EUPHAUSIA PACIFICA AND OTHER EUPHAUSIIDS IN THE COASTAL WATERS OF BRITISH COLUMBIA: RELATIONSHIPS TO TEMPERATURE, SALINITY AND OTHER PROPERTIES IN THE FIELD AND LABORATORY.

by

LANCE REGAN

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We accept this thesis as conforming to the required standard

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September, 1968
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Department of Zoology

The University of British Columbia
Vancouver 8, Canada

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ABSTRACT

During 1960-61 the abundance and distributions of four species of euphausiids (*Euphausia pacifica* Hansen, *Thysanoessa spinifera* Holmes, *Thysanoessa longipes* Brandt and *Thysanoessa raschii* M. Sars) and the developmental stages of one species, *E. pacifica* were studied each month in relation to temperature and salinity in Indian Arm, British Columbia, using the method of T-S-P diagrams.

*Euphausia pacifica* probably is a resident species and as such was the most tolerant towards environmental conditions and their fluctuations in Indian Arm, followed in order of decreasing tolerance by the expatriate species *T. spinifera, T. longipes* and *T. raschii*. All species, (whether resident or expatriates), were useful biological indicators of oceanographic changes in Indian Arm, particularly with reference to the detection of outside waters entering the inlet.

Field data indicated that temperature and salinity may have been contributory "regulatory factors" with regard to the vertical distribution of euphausiids in Indian Arm, particularly in the region of maximum temperature and salinity change in the thermocline and halocline, between about 10 m and the surface. In contrast, the occurrences and distribution of euphausiids in intermediate-depth and deeper waters and the general absence of adult specimens of *E. pacifica, T. spinifera* and *T. longipes* from the deep waters, below 120 m, and of *T. raschii* from waters below 60 m have suggested that regulatory factors other than temperature and salinity were also operative. Nauplii and metanauplii of *E. pacifica* were markedly restricted in their
distribution to deeper water when compared with the broad vertical distribution of eggs, later developmental stages (calyptopii, furcilia) and the adults of this species, a feature which may be similarly caused.

In the laboratory, experiments were conducted in attempts to determine if the variations in euphausiid distributions found in the field resulted from different reactions of species to temperature, salinity and/or combinations of temperature-salinity, or to some other property or properties acting within particular temperature-salinity ranges.

In the laboratory specimens were induced to migrate vertically in temperature which increased and salinity which decreased towards the surface. The numbers migrating decreased progressively with increase in the temperature and with decrease in the salinity. The strongest effects occurred when the rate of change of either property was the maximum obtainable and when temperature and salinity gradients were combined. These experiments indicated, also, that specimens would migrate into higher temperatures and lower salinities than usually obtained in the field (and this, despite the much steeper gradients employed in the laboratory).

In a second series of experiments temperature and salinity conditions were kept constant, or nearly so, and specimens (of E. pacifica) were induced to migrate from water originating in one area ("home") into water from another area ("foreign"). In general, specimens showed a preference towards
the properties of "home" water and would "avoid" the "foreign" waters. In survival experiments specimens survived in larger numbers and for longer periods in "home" waters than in "foreign" waters or in mixtures of the two. There were indications of a seasonal fluctuation in survival of specimens.

On the basis of the findings from the field and laboratory investigations, it is postulated that properties unique to different waters, and the reaction of euphausiids towards these "unique properties", were important in the occurrences and distribution of euphausiids in Indian Arm and their migration and survival in the laboratory.
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I. INTRODUCTION

A detailed study of the physical oceanography (Gilmartin, 1960, 1962) of Indian Arm, British Columbia, and investigations of distributions of selected species of zooplankton (McHardy, 1961; Shan, 1962) in the inlet have been undertaken during the past several years by the Institute of Oceanography, University of British Columbia. The present study is concerned with environmental factors involved in the occurrences and distribution of the euphausiids, Euphausia pacifica Hansen, Thysanoessa spinifera Holmes, Thysanoessa longipes Brandt and Thysanoessa raschii M. Sars, in Indian Arm and the migration and survival in the laboratory of E. pacifica from Indian Arm and adjacent areas in waters of diverse origin.

Taxonomic descriptions of the euphausiids investigated in the present study, along with general notes on their distributions in the North Pacific have been reported by Banner (1950) Boden, Johnson and Brinton (1955) and Brinton (1962); post-naupliar developmental stages of E. pacifica have been described by Boden (1950).

