changes, and thus profoundly influence the magnitude of zooplankton transport.

Species specific behavior patterns seemed to have a most dramatic influence on transport. This conclusion is similar to that reported by Sands and Svendsen (1980) for data collected from a Norwegian fjord. In Indian Arm this was a result of the transport mechanisms being a near surface phenomenon. The physical presence of the shallow sills, their induced vertical mixing, and the lack of a deep water intrusion precluded the exchange of water deeper than sill depth and hence of the

animals associated with it. Animals which exhibit a vertical migration, such as the diel migration of M. pacifica or the ontogenetic migration of E. bungi, were transported across the sill only during those periods when they were present in this exchangeable water. Animals which exhibit an ontogenetic depth preference such as Euchaeta japonica were transported only at that life history stage which occupied water above sill depth. Organisms whose entire life history was spent in potentially exchangeable water and were tolerant of the surface water conditions, such as Corycaeus anglicus, were exchanged at all times of the year. The magnitude of this exchange was a function of the seasonal density of the organism, and was thus closely linked with the breeding cycle.

One can speculate that a second prerequisite for transport was the ability of the organism to survive the physical and biological conditions in the exchanging water. Hydrographically, this included strong horizontal gradients in temperature and salinity induced by the intense vertical mixing over the sills. Organisms also had to be tolerant of biologically active chemical elements present in the water. This is a possible explanation for the anomalous lack of transport during the summer of E. japonica. Furthermore, both E. japonica and E. bungi were transported mainly as young copepodite stages, despite the presence of other life history stages in potentially transportable water on either side of the sill. This could be due to an increased tolerance of these stages to near surface water conditions.

The effect of transport on the populations inside Indian Arm varied with species and was dependent upon the survival of the organism in the inlet, its ability to tolerate the conditions of transport and the magnitude of that transport. For organisms which did not reproduce in Indian Arm, (e.g. E. bungi), the entire population within the inlet was a result of transport and the data showed that total seasonal transport closely balanced the total inlet population. For a species which did reproduce in Indian Arm, (e.g. E. japonica), the correlation of transport with changes in the inlet population was not so close. Natality within the inlet had a more dominant effect on population trends. In such cases the effect of transport was merely to unite populations genetically in geographically separate regions. Although it is unknown whether C. anglicus bred within the inlet, the data suggested that transport of the species had a dominant effect on the population inside Indian Arm. Vancouver Harbour seemed to be a preferred breeding site for the organism and the close proximity of this site to the sill might have led to the increased transport.

The effect of different transport mechanisms on the actual transport of zooplankton was difficult to assess. No analysis could be made of the effect of a density driven intrusion as no major intrusion of this type occurred during the study. The predominant transport mechanism during the study period was tidal exchange. Estuarine circulation was a small component of the total flow across the sill and could not be analytically separated from the tidal component. Intuitively, however, it

seemed that the effect of this flow would be manifested over a much longer time frame. Estuarine circulation would most strongly affect those species living in the surface waters of Indian Arm as currents are strongest in this shallow layer. Although the effect on subsurface organisms outside the inlet would not be so pronounced due to the slower upinlet current velocities, it would produce a net movement into the inlet. Estuarine circulation thus establishes a net upinlet flow in the subsurface waters found over the sill and a net export in the surface layers of the inlet. It can be hypothesized that this would have a greater effect on Vancouver Harbour zooplankton entering Indian Arm than the reverse; only those species in the shallow, relatively fresh surface layers of Indian Arm would be advected out, a region sparsely populated by marine zooplankton. (This was also found in Knight Inlet, Stone, 1977).

Over a single tidal cycle, distinct changes took place in the zooplankton community found over the sill. Relatively few copepod species showed any correlation to tidal height and fewer individual species showed significant changes in relation to tidal direction or time of day. Most importantly, significant differences in individual species densities did not occur in relation to tidal direction. Changes in the entire copepod community occurred in association with hydrographically discernable types of water advected over the sill during the tidal cycle. The changes which did occur seemed to be at the community level rather than at the species level. Community changes thus occurred in relation to the origin of the water, a



factor which was not directly related to tidal direction. The most profound difference in the copepod community was found towards the end of large flood tides. The hydrographic data suggested that the origin of this water was Vancouver Harbour, a suggestion supported by the presence of high densities of C. anglicus found at the same time.

Species which exhibit a diel vertical migration were found in significantly higher numbers at night. Youngbleth (1980) found higher concentrations of many species of plankton in samples taken at night which he attributed to a reduced net avoidance. In this study, however, only those species which have a known vertical diel migration were found in greater densities at night, lending credence to the proposal that these species were transported primarily at night.

Analysis of the whole zooplankton community over a tidal cycle pointed out limitations in the interpretation of the transport patterns deduced for the four study species. The transport study was carried out using the densities of the study species which occurred during the ebb and flood events of each cruise. Significant differences in the individual species densities were not seen in relation to the direction of tidal flow across the sill when the whole community was analysed. Further analysis of the zooplankton community showed, however, that very significant changes took place in association with hydrographic properties. The differences were thus related to the origin of the water. While these hydrographic properties, indicative of the origin of this water, were temporally

dissociated from tidal direction, it was still the tidal flow which was responsible for the advection of the water over the sill and the resultant exchange. Thus when extrapolated over much longer time scales it was the origin of the water, and its associated zooplankton, which resulted in the resolution of seasonal transport patterns.

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## TABLES

Table I: Cruise dates and numbers.

Cruise	Date
80/1	January, 1980
80/2	February, 1980
80/12	July, 1980
80/18	October, 1980
81/1	January, 1981
81/6	March, 1981
81/33	November, 1981

Table II: Sampling Depths.

Station	Hydrographic Data	Clarke-Bumpus Tows	Vertical Hauls	
GEO 1748	0		375-50	50-0
	5	X		
	10			
	20	X		
	50	X		
	75			
	100	X		
	150	X		
	200			
	250	X		
	300			
	350	X		
	375			
FRA 1	0		200-50	50-0
	5	X		
	10			
	20	X		
	30			
	50	X		
	75			
	100	X		
	150	X		
	200	X		
VAN 24	0		50-0	
	5	X		
	10			
	20	X		
	30			
	50	X		
IND 0	0		20-0	
	5	X		
	10	X		
	20	X		
IND 1.5	0		175-50	50-0
	5	X		
	10			
	20	X		
	30			
	50	X		
	75			
	100	X		

	150	X		
	175	X		
IND 2.0	0		200-50	50-0
	5	X		
	10			
	20	XX		
	30			
	50	X		
	75			
	100	XX		
	150	X		
	200	XX		

---

Note XX indicates depths at which replicate samples were taken for statistical treatment.

Table III: Animals and Taxonomic Groups Identified for the  
Community Analysis at IND 0 (Cruise 80/18)

-----  
Copepods

Microcalanus pygmaeus  
Pseudocalanus minutus  
Paracalanus parvus  
Oithona spinirostris  
Oithona helgolandica  
Oncaea borialis  
Corycaeus anglicus  
Scolecithricella minor  
Metridia pacifica  
Calanus pacificus  
Acartia longiremis  
Acartia clausi  
Tortanus discaudatus  
Aetideus armatus  
Euchaeta japonica  
Bradyidius saanichi

Other Invertebrates (where known, the number of species  
in each group is given)

Nauplius larvae

Ostracods

Conchoecia elegans  
Philomedes sp. 1  
Paradoxostoma striungulum

Siphonophores 4

Pteropods

Limacina helicina

Larvaceans 2

Harpacticoid copepods

Isopods

Amphipods

Parathemisto sp. 1  
Stilipes sp. 1

Medusae

Phialidium sp. 1

Proboscidactyla sp. 1  
Aegina sp. 1  
Aequorea sp. 1

Decopod Larvae

Ctenophores 1

Cumaceans

Euphausiids 1

---



Table IV: Animal densities per cubic meter at the sampling depths on cruise 81/33.

Depth	<i>Euchaeta japonica</i>	<i>Eucalanus bungi</i>	<i>Metridia pacifica</i>	<i>Corycaeus anglicus</i>
200		0.83	0.83	0.14
100	1.96		93.97	0.39
20				0.75
200		0.40	2.46	0.20
100	2.23		78.06	1.59
20				0.18
200		0.19	2.53	
100	5.40		109.90	0.64
20				0.55
200		0.90	0.36	
100	3.02		122.59	1.26
20			0.13	1.44
200		1.26	1.69	0.42
100	4.62		139.47	0.12
20				1.13
200		0.60	0.20	
100	3.77		149.95	0.92
20			0.16	1.17

Table V: Statistical treatment of replicates.

Species	total	mean	S.D.	CV	95% Confidence Limits	
					Upper	Lower
At 200m						
E.bungi	4.18	0.70	0.38	54.57	1.68	-0.28
M.pacifica	8.07	1.35	1.03	76.64	4.00	-1.30
C.anglicus	0.76	0.13	0.17	131.98	0.57	-0.31
At 100m						
E.japonica	21.00	3.50	1.35	38.66	6.97	0.03
M.pacifica	693.93	115.66	127.23	23.55	185.67	45.65
C.anglicus	4.92	0.82	0.55	66.88	3.39	-0.59
At 20m						
C.anglicus	5.22	0.87	0.46	53.31	2.05	-0.31

## Transformed Data

	Derived Geometric Mean	log S.D.	CV'	Log 95% Confidence Upper	Limits Lower
At 200m					
E.bungi	0.66	0.10	25.8	2.00	-0.08
M.pacifica	1.15	0.20	58.5	6.02	-0.34
C.anglicus	0.12	0.06	14.8	0.59	-0.22
At 100m					
E.japonica	3.33	0.13	34.9	8.35	1.00
M.pacifica	112.89	0.11	28.8	217.41	58.38
C.anglicus	0.75	0.14	38.0	3.00	-0.24
At 20m					
C.anglicus	0.82	0.12	31.8	2.70	-0.11

\* Note Transformation  $x = \log_{10}(x+1)$   
 CV = Coefficient of Variation  
 CV' = Logarithmic Coefficient of Variation  
 Log Confidence Limits = 95% confidence limits  
 for a hypothetical sample containing  
 an animal density equal to 'Mean'

Table VI: Volume transport of water across the Indian Arm sill, calculated from current meter readings.

Cruise	Volume Transport (Cubic Meters)		
	80/18	81/1	81/6
Ebb			$-2.25 \times 10^7$
Flood	$1.55 \times 10^7$	$4.33 \times 10^7$	$8.35 \times 10^7$
Ebb	$-3.09 \times 10^7$	$-2.15 \times 10^7$	$-3.06 \times 10^7$
Flood	$1.44 \times 10^8$	$7.10 \times 10^7$	$3.68 \times 10^7$
Ebb	$-1.70 \times 10^6$	$-1.04 \times 10^8$	
Net Transport	$1.27 \times 10^8$	$3.18 \times 10^7$	$6.72 \times 10^7$
*Note    - denotes flow out of the inlet (southward) + denotes flow into the inlet (northward)			

Table VII: Average volume transport for large and small tidal exchanges, calculated from the model predictions.

Date	Cruise	Large Tide	Small Tide
Feb. 1980	80/2	$7.59 \times 10^7$	$4.92 \times 10^7$
July 1980	80/12	$1.00 \times 10^8$	$3.37 \times 10^7$
Oct. 1980	80/18	$9.13 \times 10^7$	$4.27 \times 10^7$
Jan. 1981	81/1	$7.42 \times 10^7$	$2.69 \times 10^7$
March 1981	81/6	$7.34 \times 10^7$	$4.31 \times 10^7$

Table VIII: Density of Corycaeus anglicus in the study area.

Densities are in number per cubic meter.

February (Cruise 80/2)				Station			
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth	1748		Narrows				
(m)							
5		1.3		0.3	0.0	0.1	0.0
10					0.0		
20		0.8	---	0.4	0.9	0.3	0.1
50		0.0		0.0		0.1	0.4
100		0.2				0.4	0.0
150		0.0				0.0	0.0
175						0.2	
200		1.0					0.0
250							
300							
350							
400	---						
July (Cruise 80/12)				Station			
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth	1748		Narrows				
(m)							
5	0.0	0.1		0.0	0.7	0.0	0.0
10					1.4		
20	0.4	1.4	-	0.0	1.4	0.0	0.0
50	0.0	0.8		1.2		0.6	0.0
100	0.0	0.0				0.0	0.0
150	0.0	0.0				0.0	0.0
175						0.0	
200		0.0					0.0
250	0.0						
300							
350	0.0						
400	---						

-----  
 October (Cruise 80/18) Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	0.0	0.1		3.9	4.0	1.2	1.5
10					6.1		
20	1.0	1.4	---	16.6	11.5	2.6	0.7
50	0.8	0.8		25.5		2.6	0.7
100	0.2	0.3				0.2	1.0
150	0.2	1.5				0.0	1.6
175						0.1	
200		1.0					0.7
250	0.0						
300							
350	0.4						
400	---						

-----  
 January (Cruise 81/1) Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	0.0	0.0		4.2	1.3	0.6	0.1
10					1.1		
20	0.0	0.0	---	0.6	0.4	0.2	0.6
50	0.0	0.0		0.1		0.1	0.2
100	0.0	0.0				1.5	0.0
150	0.0	0.0				0.0	0.0
175						0.0	
200		0.0					0.5
250	0.0						
300							
350	0.0						
400	---						

-----  
 March (Cruise 81/6) Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	0.0	0.0		0.8	0.3	0.5	0.2
10					0.2		
20	0.0	0.1	---	0.6	0.2	0.1	0.2
50	0.4	0.0		0.0		0.0	0.0
100	0.0	0.7				1.0	0.3
150	0.0	0.4				0.0	0.4
175						0.0	
200		0.1					0.0
250	0.0						
300							
350	0.0						
400	---						

-----

Table IX: Transport of Corycaeus anglicus across the Indian Arm sill during the study period.

Cruise Interval	Tidal Cycles	Averaged Transport Between Cruises	Indian Arm Population (Second Cruise)	Confidence Intervals	
				Upper	Lower
80/2-80/12	132	$6.34 \times 10^9$	$6.32 \times 10^8$	$7.75 \times 10^8$	0
80/12-80/18	108	$5.94 \times 10^9$	$2.72 \times 10^9$	$8.74 \times 10^9$	$3.79 \times 10^8$
80/18-81/1	74	$2.37 \times 10^8$	$7.58 \times 10^8$	$3.57 \times 10^9$	$3.70 \times 10^7$
81/1-81/6	61	$-6.34 \times 10^8$	$5.30 \times 10^8$	$2.73 \times 10^9$	0

Note + indicates transport into the inlet  
 - indicates transport out of the inlet





October (Cruise 80/18)				Station			
Sample	GEO 1748	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth(m)	Narrows						
5	7.8	25.8		0.0	0.0	0.0	0.0
10					0.0		
20	2.9	3.7	---	0.0	0.0	4.2	0.1
50	10.9	5.8		0.0		8.4	5.4
100	2.6	1.2				4.7	13.1
150	1.1	1.0				8.2	5.8
175						4.8	
200		1.8					1.5
250	2.4						
300							
350	4.9						
400	---						

January (Cruise 81/1)				Station			
Sample	GEO 1748	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth(m)	Narrows						
5	8.6	9.5		0.2	0.8	0.0	2.2
10					1.0		
20	0.4	1.0	---	0.6	0.9	0.2	3.5
50	2.8	0.9		0.7		1.7	0.5
100	0.3	0.8				5.0	0.3
150	1.4	0.9				1.2	0.0
175						0.8	
200		0.6					1.0
250	0.4						
300							
350	0.0						
400	---						

March (Cruise 81/6)				Station			
Sample	GEO 1748	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth(m)	Narrows						
5	4.5	4.5		0.1	0.0	0.0	0.0
10					0.0		
20	1.2	1.8	---	0.0	0.0	0.0	0.0
50	2.8	2.1		0.0		0.0	0.0
100	0.5	0.3				0.0	0.3
150	0.6	0.5				4.2	0.5
175						2.2	
200							
250	2.0						
300							
350	3.9						
400	---						

Table XI: Euchaeta japonica seasonal transport across the Indian Arm sill and population in Indian Arm.