Euphausia pacifica and T. longipes appear to be primarily oceanic species, widely distributed throughout the North Pacific, but also occurring in neritic waters; T. spinifera and T. raschii appear to be restricted to waters along the coasts bordering the northeastern Pacific. No information is available in the literature concerning detailed studies of either the distribution of euphausiids, or of factors involved in this, for
British Columbia. In British Columbia coastal waters *E. pacifica* is almost always the dominant species and can occur in very large numbers.

There is a large body of literature attesting the importance of temperature and salinity in the physiological reactions of organisms towards marine and brackish-water environments. Recent reviews of papers on or including the effects of temperature and salinity on the metabolism, reproduction, development and activity of aquatic organisms have been provided by Prosser and Brown (1961) and Kinne (1963, 1964). These summarize the consensus of many workers that temperature and salinity are probably two of the most important physical factors in the life of marine and brackish-water animals. Ekman (1953), Sverdrup, Johnson and Fleming (1942) and Hedgpeth (1957), among others, have divided the oceans and their faunas into horizontal (e.g., boreal, temperate, Arctic) and vertical, (e.g., epipelagic, bathypelagic, abyssal) zoogeographical zones dependent for their demarcation on temperature as shown by particular isotherms. Additional literature concerns primarily the effects of temperature on the vertical distribution of zooplankton (Moore, 1950, 1952; Moore, Owre, Jones and Dow, 1953; Moore and Corwin, 1956; Moore and Foyo, 1963). Several attempts have been made to classify marine and brackish waters and their faunas on differences in average salinity (Ekman, 1953; Hedgpeth, 1957). Lance (1962) demonstrated experimentally that salinity *per se* effects the vertical migration and distribution of zooplankton and this is pertinent to the present study.

It has been demonstrated in recent studies dealing with
effects of temperature and salinity on reactions of organisms that both factors should be considered together, in a bifactorial approach (Kinne, 1964). Some of the data are derived from the survival of marine and brackish-water animals in the laboratory (McLeese, 1956; and Costlow, Bookhout and Monroe, 1960, 1962). On the other hand Pickford (1946, 1952), Haffner (1952), David (1955, 1958), McGowan (1959) and Bary (1959, 1963 a, c and d, 1964) have developed and modified techniques of relating the distribution of marine organisms in the field to those bodies of water (water masses), characterized by their temperatures and salinities by means of temperature-salinity (T-S) diagrams. Basically these techniques directly relate the occurrences of organisms to the temperature-salinity conditions in which they are living.

There has been continuing speculation whether the temperature and/or salinity (used to characterize the environmental water "bodies") in fact "control" the occurrences and distribution of the organisms, or whether the "control" might be exercised by means of other factors inclusive in the "bodies" of water. Thus Bary (1963 a, 1964) has shown that distributions of pelagic organisms in the northeastern Atlantic were associated with identifiable bodies of water, but that neither the temperature nor the salinity defining these waters appeared to be the factors responsible for the particular species-water body associations. Other undetermined factors, the "unique properties" (Bary, 1963 a, p.64), were hypothesised as integral to these water bodies, and that these combined with the differences in "tolerance" among species,
were responsible for the association between the species and the water-body.

Wilson (1951) and Wilson and Armstrong (1952, 1954) were among the first investigators to demonstrate experimentally that "biological differences" existed between natural waters of diverse origin. In general these studies indicated that English Channel water (near Plymouth) either lacked some vital substance, or contained in minute amounts something harmful to the development and survival of certain species of sea-urchins and polychaetes. In Celtic Sea and Clyde Sea water brought into the laboratory, development generally approached normal and the specimens survived considerably better than in the water from the English Channel. More recently Johnston (1962, 1964) has demonstrated experimentally that the growth of phytoplankton can be affected favourably or adversely depending on the "quality" of seawaters from the North Sea and North Atlantic. Seawater, as a natural medium for phytoplankton, changed according to the location, depth and season at which the water was collected. "Quality" might be traced to gross differences in composition of the dissolved organic matter in the respective waters (Johnston, 1962), and in particular to the chelation of trace metals by dissolved organic substances (Johnston, 1964).

It appears therefore that there is a large body of field and experimental data concerned with the role of temperature and salinity as the controlling processes of distributions of marine and brackish-water organisms. However, the importance of other undetermined factors (be they referred to as "unique properties" or "biological differences" or "qualities") in seawater, and the
reactions of organisms to such factors, is increasingly evident in the more recent literature.