<u>Transport</u>				
Feb. (80/2 Data)	Jan. (81/1 Data)	Total Seasonal Transport=3 Months =86 Tidal Cycles (Jan. Data only)		
Number per Tidal Cycle	Number per Tidal Cycle			
$1.52 \times 10^6$	$7.51 \times 10^7$	$6.46 \times 10^9$		
95% confidence limits				
$-2.61 \times 10^7$ 0	$1.71 \times 10^8$ $2.35 \times 10^7$	$1.47 \times 10^{10}$ $2.02 \times 10^9$		
<u>Population</u>				
Feb(80/2)	July(80/12)	Oct(80/18)	Jan(81/1)	March(81/6)
$3.29 \times 10^9$	$1.90 \times 10^9$	$1.19 \times 10^{10}$	$2.85 \times 10^9$	$8.78 \times 10^8$
95% confidence limits				
$9.44 \times 10^9$ $5.18 \times 10^8$	$5.77 \times 10^9$ $2.40 \times 10^8$	$2.80 \times 10^{10}$ $4.55 \times 10^9$	$9.73 \times 10^9$ $8.16 \times 10^8$	$2.44 \times 10^9$ $2.30 \times 10^8$

Table XII: Percent composition of Euchaeta japonica density in potentially exchangeable water, January, 1981. Deduced from Figure 10.

Location	Copepodite Stage					
	I	II	III	IV	V	VI
Sill						
density	0	2.2	15	4.2	1.5	0.1
%	0	9.5	65.2	18.3	6.5	0.4
Harbour						
density	0	0.2	0	0	0	0
%	0	100	0	0	0	0
Indian Arm						
density	0	1.4	0.3	0.1	2.8	1.2
%	0	24.1	5.1	1.7	48.3	20.7
Strait						
density	0	0.9	10	1.9	3.3	1.9
%	0	5	55.6	10.6	18.3	10.6

\*Note

'Indian Arm' refers to the sum from both Indian Arm stations

'Strait' refers to the sum from both Strait of Georgia stations

Table XIII: Percent composition of Euchaeta japonica density in potentially exchangeable water, October, 1980. Deduced from Figure 18.

Location		Copepodite Stage					
		I	II	III	IV	V	VI
Indian Arm	density	0	6.3	3.8	2.2	4.5	1.3
	%	0	34.8	21.0	12.1	24.9	7.2
Strait	density	0	9.2	12.5	9.3	19.5	6.4
	%	0	16.2	2.2	16.3	34.3	11.2

\* Note Values refer to the sum of both stations in each location.

Table XIV: Density of Euchaeta japonica copepodite Stages I, II, and III in the Strait of Georgia and Indian Arm in October (Cruise 80/18).

Sample Depth(m)	Station			
	GEO 1748	FRA 1	IND 1.5	IND 2.0
5	2.1	4.8		
10				
20	1.6	0.3		0.1
50	8.6	4.3	5.4	4.6
100	1.8	0.8	2.9	4.1
150	0.9	0.4	6.3	2.2
175			<u>4.6</u>	
200		<u>0.3</u>		<u>0.8</u>
250	1.3			
300				
350	4.8			
400	---			

Table XV: Density of Metridia pacifica in the study area.

-----								
February (Cruise 80/2) Station								
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0	
Depth	1748		Narrows					
(m)								
-----								
5		65.9		9.3	10.2	49.0	18.0	
10					17.3			
20		1.4	---	8.3	12.9	31.1	15.7	
50		1.7		2.5		11.3	9.6	
100		5.8				13.6	40.0	
150		31.5				12.0	18.5	
175						6.9		
200		6.0					0.9	
250								
300								
350								
400	---							
-----								
July (Cruise 80/12) Station								
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0	
Depth	1748		Narrows					
(m)								
-----								
5	0.7	0.1		0.2	9.7		1.4	
10					0.5			
20	146.7	56.2	---	1.3	9.4	7.1	41.2	
50	4.0	9.4		0.0		10.0	0.0	
100	23.5	297.4				58.6	70.5	
150	67.3	26.7				24.1	16.3	
175						0.0		
200		45.6					13.1	
250	11.4							
300								
350	1.3							
400	---							

-----  
 October (Cruise 80/18) Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	17.1	13.6		2.6	1.4	49.7	0.0
10					8.2		
20	39.4	56.5	---	3.2	1.8	14.3	0.1
50	2.4	4.8		5.5		8.3	24.7
100	15.7	4.7				29.4	61.1
150	13.0	16.5				24.9	34.4
175						57.3	
200		27.4					105.5
250	22.1						
300							
350	53.5						
400	---						

-----  
 January (Cruise 81/1) Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	56.3	302.7		0.2	6.2	0.6	3.5
10					5.1		
20	27.8	10.7	---	1.2	5.2	28.4	22.0
50	5.8	6.3		6.3		4.3	12.5
100	13.0	15.3				75.2	1.3
150	17.5	14.7				17.2	18.4
175						10.0	
200		11.9					95.2
250	17.9						
300							
350	11.5						
400	---						

-----  
 March (Cruise 81/6) Station

Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m) Narrows  
 -----

5	31.3	193.4		13.2	6.3	1.9	4.0
10					10.0		
20	77.2	20.6	---	15.3	6.6	3.1	1.7
50	13.8	9.5		12.3		1.1	4.8
100	23.4	10.1				22.7	4.3
150	56.8	9.0				3.7	0.6
175						8.0	
200		5.7					1.4
250	2.3						
300							
350	1.4						
400	---						

-----





Table XVII: Transport of Metridia pacifica across Indian Arm sill.

Net Transport (animals)	Tidal Cycles Between Cruises	Average Transport	Total Population in Indian Arm	Population Confidence Limits
Cruise 80/2 $+1.02 \times 10^9$			$3.84 \times 10^{10}$	$8.75 \times 10^{10}$ $2.22 \times 10^{10}$
	132	$+6.45 \times 10^{10}$		
Cruise 80/12 $-4.20 \times 10^7$			$5.64 \times 10^{10}$	$1.02 \times 10^{11}$ $2.65 \times 10^{10}$
	108	$-3.07 \times 10^9$		
Cruise 80/18 $-1.49 \times 10^7$			$5.91 \times 10^{10}$	$1.06 \times 10^{11}$ $2.99 \times 10^{10}$
	74	$-1.56 \times 10^9$		
Cruise 81/1 $-2.73 \times 10^8$			$5.33 \times 10^{10}$	$9.04 \times 10^{10}$ $2.29 \times 10^{10}$
	61	$-6.19 \times 10^9$		
Cruise 81/6 $+7.02 \times 10^7$			$1.12 \times 10^{10}$	$2.36 \times 10^{10}$ $4.80 \times 10^9$
Note + indicates transport into the inlet - indicates transport out of the inlet				
Tidal Volumes for each cruise in cubic meters (large tide and small tide)				
Cruise 80/2		$7.59 \times 10^7$	$4.92 \times 10^7$	
Cruise 80/12		$1.00 \times 10^8$	$3.37 \times 10^7$	
Cruise 80/18		$9.13 \times 10^7$	$4.27 \times 10^7$	
Cruise 81/1		$7.42 \times 10^7$	$2.69 \times 10^7$	
Cruise 81/6		$7.34 \times 10^7$	$4.31 \times 10^7$	

Table XVIII: Density of Eucalanus bungi in the study area.

February (Cruise 80/2)				Station			
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth	1748		Narrows				
(m)							
5		0.0		0.0	0.0	0.0	0.0
10					0.0		
20		0.0	---	0.0	0.0	0.0	0.0
50		0.0		0.0		0.0	0.0
100		0.0				0.0	0.0
150		0.2				0.0	0.0
175						0.5	
200		0.0					0.0
250							
300							
350							
400	---						
July (Cruise 80/12)				Station			
Sample	GEO	FRA 1	1st	VAN 24	IND 0	IND 1.5	IND 2.0
Depth	1748		Narrows				
(m)							
5	0.0	0.0		0.0	0.01	0.0	0.0
10					0.03		
20	11.5	1.8	---	0.6	0.14	0.0	0.0
50	1.0	2.7		0.0		0.0	0.0
100	0.6	0.2				0.0	0.0
150	0.0	0.3				1.5	1.0
175						0.0	
200		5.0					5.8
250	1.4						
300							
350	13.7						
400	---						

-----  
 October (Cruise 80/18)                      Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth(m)                      Narrows  
 -----

5	0.0	0.0		0.0	0.0	0.0	0.0
10					0.0		
20	0.2	0.3	---	0.0	0.0	0.0	0.0
50	0.0	0.0		0.0		0.1	0.0
100	0.0	0.0				0.0	0.0
150	0.2	0.0				1.0	0.8
175						6.6	
200		0.1					4.5
250	0.2						
300							
350	6.2						
400	---						

-----  
 January (Cruise 81/1)                      Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth (m)                      Narrows  
 -----

5	0.0	0.0		0.0	0.0	0.0	0.0
10					0.0		
20	0.0	0.0	---	0.0	0.0	0.0	0.0
50	0.0	0.0		0.0		0.0	0.0
100	0.0	0.0				0.2	0.8
150	0.0	0.0				3.5	1.2
175						3.5	
200		0.0					0.0
250	0.4						
300							
350	7.2						
400	---						

-----  
 March (Cruise 81/6)                      Station  
 Sample GEO 1748 FRA 1 1st VAN 24 IND 0 IND 1.5 IND 2.0  
 Depth (m)                      Narrows  
 -----

5	0.0	0.0		0.0	0.0	0.0	0.0
10					0.0		
20	0.0	0.0	---	0.0	0.0	0.0	0.0
50	0.0	0.0		0.1		0.0	0.0
100	0.1	0.0				0.0	0.0
150	0.0	0.1				0.6	0.2
175						0.0	
200		0.6					0.4
250	2.9						
300							
350	0.2						
400	---						

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Table XIX: Seasonal transport of Eucalanus bungi across the Indian Arm sill and the overwintering population in Indian Arm.

Transport per Tidal Cycle (from 80/12)	Tidal Cycles	Total Seasonal Transport	Indian Arm Population	
			Jan(81/1)	March(81/6)
$3.85 \times 10^6$	73	$2.80 \times 10^8$	$1.10 \times 10^9$	$1.40 \times 10^8$
Upper Confidence Limit				
$1.60 \times 10^7$		$1.17 \times 10^8$	$2.64 \times 10^9$	$5.25 \times 10^9$
Lower Confidence Limit				
0.00		0.00	$3.27 \times 10^8$	0.00



Table XXI: U-Test results for community parameters over the tidal cycle at IND 0 (Cruise 80/18).

	EBB / FLOOD	DAY / NIGHT
Sample	11,14,15,19/ 12,13,16,17,18	11,12,13,18,19/ 14,15,16,17
%Dominance copepods	15	14
S.W. Div. copepods	16	12
Simpsons Div. copepods	15	
Total copepods	11	
%Dominance other Invert.	15	12
S.W. Div. other Invert.	20*	
Simpsons Div. other Invert.	19*	
<u>Metridia pacifica</u>	10	16
<u>Psuedocalanus minutus</u>	12	
<u>Acartia clausi</u>	11.5	
<u>Paracalanus parvus</u>	12	
<u>Oithona helgolandica</u>	14	
<u>Corycaeus anglicus</u>	11	19*
<u>Microcalanus pygmaeus</u>	13	
<u>Calanus pacificus</u>	15	
Siphonophores	20*	11
Total Ostracods	13	
Euphausiids	12	20*
Parathemisto (Amphipoda)	13.5	14.5

\*\* Critical value for U test was 18 (p=0.05)

Table XXII: Kruskal Wallis results for zooplankton community changes over the tidal cycle at IND 0 (Cruise 80/18).

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Parameter	value
%Dominance copepods	5.8
Simpsons Div. copepods	6.35*
S.W. Div. copepods	7.00*
Total copepod densities	1.5
%Dominance other Invert.	1.84
Simpsons Div. other Invert.	0.98
S.W. Div. other Invert.	3.84
<u>Metridia pacifica</u>	3.26
<u>Pseudocalanus minutus</u>	3.11
<u>Paracalanus parvus</u>	4.00
<u>Oithona helgolandica</u>	4.44
<u>Corycaeus anglicus</u>	6.30*
<u>Acartia clausi</u>	1.39
<u>Microcalanus pygmaeus</u>	5.40
<u>Calanus pacificus</u>	4.17
Euphausiids	6.67*
Siphonophores	0.81
Ostracods	0.78

---

\*Note      Critical value for Kruskal Wallis test was 6.0  
               (p=0.05)

**FIGURES**



Figure 1; The study area, showing station positions, points of reference and transect S7 used in the model volume transport prediction.

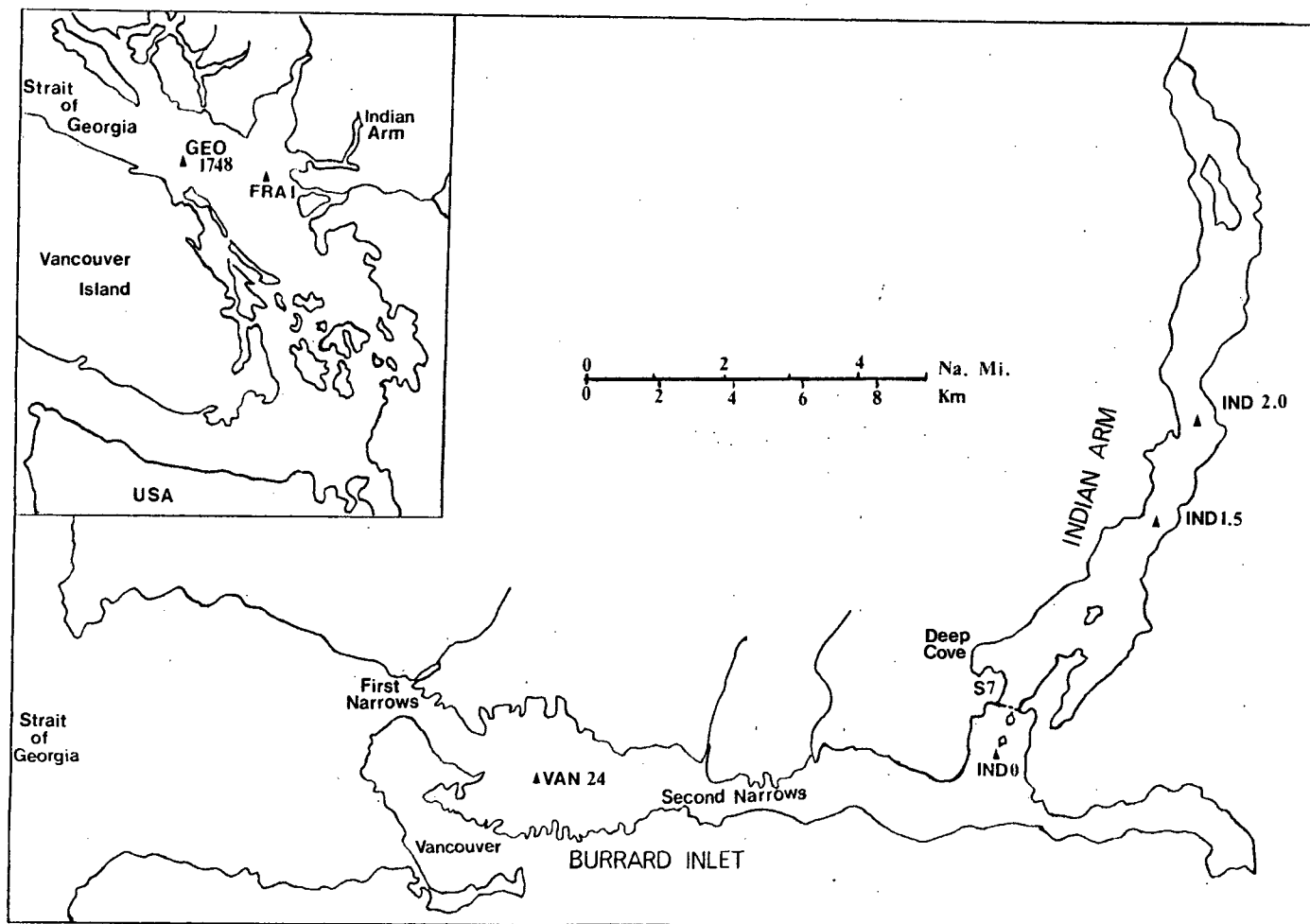


Figure 2; Longitudinal depth profile through the study area, showing the position of the shallow sills in relation to the deeper water. (Lateral distances not to scale).