The present study has consisted of two parts. Firstly, an attempt has been made from field data to resolve whether, for the coastal waters of British Columbia, temperature and salinity play a part in the distributions of selected species and if so to what extent this applies. Secondly, from laboratory studies, it has been desired to show whether other factors might be playing a primary or a secondary role and either control occurrences or modify the effects of temperature and/or salinity.

On the basis of the evidence two general statements can be made. Firstly, temperature and salinity, particularly when combined, can affect the vertical distribution and migration of specimens in regions of extreme change (thermocline and halocline) both in laboratory experiments and in near-surface waters in the field. Secondly, the effects of temperature and salinity (in intermediate-depth and deep waters of Indian Arm and in seawaters of diverse origin) appeared to be secondary to other unidentified factors, particularly when tests were carried out between waters of diverse origins. The evidence obtained tends to support Wilson et al (1951, 1954) in that "biological differences" were demonstrated between waters from different, but on occasion adjacent areas in British Columbia coastal waters.
PART A:

FIELD PROGRAMME

To determine the relationships between the distribution of euphausiids and temperature and salinity in Indian Arm the following were studied:


3. the monthly distribution of temperature, salinity and density ($\sigma_t$), and the movement of waters into and out of the inlet between January, 1960 and July-August, 1961.

4. the relations between the occurrences of euphausiids and the distribution of temperature, salinity and density ($\sigma_t$).

5. the relations between changes in occurrences of euphausiids and concurrent changes in oceanographic conditions indicated by temperature, salinity and density ($\sigma_t$).
II. MATERIALS AND METHODS

COLLECTION OF DATA

Concurrent collections of temperatures, salinities and plankton were made in Indian Arm at approximately monthly intervals between June, 1960, and July-August, 1961 (I.O.U.B.C., 1960, 1961). To include periods in which there were gross changes in water conditions, as well as periods of relative stability, it was necessary to extend the investigation and to this end data and samples collected between January and April, 1960, were examined.

During the monthly cruises, six selected stations were occupied during night and day. Four sampling runs of each were made in which temperature, salinity and plankton data were collected; during some additional runs, only plankton was collected. Whenever possible, stations were sampled during both flood and ebb tides.

The six stations (Stations 2, 6, 9, 12, 15 and 23, Fig. 1a) were located along the mid-line of Indian Arm at the same positions as sampled by Gilmartin (1960), McHardy (1961) and Shan (1962). The positions, chosen with respect to the physiography of and circulation in the inlet, are believed to have provided representative data. They are situated (Fig. 1a) over the sill (Station 23) in the deep basin (Stations 6 and 9), in shoaling waters (Stations 2 and 12), and in a region of maximum mixing (Station 15). Exchanges of water between Indian Arm and Burrard Inlet occur through the positions of Stations 15 and 23.
During the present study, extensive fog in December, 1960, and January, 1961, prevented ship manoeuvring in the shallow and narrow regions of Station 23 and 15; prior to the present study, Station 23 was not sampled in January, February and March, 1960 (McHardy, 1961). In April, 1961, no collections were made during darkness.

Standard oceanographic techniques were used. Water samples for salinity and oxygen determinations were obtained using Atlas water bottles at the standard depths of 0, (5), 10, 20, (30), 50, 75, 100, 150 and 200 m; in situ temperatures were recorded using reversing thermometers. In addition, vertical temperature-depth profiles were obtained using the bathythermograph. Salinities were determined by the Mohr titration method and oxygen content by the Winkler titration method (for description of methods, see Strickland and Parsons, 1961). Density was derived from temperature and salinity by means of nomograph tables. The monthly presentations of temperature, salinity and density (σ_t) (Figs. 3-20) for Indian Arm are the means of values from two sampling runs, one made during the flood and the other during the ebb of a tide.

The plankton-sampling programme was designed to demonstrate the spatial, diel, and seasonal distributions of euphausiids in Indian Arm. The plankton sampler was the Clarke-Bumpus Sampler (Clarke and Bumpus, 1950), modified according to Paquette and Frolander (1956) and fitted with

1. Depth of 5 m not sampled between January and April, 1960
2. Depth of 30 m not sampled between January and October, 1960.
nylon nets with mesh apertures of either 0.40 mm (No. 2 mesh) or 0.12 mm (No. 10 mesh). During each cruise, nets of No. 2 mesh were used for the first 24-hour period and No. 10 for the second. The No. 2 mesh was used for collecting adults euphausiids and No. 10 primarily for eggs and developmental stages.