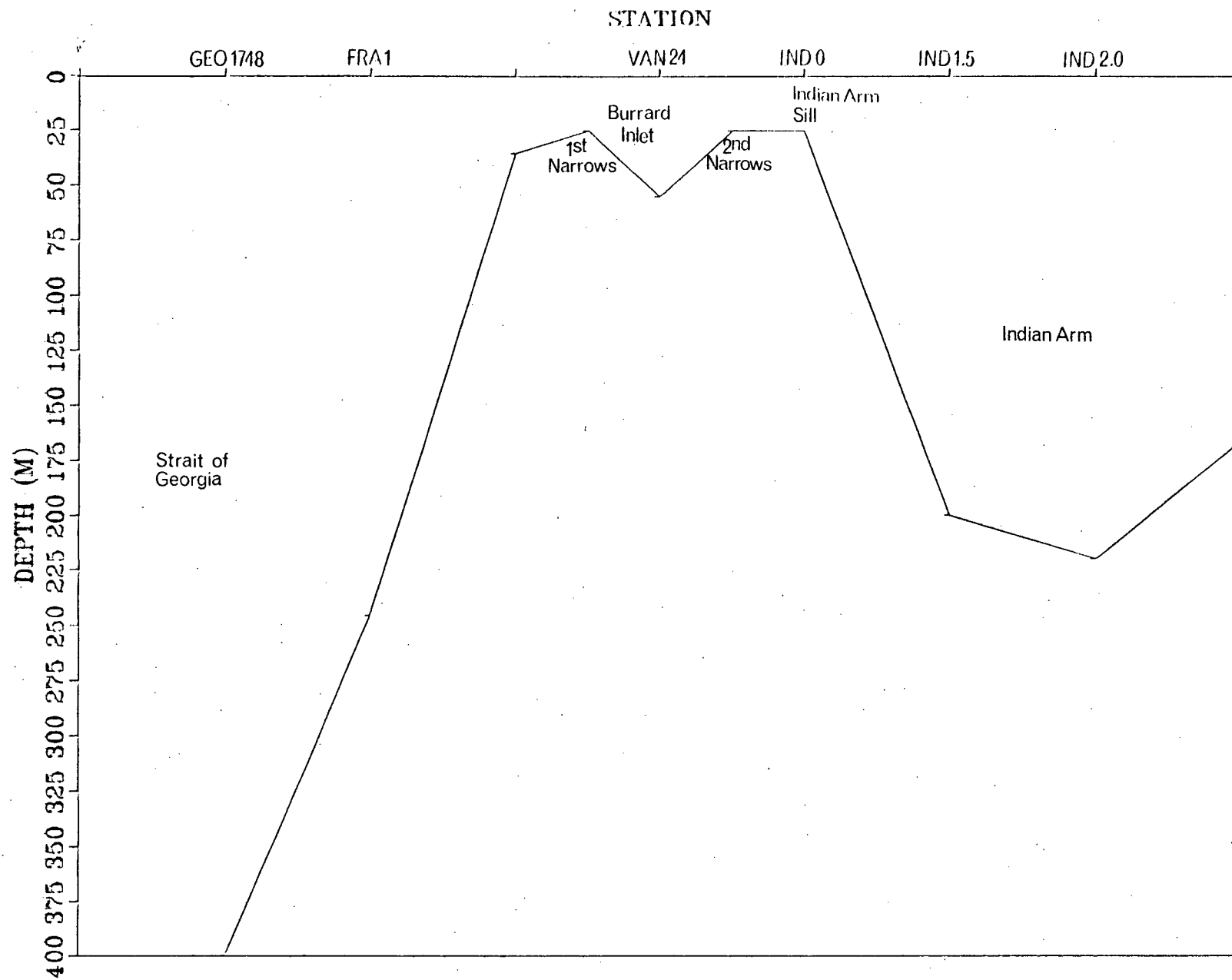


Figure 3; Density structure in the study area during winter,  
1981 (January data, Cruise 81/1) (Density in Sigma T)

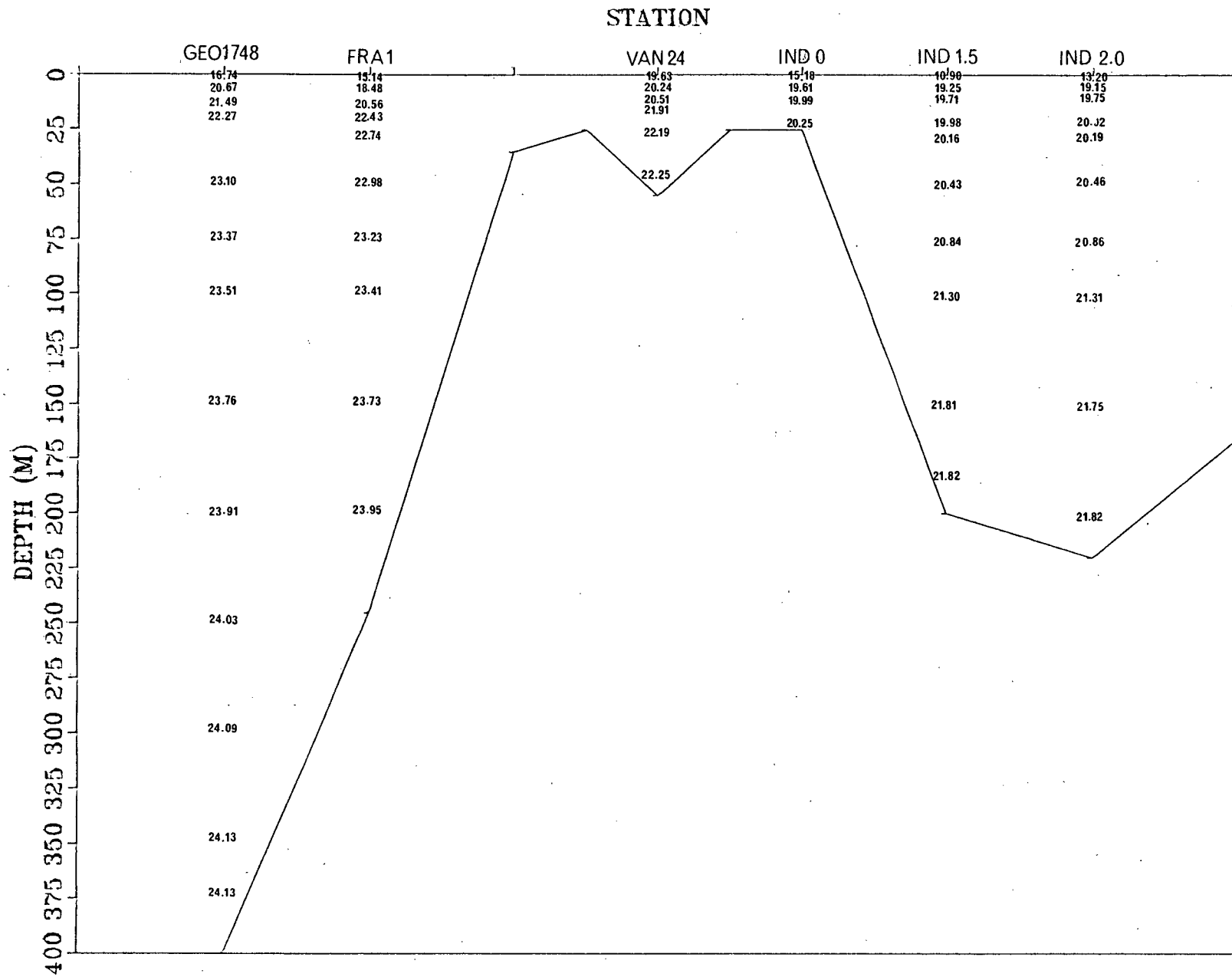


Figure 4; Density structure in the study area during winter,  
1980 (February data, Cruise 80/2) (Density in Sigma T)

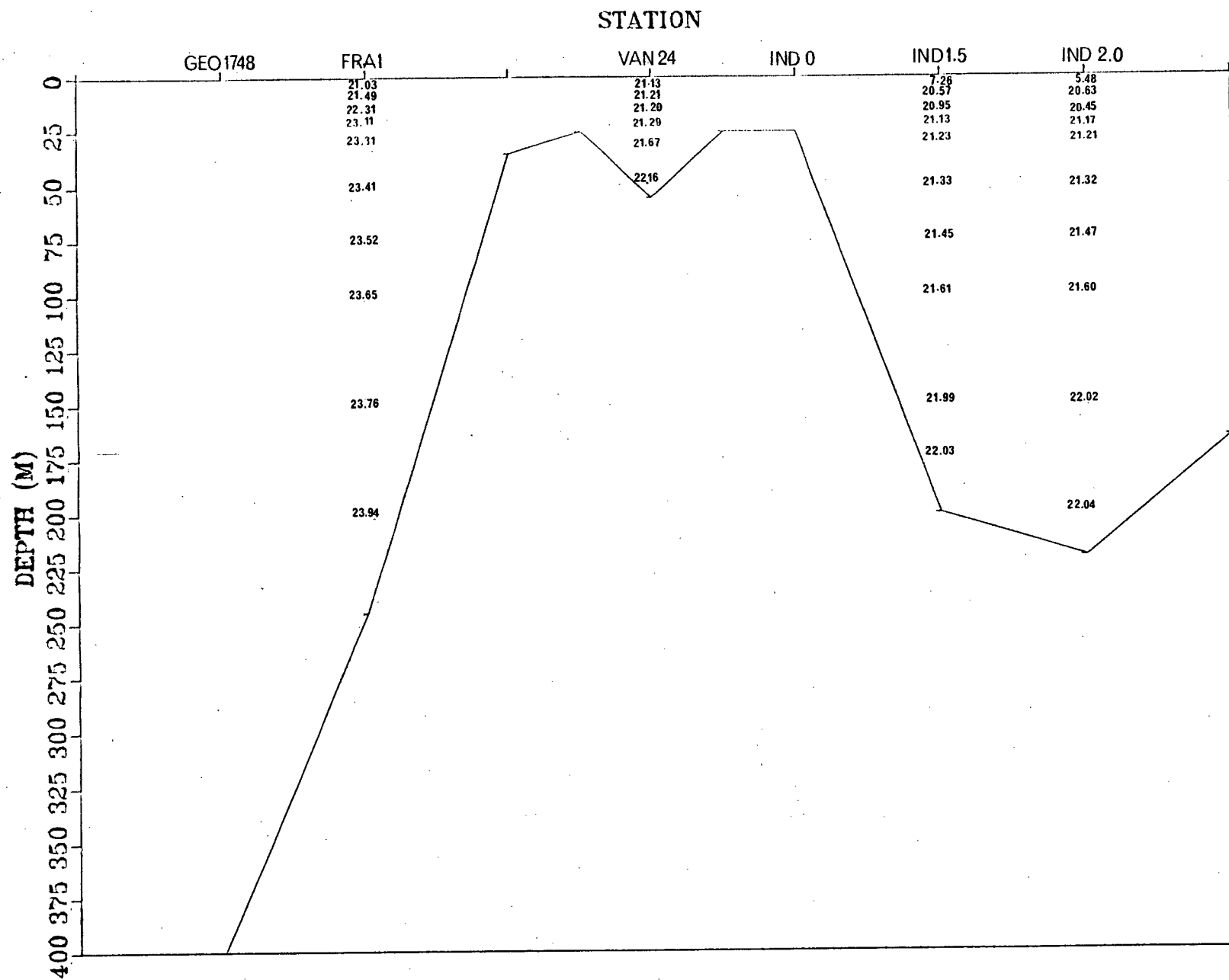




Figure 5; Oxygen concentration in water below 150 meters at Station IND 2.0, over time, showing the effect of a winter density driven intrusion on the oxygen concentration in Indian Arm deep water.

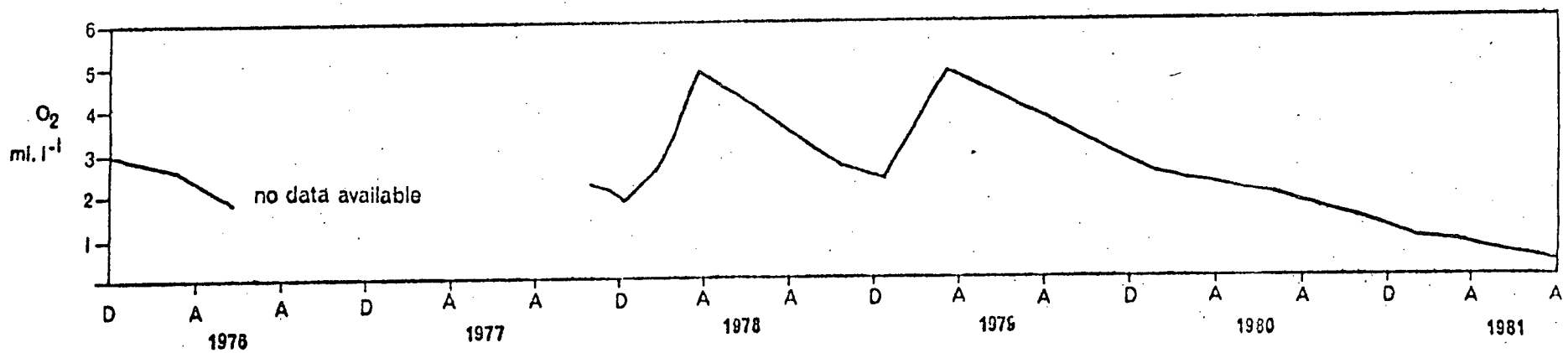
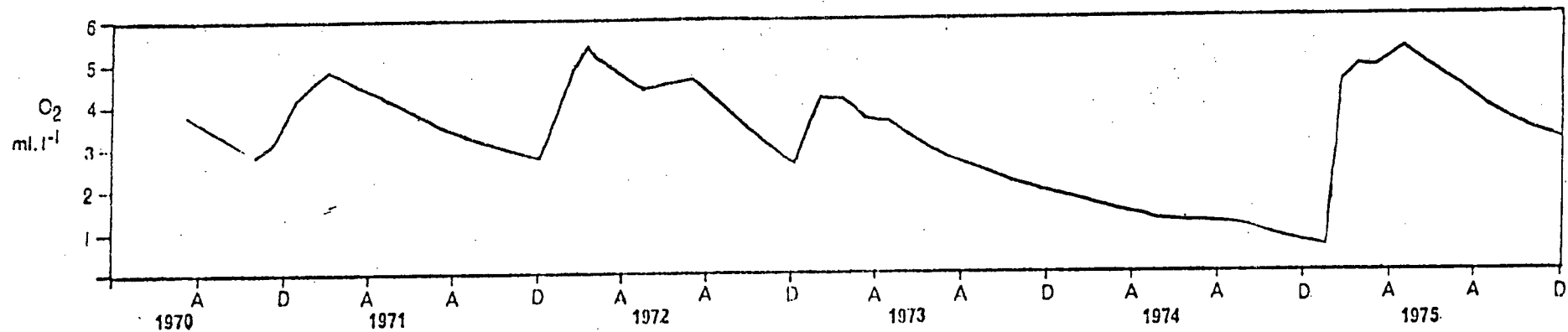


Figure 6; Current vectors derived from the current meter  
deployed at IND 0 over a tidal cycle. (Data from Cruise  
81/6, 1cm = 0.1 knots).

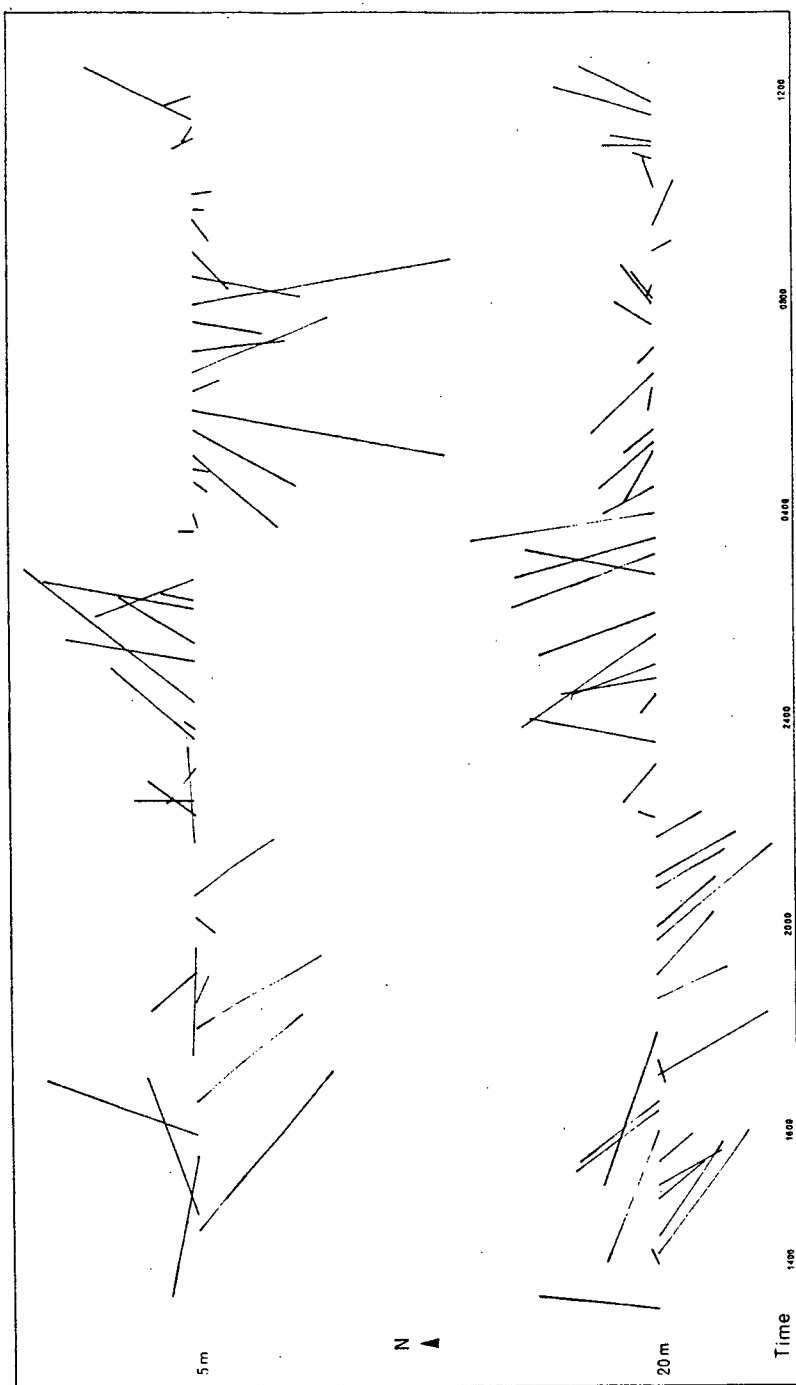


Figure 7; North-south components (along the channel) of current vectors over a tidal cycle at IND 0 (Data from Cruise 81/6, 1cm = 0.1 knots).

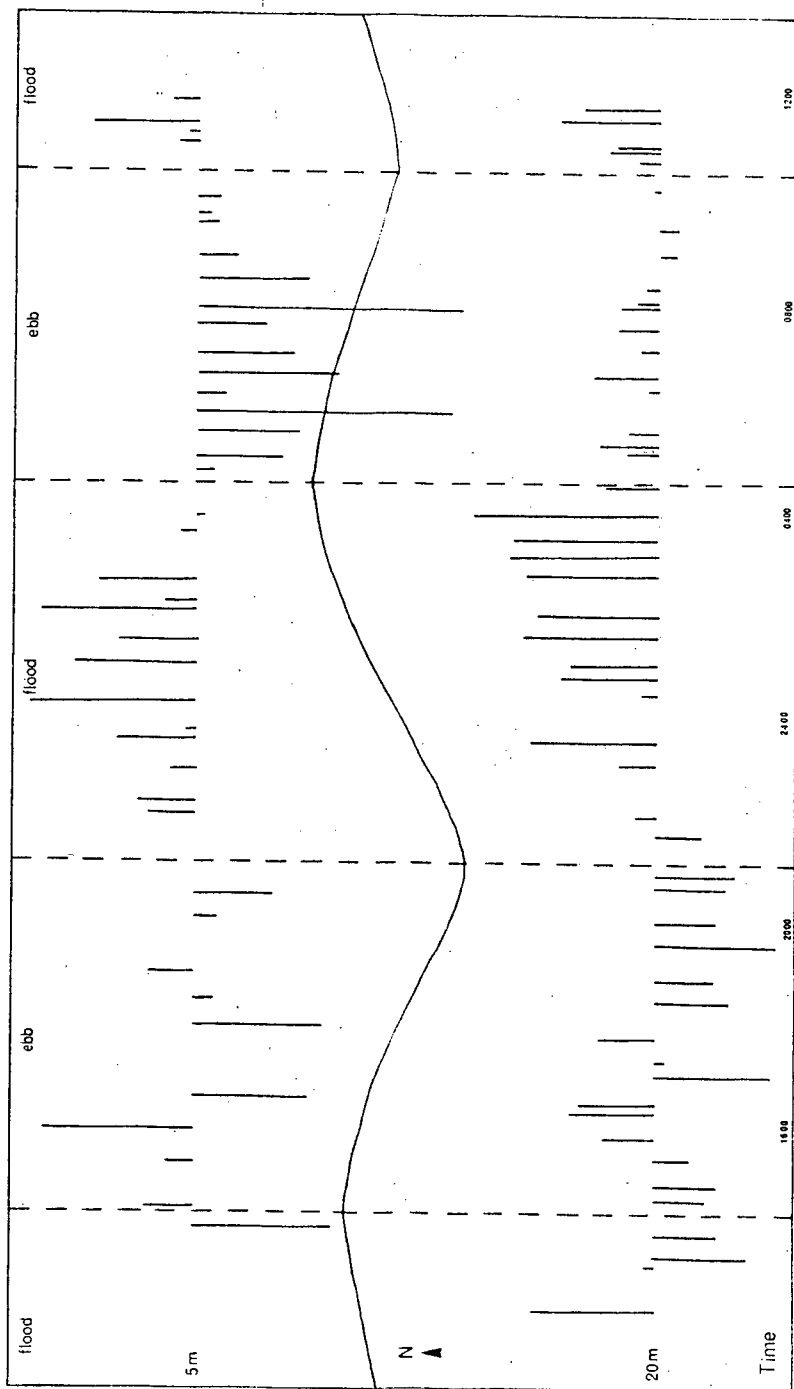


Figure 8; Total and net transport of Corycaeus anglicus across the Indian Arm sill during each cruise.

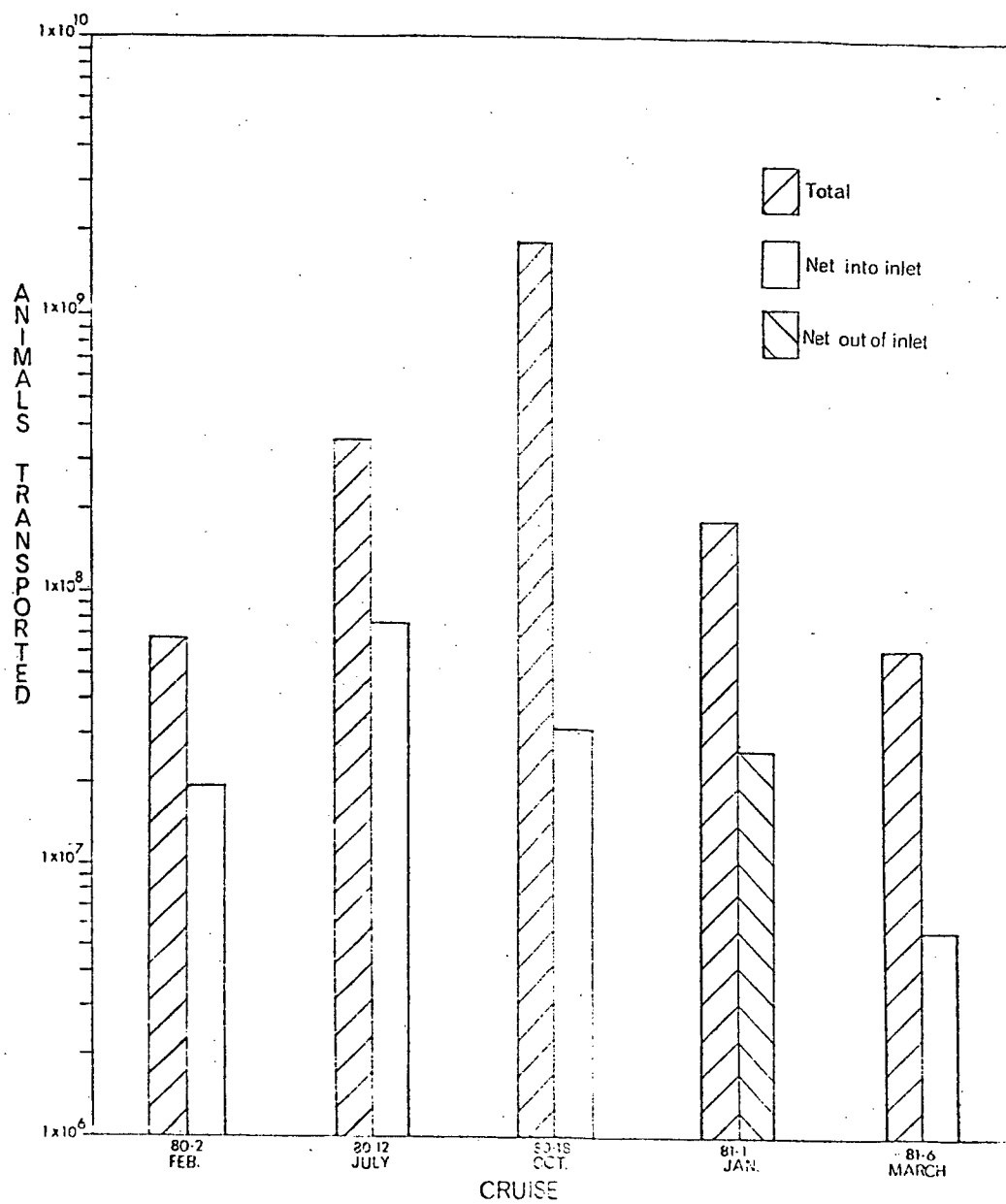




Figure 9; Mean concentration of Corycaeus anglicus in the study area in October in number per cu. meter from samples taken above 50 meters showing 95% confidence limits.

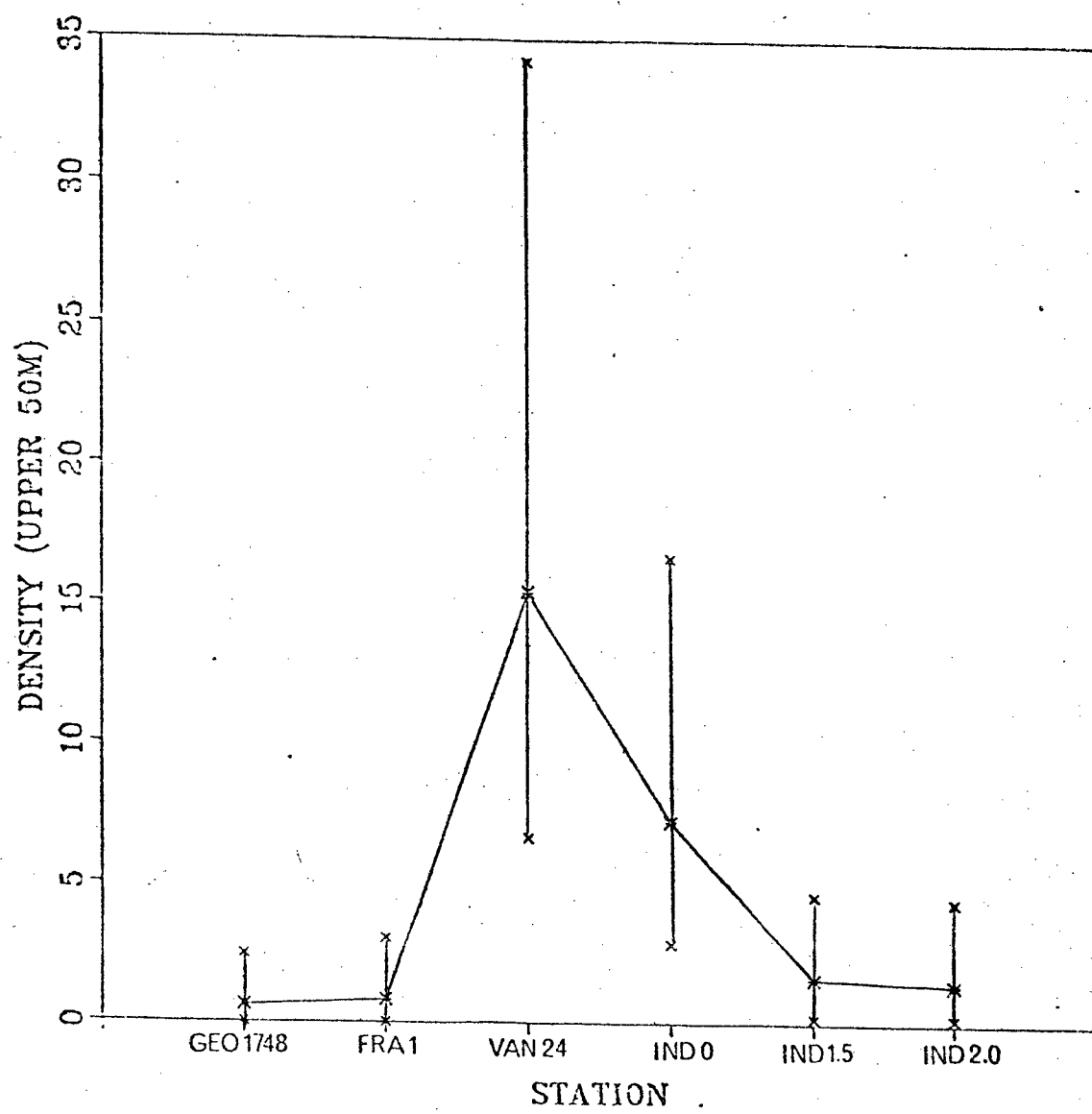


Figure 10; Temperature/Salinity plot of study area water during January, 1981 (Cruise 81/1) showing the T/S properties of water exchanged across the Indian Arm sill over a tidal cycle.