The plankton samplers were lowered closed to a series of selected depths, opened with a messenger, towed horizontally over a radar-measured distance of five cables (about 0.93 km), and finally closed with a second messenger and retrieved. Duration of the tows was between 10 and 15 minutes at a speed of two to three knots. A Tsurumi-Seiki-Kosakuso (T-S-K) maximum depth recorder was used on several occasions to check the depth of tow as calculated from the angle of the towing cable (Regan, 1963). A flow-meter present in each plankton sampler enabled estimations to be made of the volume of water filtered during all plankton tows. It was possible, therefore, to treat the plankton samples quantitatively.

Plankton was collected from the estimated depths of 0, 30, 60, 90, 120, 150 and 180 m at Stations 2, 6, 9 and 12, when depth permitted. At Station 15, collections were from 0, 30 and 50 m and, at Station 23, from 0 and 20 m. Additional samples were collected from depths of 15 m (beginning in February, 1961), 45 m (beginning in March, 1961), and 8 and 75 m (beginning in June, 1961); this extra sampling was introduced to provide more detailed information on the vertical distribution of the euphausiids in the upper waters and was continued until July-August, 1961. Information on whether euphausiids occurred near the bottom of Indian Arm. was based on collections made from approximately one
metre above the bottom, October, 1960, to July-August, 1961; a Clarke-Bumpus sampler was attached to a large, flat weight which was towed along the bottom.

A secondary project, pertaining to the testing and evaluation of the Clarke-Bumpus Plankton Sampler in the collection of euphausiids, was undertaken in 1961. A full report of this study has been presented in a manuscript report (Regan, 1963).

A large number of plankton samples accumulated from the intensive sampling programme. It was necessary, therefore, to select samples for subsequent analysis. In general, the selected samples were those collected concurrently with oceanographic data. To obtain more specimens of the less abundant species (*Thysanoessa longipes* and *T. raschii*) additional samples, from the runs in which only plankton was collected, were examined. Counts of the adults were restricted to samples collected with the 0.40 mm mesh and the developmental stages to collections made with the 0.12 mm mesh.

Plankton samples were fixed and preserved in a 1:10 solution of 40 % neutralized formalin and seawater. All adult euphausiids were removed from the sample, sorted for species and counted. A vacuum-assisted subsampler (McHardy, 1964) was used to obtain a 10 % subsample, from which the developmental stages were sorted to species and growth stages and counted.

Results of analyses are reported as numbers collected per cubic metre of water filtered for *Euphausia pacifica*, but because of the small numbers present, analyses for *Thysanoessa spinifera*, *T. longipes* and *T. raschii* are reported as numbers
per 10 m$^3$ of water filtered. In three instances (Figs.118 - 120) an exception to the above was made and *E. pacifica* was also reported in numbers per 10 m$^3$.

Examinations and measurements of the unmounted specimens were made using a Leitz binocular microscope fitted with an ocular scale calibrated against a stage micrometer. Specimens for morphological examination were dissected and mounted in polyvinyl-lactophenol medium (Salmon, 1949) in which a few drops of one per cent chlorasol black or lignin pink had been previously mixed. These specimens were checked for the detailed, diagnostic characters appropriate to particular developmental stages and species.
Indian Arm is approximately 22 km long and 1 km wide. It extends due north from 48° 18' 10" N and 122° 56' 20" W, and is one of the southern, mainland inlets of British Columbia (Fig. 1). It is bounded by precipitous mountains, and at its southern end opens into Burrard Inlet which in turn connects with the Strait of Georgia. A basin, with an average depth of 200 m, occupies the major part of the inlet. It shoals at the head of the inlet towards the delta of the Indian River, northwards from Station 2 (Fig. 1a). A sill across the inlet's mouth is about 26 m deep (Fig. 1a, Station 23). This is considerably shallower than the average sill-depth of 106 m determined for other mainland inlets of British Columbia (Pickard, 1961).