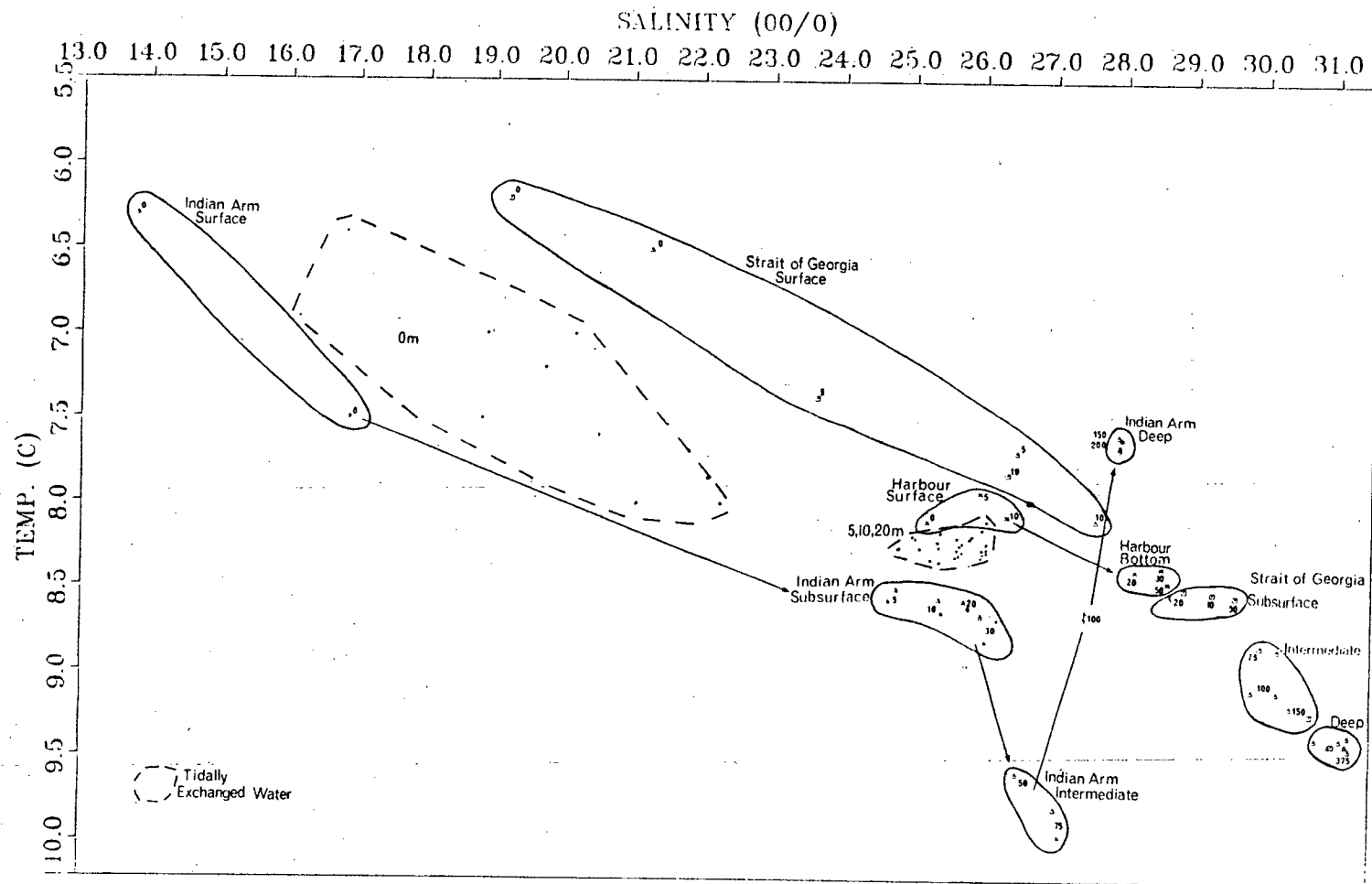


Figure 11; Depth distribution of Metridia pacifica at Station FRA 1 during the day and during the night.

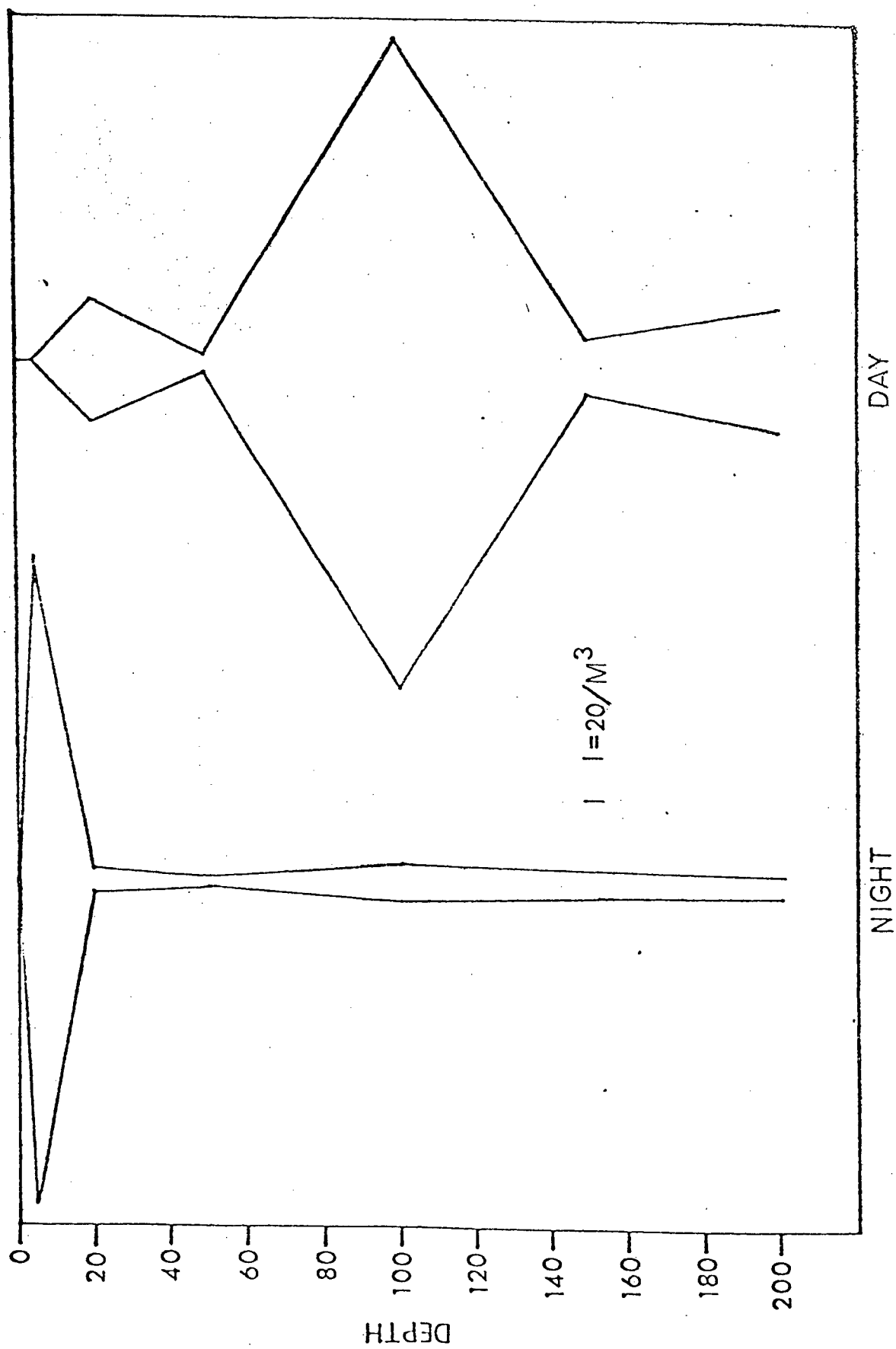


Figure 12; Total and net transport of Eucalanus bungi across the Indian Arm sill during each cruise.

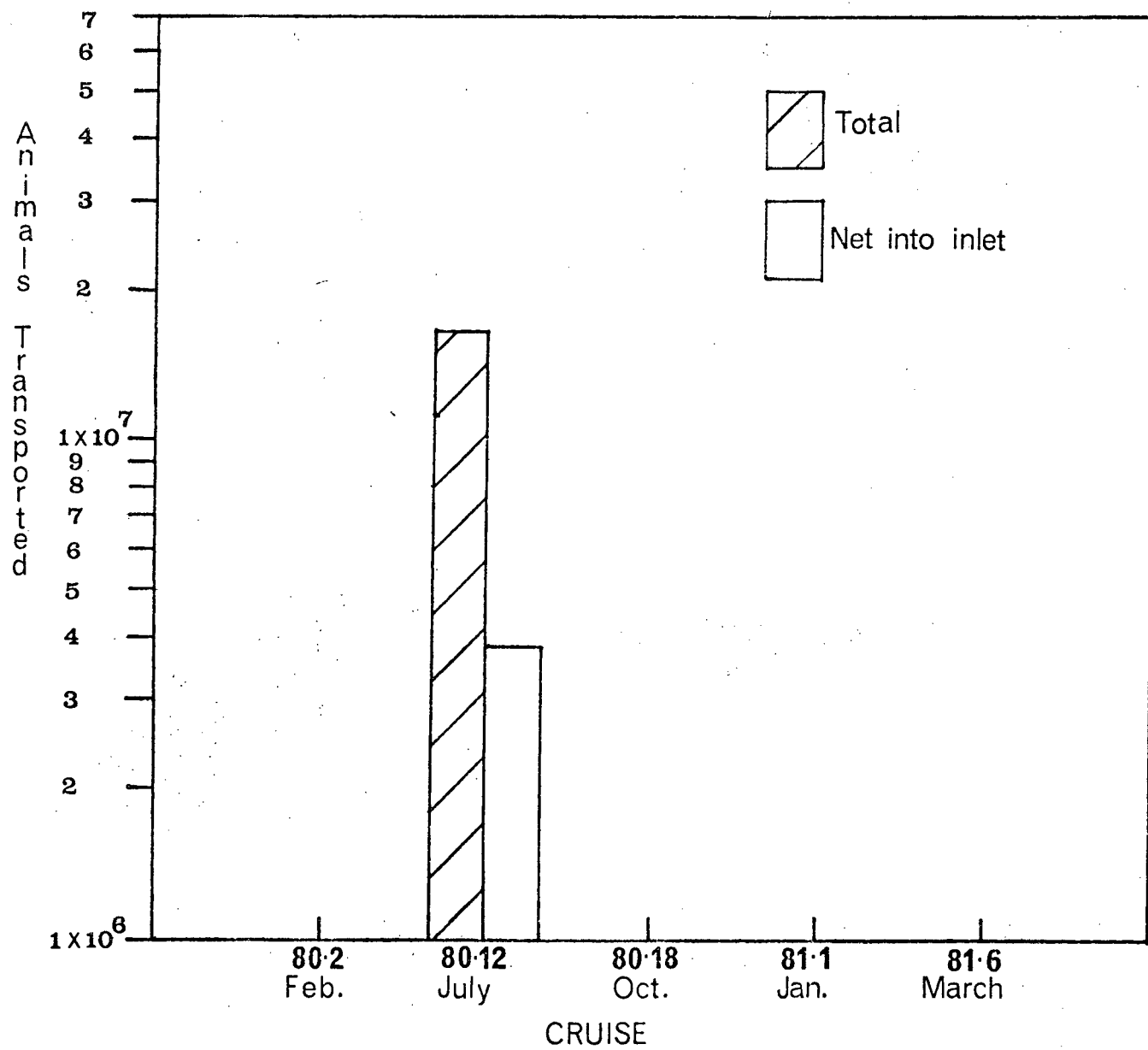




Figure 13; Temperature/Salinity plot of study area water during July, 1980 (Cruise 80/12) showing the T/S properties of water exchanged across the Indian Arm sill over a tidal cycle.

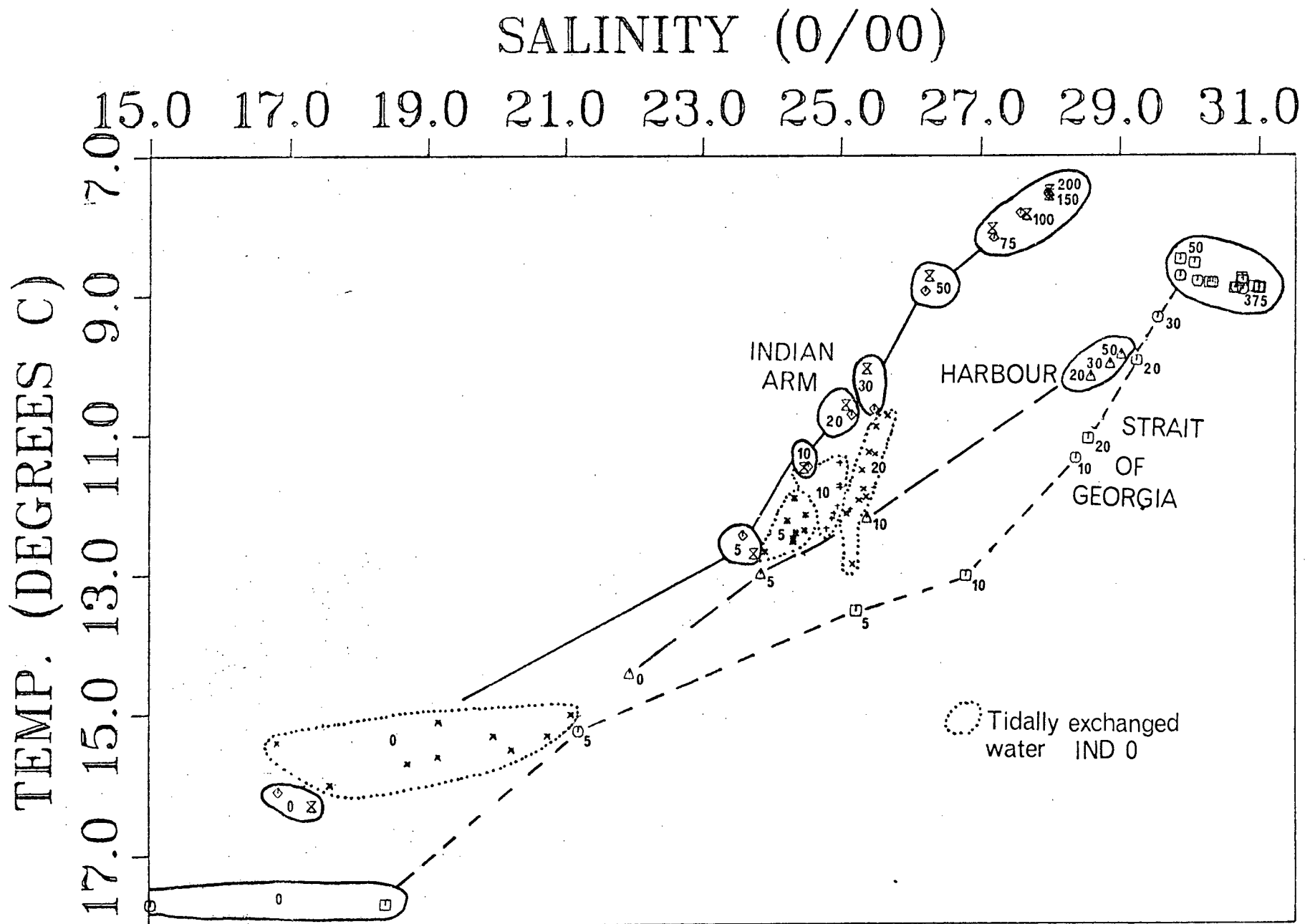


Figure 14; Temperature/Salinity plot of water at IND 2.0 showing changes during the study period in the deep water of Indian Arm.

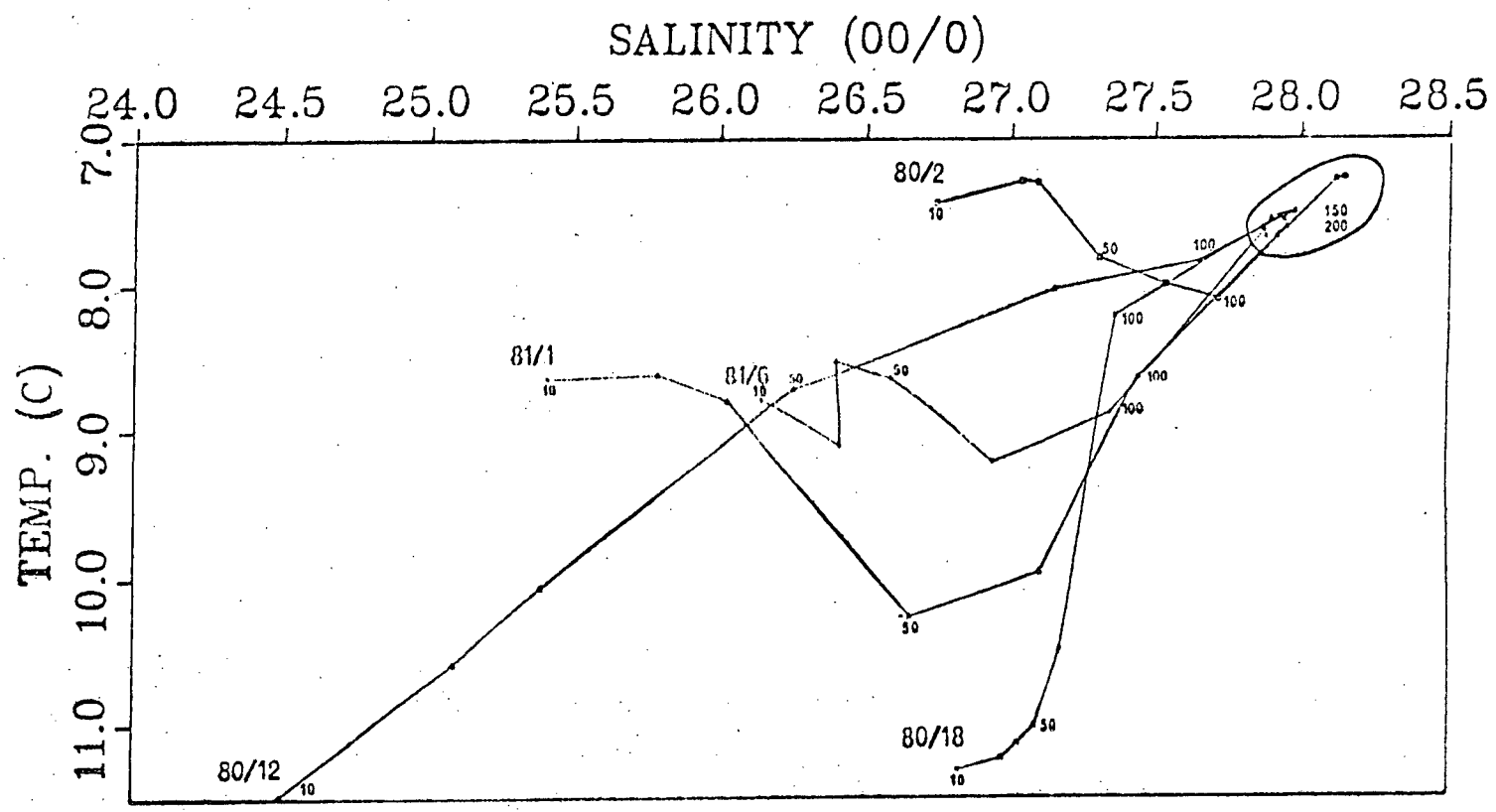


Figure 15; The tidal cycle at IND 0 during Cruise 80/18 (October, 1980) over which data for the community analysis was taken. Times and labels of samples are shown. Hour 0 was at 0800 hrs on October 28, 1980.

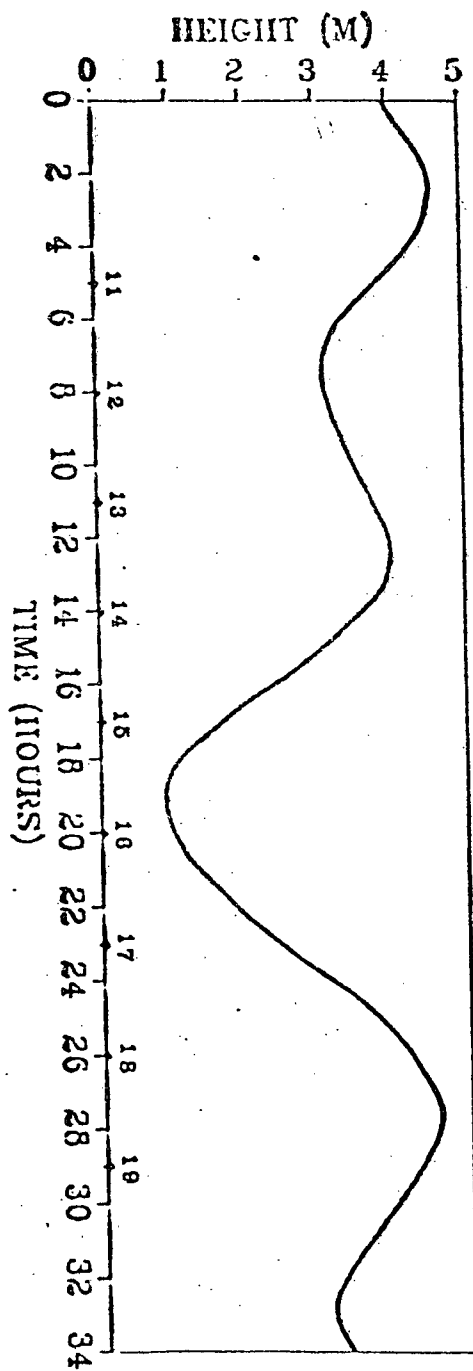


Figure 16; Temperature at each sampling depth at IND 0 over the tidal cycle (Cruise 80/18). Hours are given as in Fig. 15.

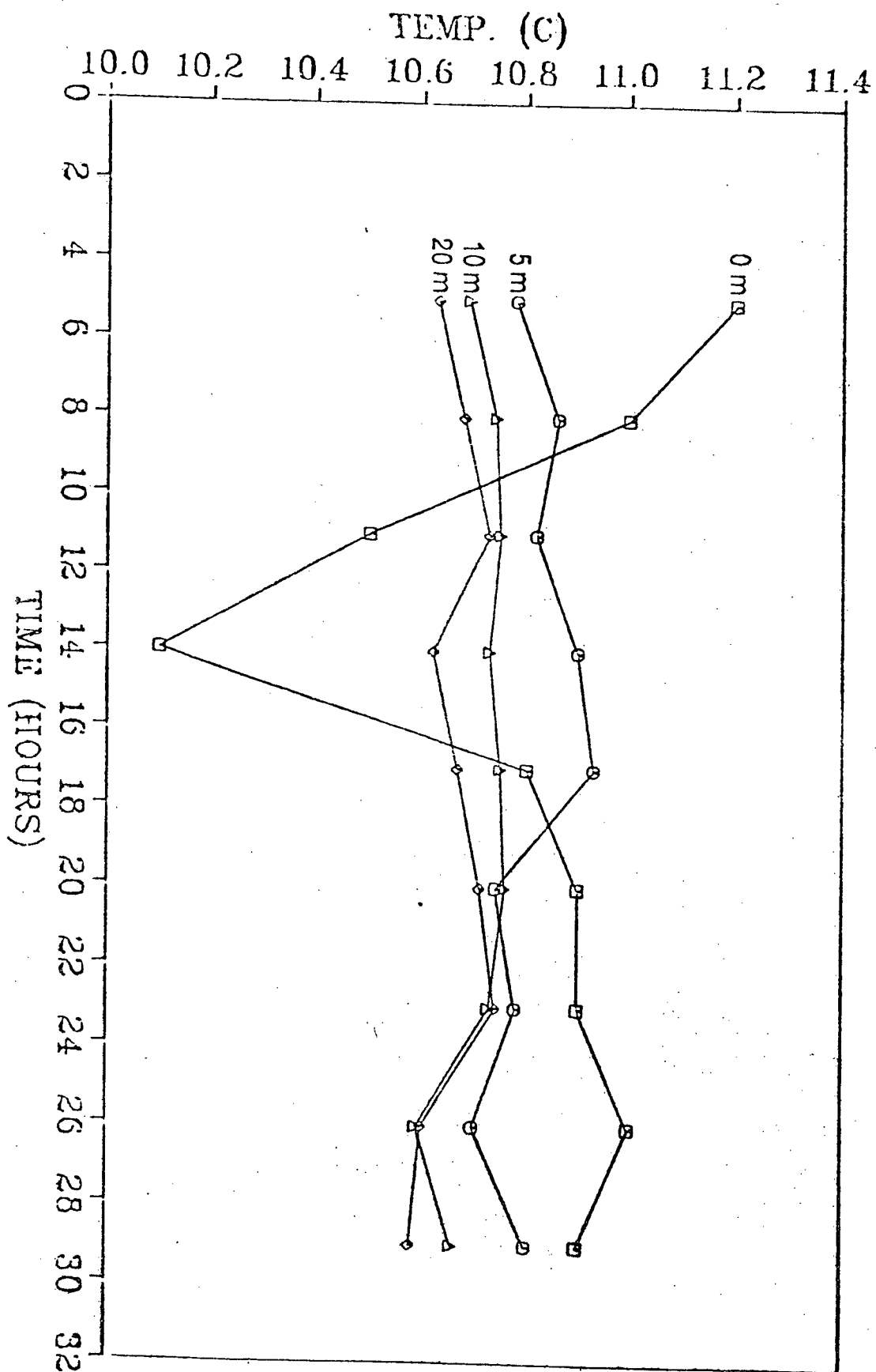




Figure 17; Salinity at each sampling depth at IND 0 over the tidal cycle (Cruise 80/18). Hours are given as in Fig. 15.

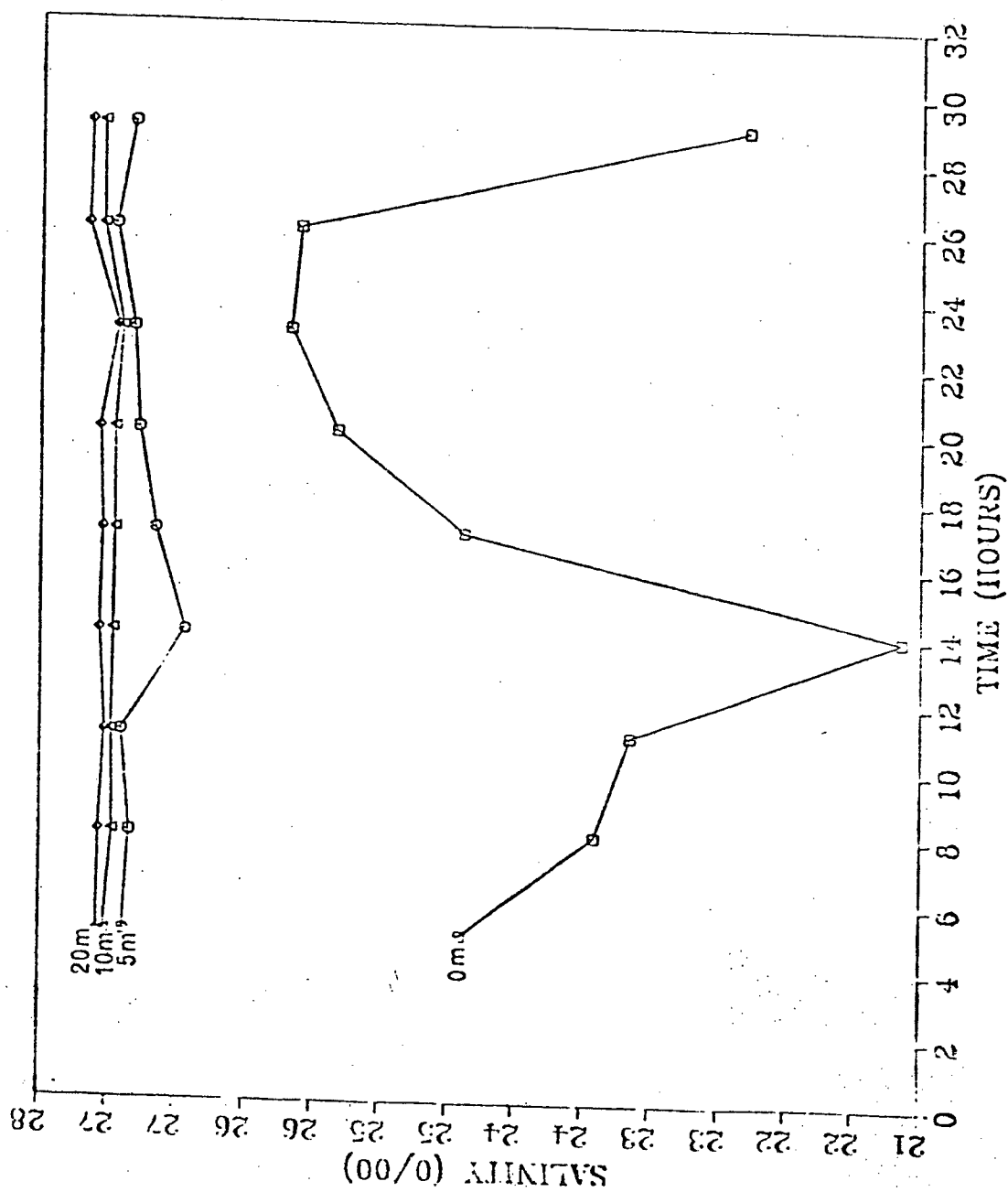


Figure 18; Temperature/Salinity plot of the study area water during October, 1980 (Cruise 80/18) showing the T/S properties of water exchanged over the Indian Arm sill during a tidal cycle, and its relation to water in surrounding areas.

SALINITY (0/00)

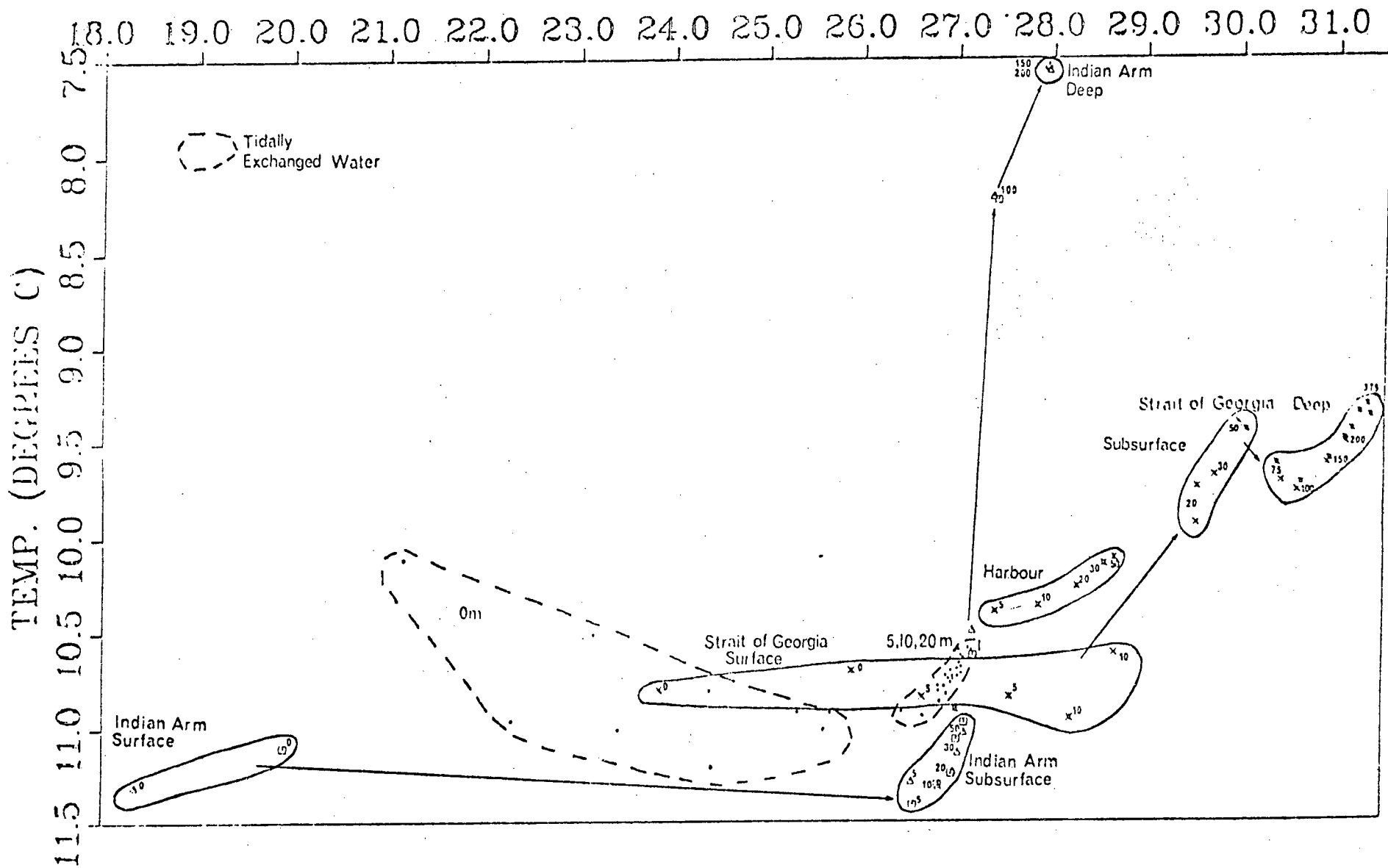


Figure 19; Temperature/Salinity plot of water from 0 meters at the Indian Arm sill over the tidal cycle. Sample numbers correspond to those given in Fig. 15.

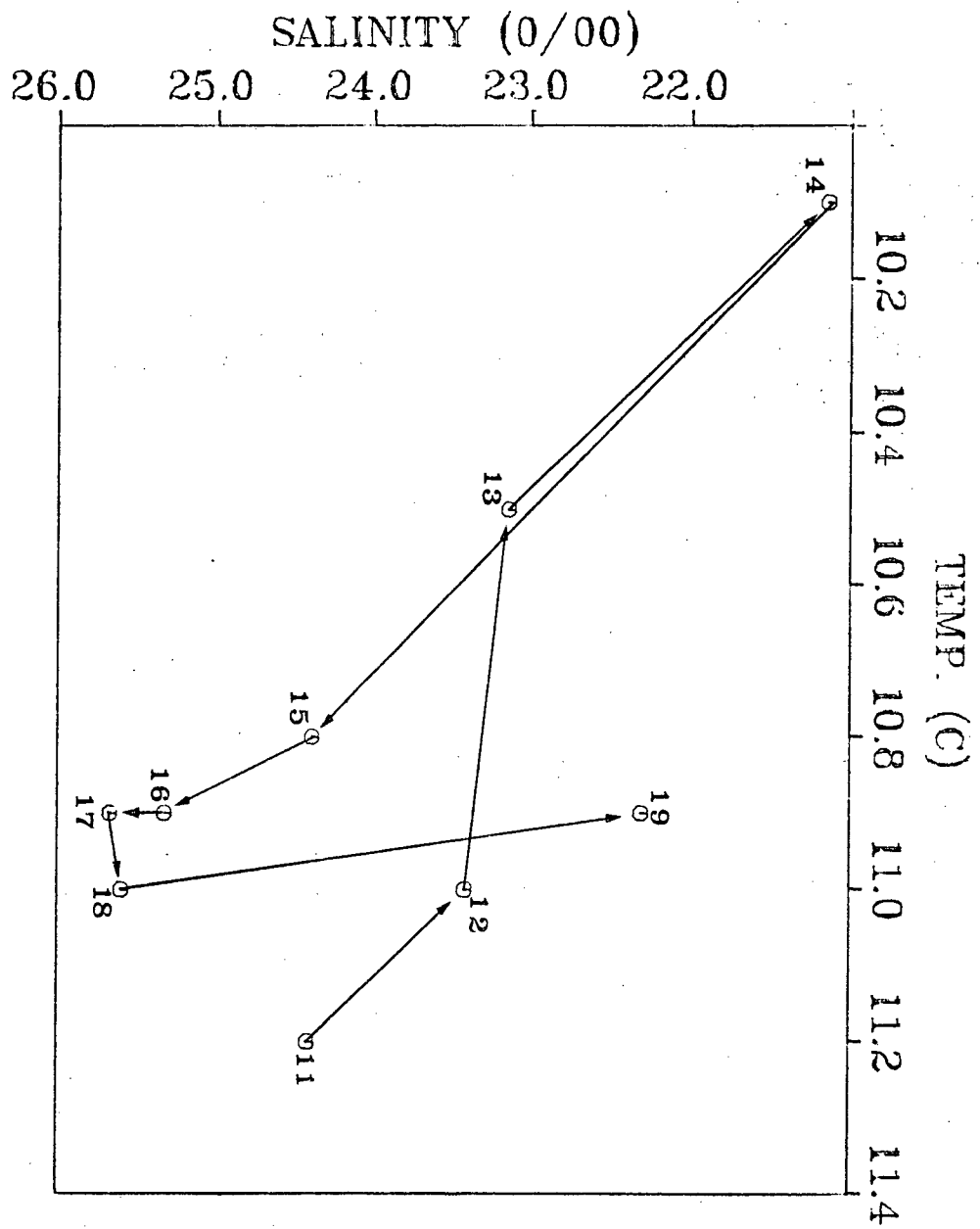


Figure 20; Temperature/Salinity plot of average T/S properties from 5, 10, and 20 meters (below the pycnocline) at the Indian Arm sill over the tidal cycle. Sample numbers correspond to those given in Fig. 15.

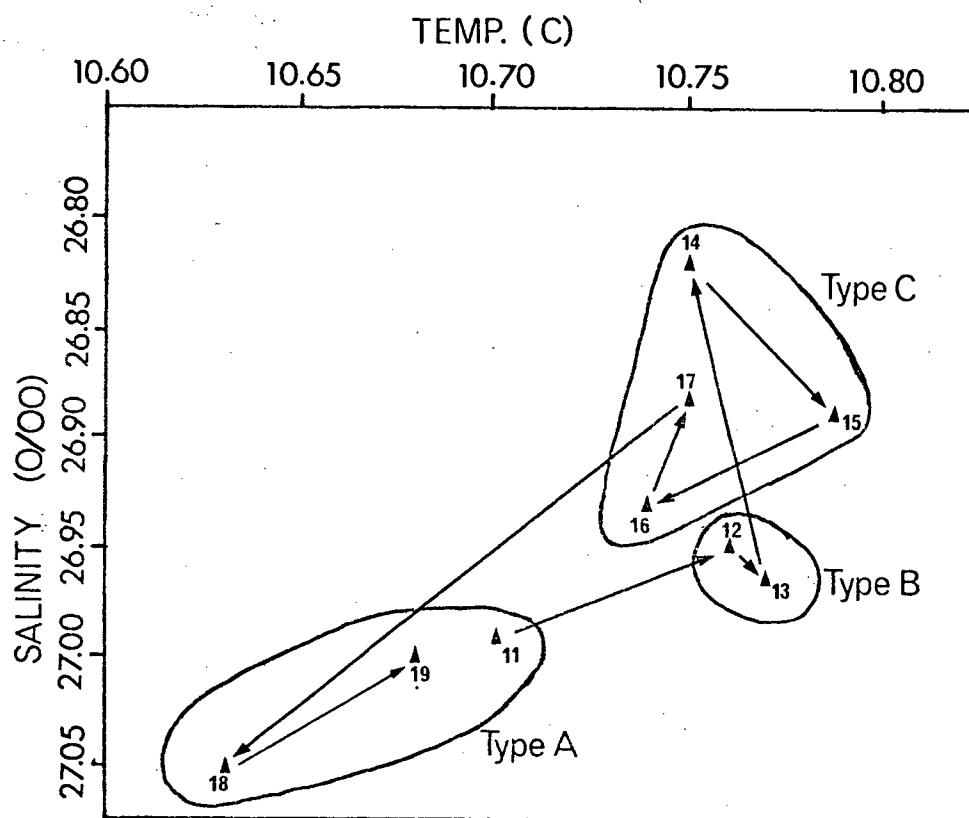




Figure 21; Density of the four most abundant copepods at IND 0 over the tidal cycle (Cruise 80/18). Hours and tidal height as in Fig. 15.  $\square$  = Paracalanus parvus ,  $\triangle$  = Microcalanus pygmaeus ,  $\times$  = Oithona helgolandica ,  $\diamond$  = Pseudocalanus minutus .

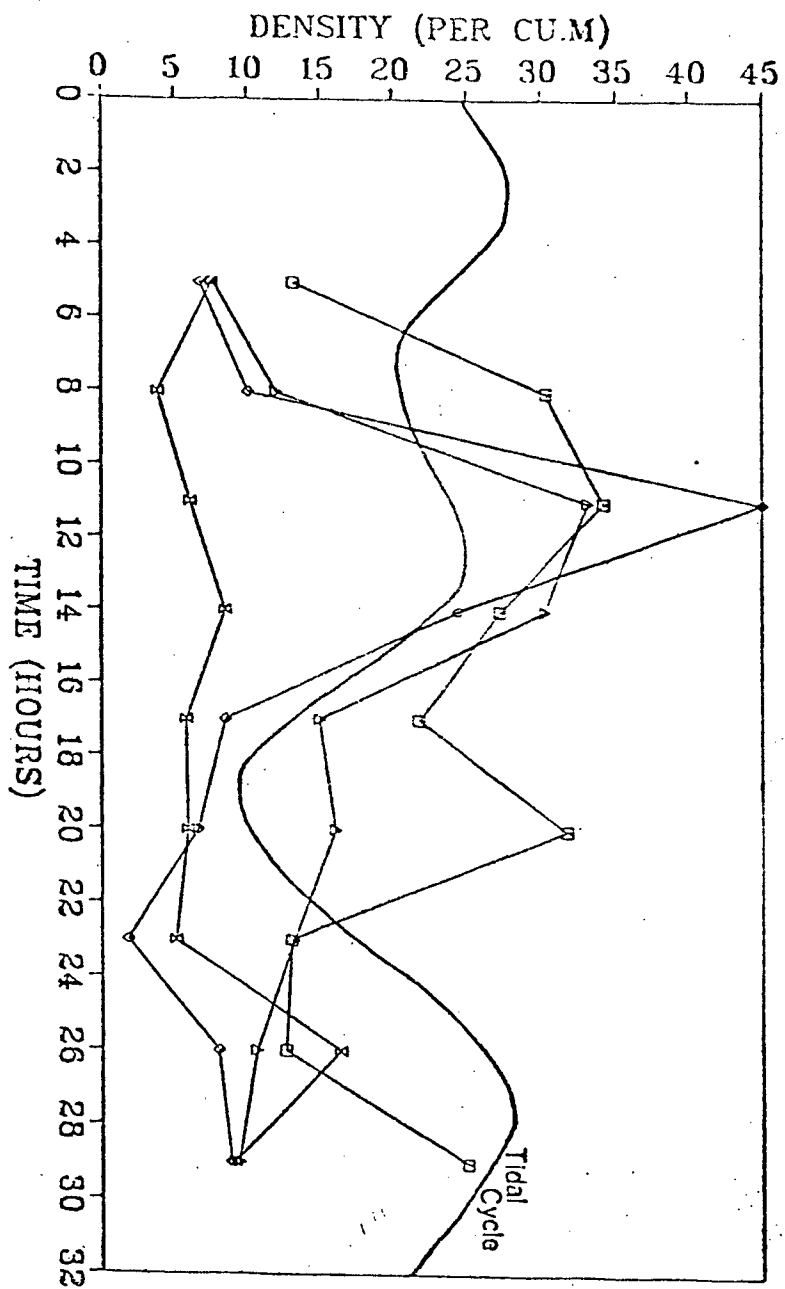


Figure 22; Density of the second four most abundant copepods at IND 0 over the tidal cycle (Cruise 80/18). Hours and tidal height as in Fig. 15.  $\Sigma$  = Corycaeus anglicus ,  $\diamond$  = Calanus pacificus ,  $\Delta$  = Acartia clausi ,  $\square$  = Metridia pacifica .

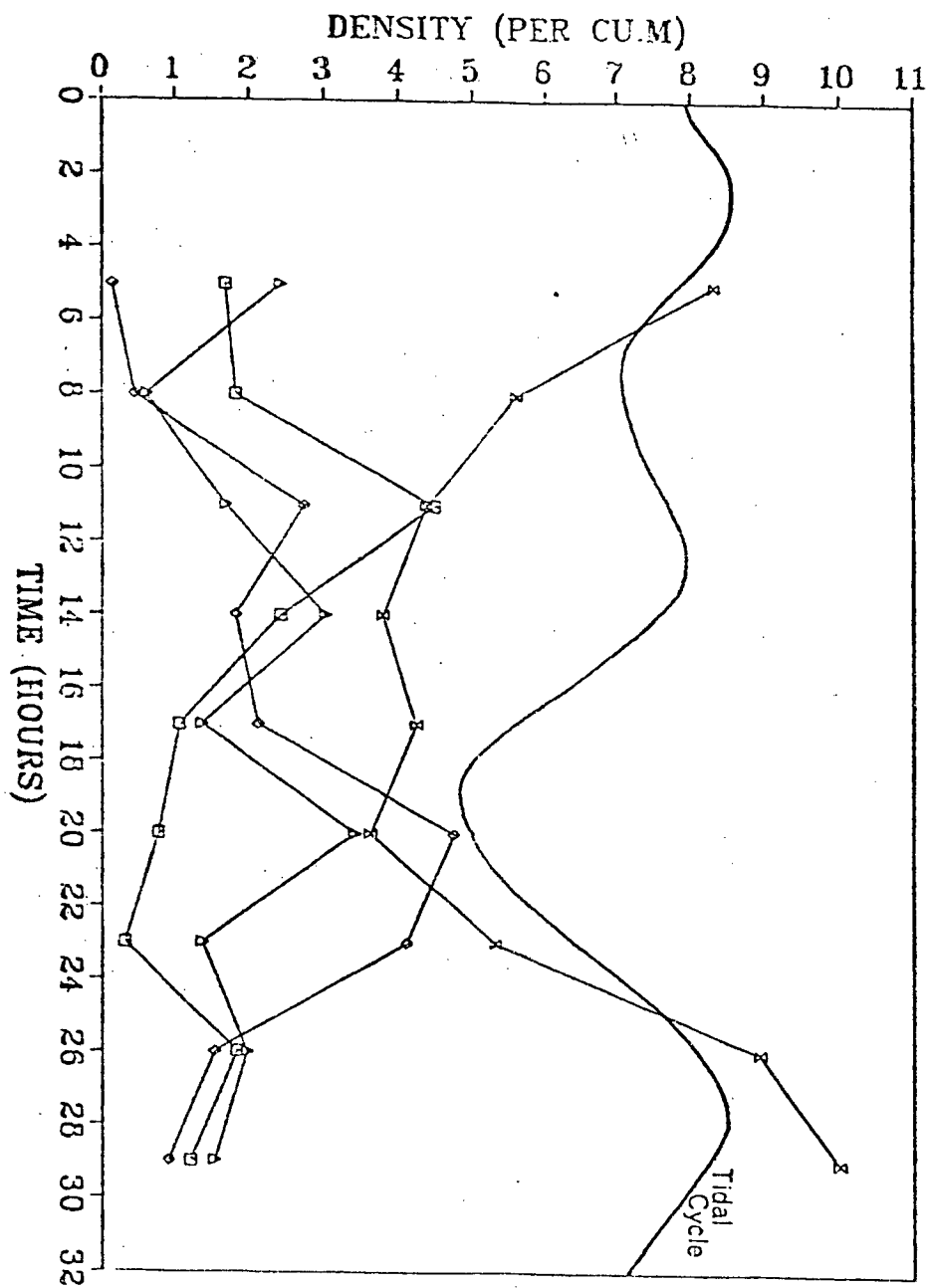


Figure 23; Total zooplankton diversity and dominance over the tidal cycle at IND 0 (Cruise 80/18). Hours and tidal height as in Fig. 15.

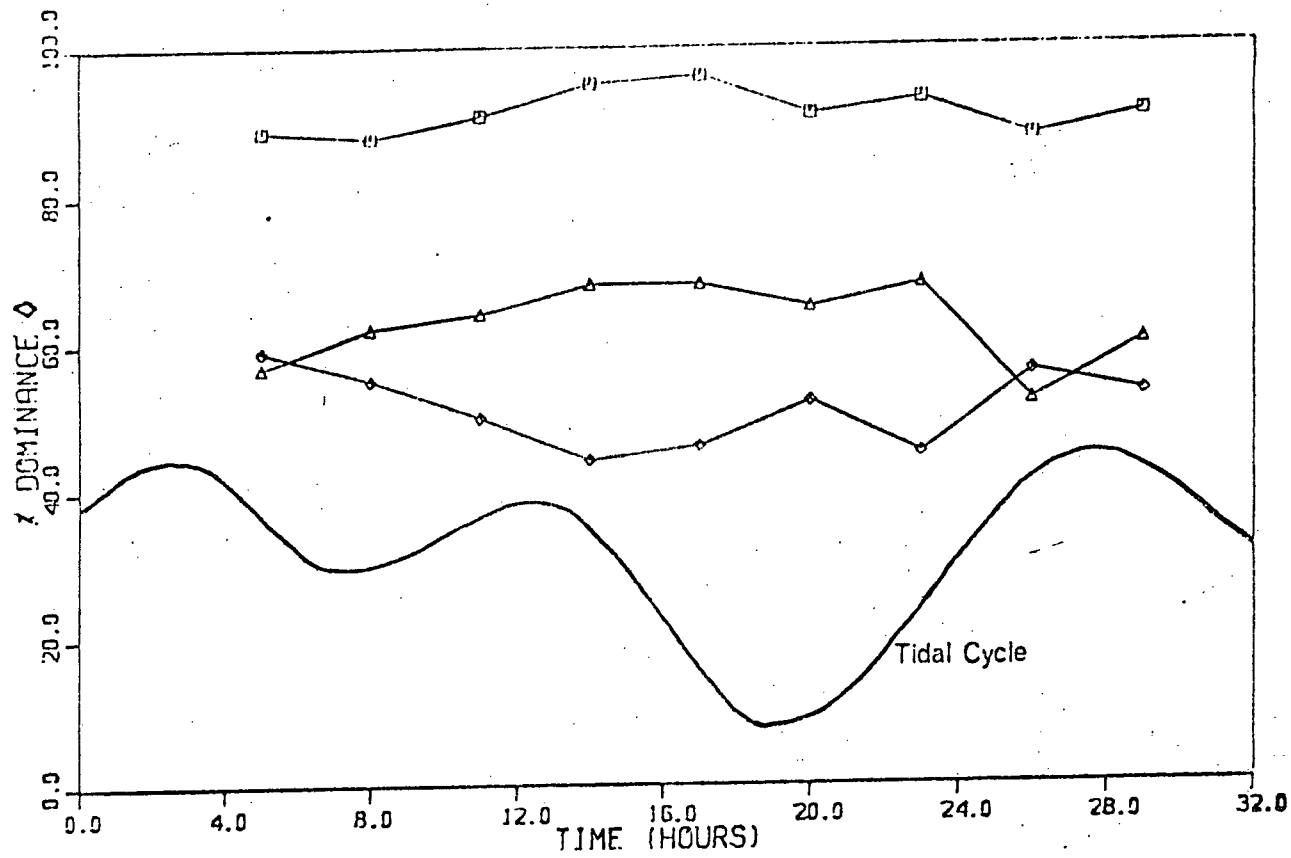
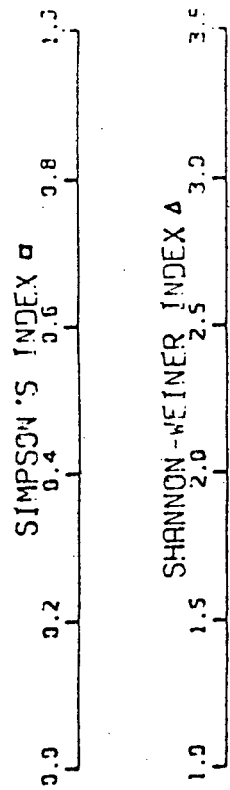


Figure 24; Diversity and dominance of the copepod community over the tidal cycle at IND 0 (Cruise 80/18). Hours and tidal height as in Fig. 15.

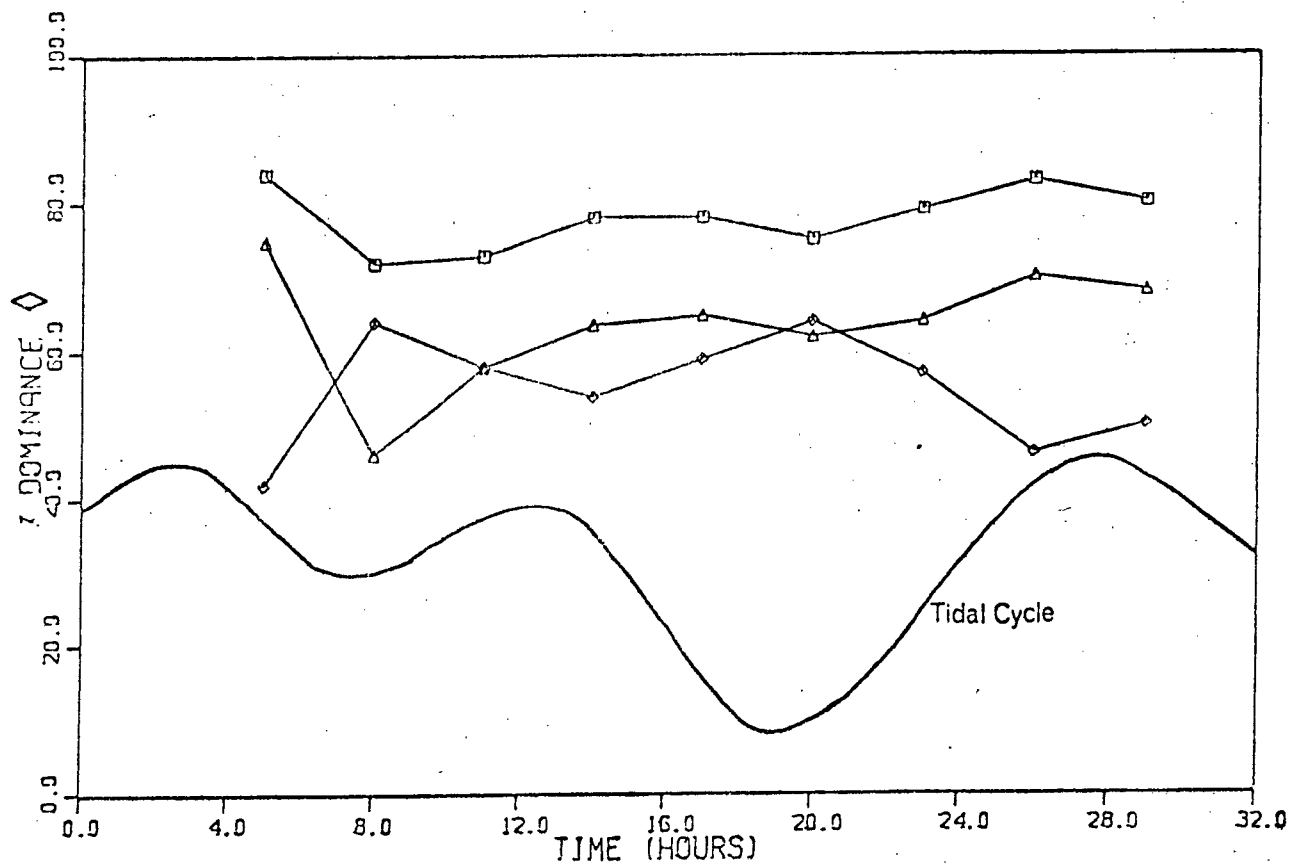
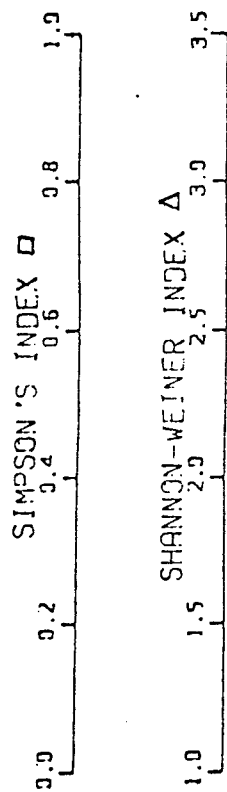




Figure 25; Diversity and dominance of all other invertebrate zooplankton over the tidal cycle at IND 0 (Cruise 80/18). Hours and tidal height as in Fig. 15.

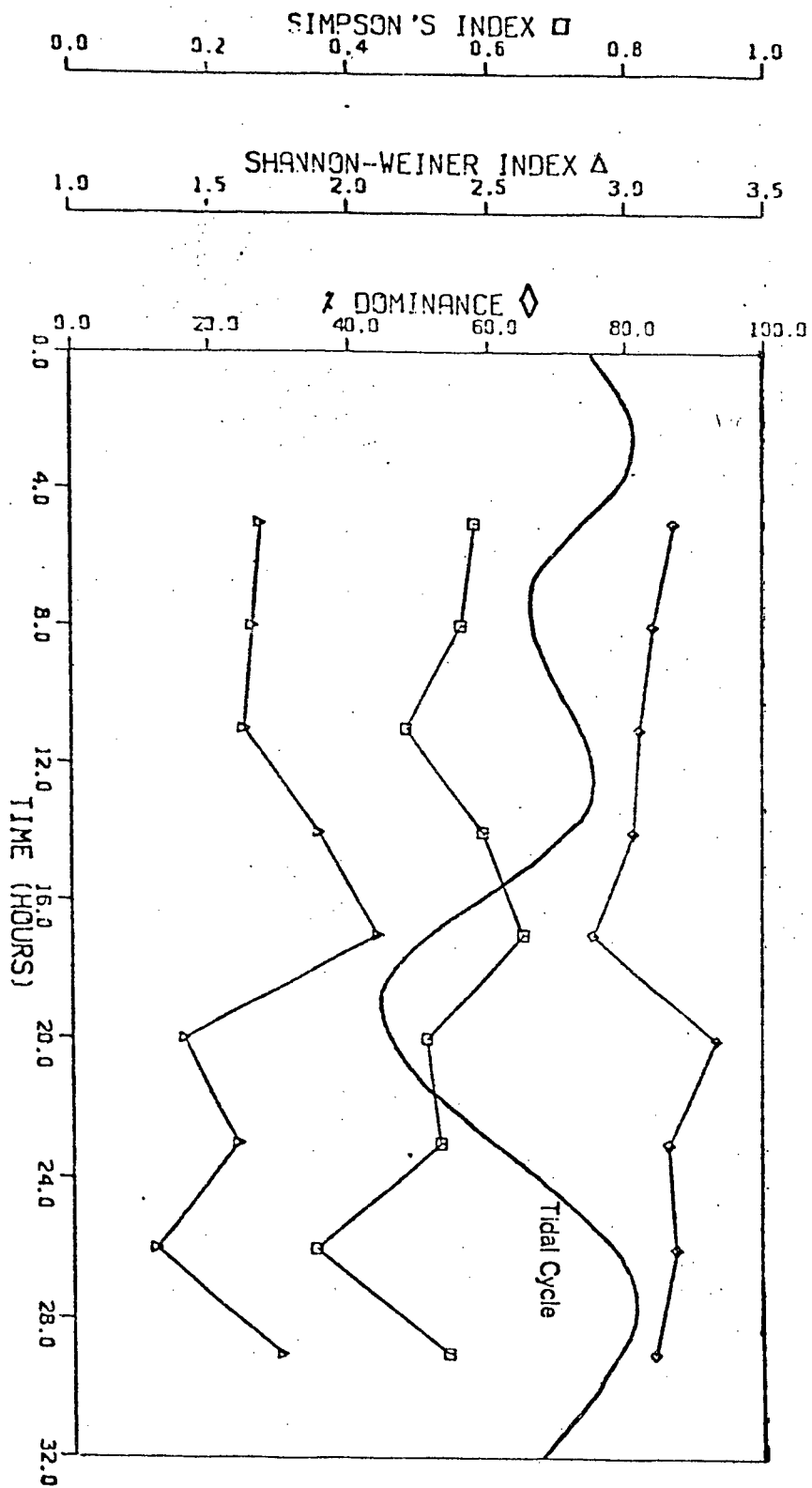


Figure 26; Diversity and dominance of invertebrate zooplankton (minus larvaceans and siphonophores) over the tidal cycle at IND 0 (Cruise 80/18). Hours and tidal height as in Fig. 15.

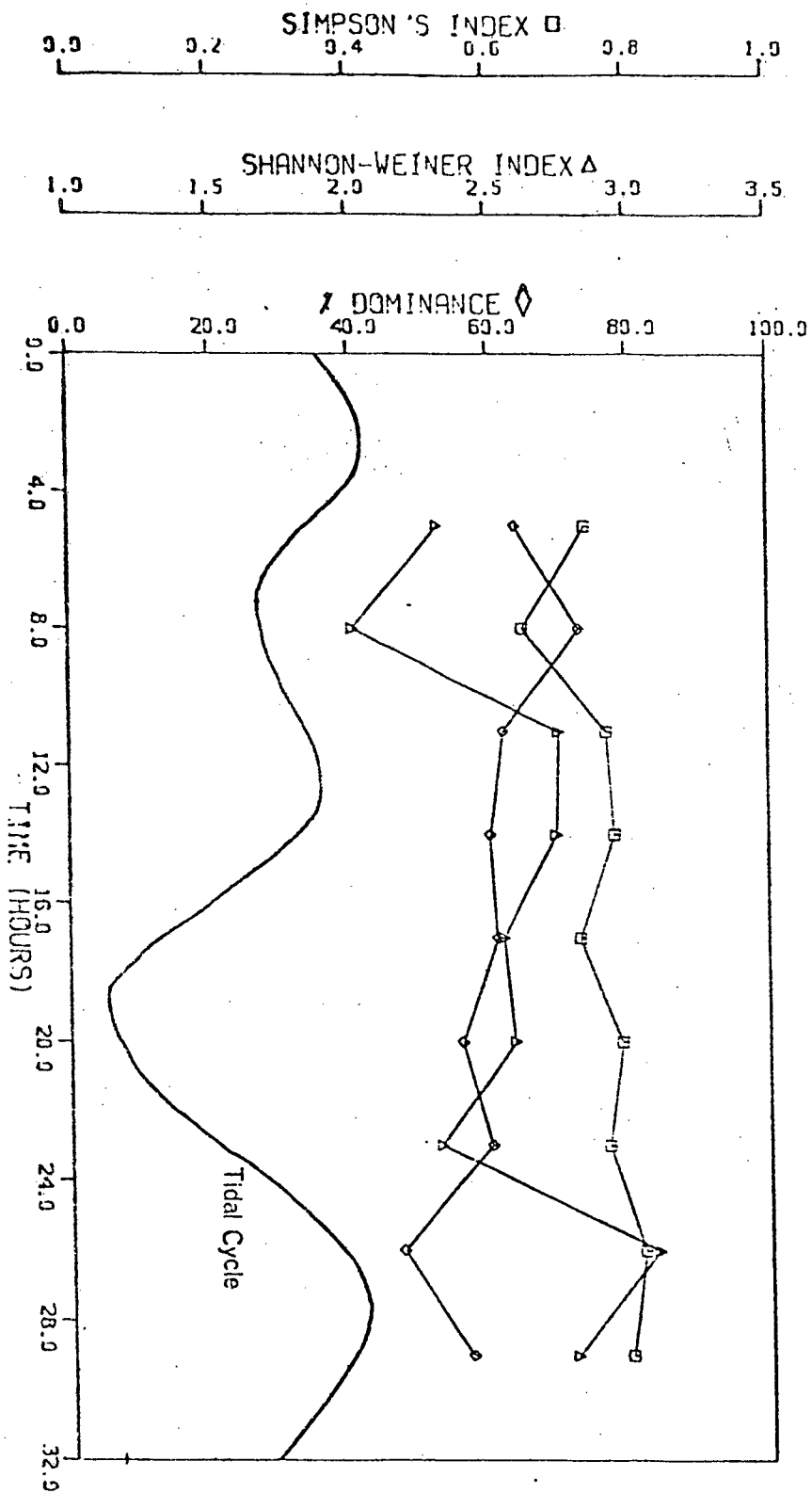


Figure 27; Kendalls coefficient of concordance between time adjacent samples over the tidal cycle at IND 0 (Cruise 80/18). Hours and tidal height as in Fig. 15.