Indian Arm is included in the group of inlets with medium volumes of freshwater runoff (Pickard, 1961). Freshwater enters from precipitation, the Indian River, peripheral streams and from the discharge at the Buntzen power plant, situated mid-way along the inlet. Because its density is lower than the saline waters, the freshwater forms a surface layer which flows southward towards the mouth. The volume of this surface layer varies seasonally (Gilmartin, 1960, 1962). The periods of freshwater runoff consist of a maximum in the spring (approximately April to June), followed by minimum in the mid-summer (approximately July to September), a secondary maximum in the early winter (approximately October to December) and a secondary minimum in the later winter (approximately January to March). During the seaward movement of the surface water, mixing occurs between it and the more saline waters immediately below; the result is that the surface water becomes increasingly brackish (saline) from the head towards the mouth of the inlet, which is
typical of British Columbia inlets (Pickard, 1955). The seaward movement of this surface, brackish layer entrains more saline water from the underlying water of the inlet (Gilmartin, 1960). Considerations of continuity require that the saline water removed from the inlet in the resulting outflow is replaced by a compensating inflow at some subsurface depth of saline water from Burrard Inlet. This inflow may be expected to be greater during the spring and early winter maxima of surface runoff than during the mid-summer and late winter minima. Water from Burrard Inlet also enters during the tidal cycle. In addition occasional intrusions of larger amounts of water have been detected (Gilmartin, 1960, 1962; and McHardy, 1961). The surface, brackish water and the subsurface water of higher salinity is essentially the two-layered system described for Indian Arm by Gilmartin (1960, 1962).

DISTRIBUTION OF TEMPERATURE, SALINITY AND DENSITY ($\sigma_t$)

The maximum and minimum values of temperature, salinity and oxygen recorded in Indian Arm between January, 1960 and July-August, 1961, are summarized in Table 1. The extremes of temperature were observed in surface waters and were 3.08 and 20.21°C. The lowest salinity was 2.42°/oo at the surface, and the highest, 27.32°/oo in deep water; oxygen ranged between 1.31 and 9.53 ml/l.

Figure 2 is a series of monthly, temperature-salinity (T-S) curves based on the mean values from the standard depths at the six stations, for the period from September, 1960, to July-August, 1961. In general, temperature decreased and salinity increased with increasing depth in Indian Arm, excepting between December and March when temperatures were very low at the surface. This general situation is typical of British Columbia inlets.
(Pickard, 1961). The temperature and salinity values located towards the left of the various curves (Fig. 2) include waters from the surface to approximately 5 m depth and as indicated by the broadness of the pattern, they varied appreciably in temperature and salinity from month to month. These waters include the regions of maximum temperature and salinity change (i.e., thermocline and halocline), the nature of which is closely related to seasonal runoff and heat input in the surface waters.

The water from the intermediate depths, approximately 5 to 75 m, is located in the central part (dotted lines) of the temperature-salinity diagram (Fig. 2). This has been named transition water and is considered to result from vertical mixing of surface and deeper high-salinity waters. The depth range over which the transition water occurs has been somewhat arbitrarily determined because of the difficulty of precisely demarcating its properties from those of surface and deep waters. For any given month, however, temperatures and salinities fall between the values for surface and deep waters, but the chief distinguishing characteristic is that the total range of temperature and salinity in the transition water for the year is substantially less than for surface waters, and greater than for deep water. The assigned range of temperature lies between approximately 7.5 and 13.5°C, and of salinity between approximately 23.0 and 27.0 ‰ (Fig. 2).

The compact group of temperature and salinity values for the deep water (from about 75 to 200 m) suggests that this water was relatively stable in its properties from September, 1960, to July-August, 1961. Temperatures ranged from approximately 7.5 to 8.0°C, and salinities from approximately 26.8 to 27.32‰ (Fig. 2).
The monthly and seasonal changes in the temperature and salinity of surface waters are clear from Fig. 2. From June to October inclusive the curves form a group in which both temperature and salinity vary widely. In June, high temperatures combined with low salinities, the combination resulting from surface heating and from dilution by large volumes of freshwater runoff. In contrast, the lower temperature and higher salinity in October reflect cooling of surface water and low runoff.

Conditions between December and April (Fig. 2) form a second group in which salinity is the dominant variable. In this group, relatively isothermal conditions prevailed throughout the water column. The winter runoff of freshwater diluted the surface water to the low salinities of December and February; these values were much lower than the salinities for transition and deep waters. In January, March and April the relatively high salinities in surface waters resulted from reduced runoff, but because of the small range of temperature in the water column for this period, salinity remained the dominant variable.

Figures 3 to 17 present monthly, temperature-salinity (T-S) scatter diagrams for Indian Arm from January, 1960 to July-August, 1961. Depth intervals, in metres, indicate the appropriate ranges of depths for groups of intercepts (points) of temperature and salinity. In the accompanying inserts (e.g., Fig. 3, inserts a and b) isotherms and isohalines show the distributions of the properties for longitudinal sections of Indian Arm.

The distribution of density ($\sigma_t$) is shown in longitudinal sections of the inlet in Figs. 18, 19 and 20. In general, it has been demonstrated (Tabata and Pickard, 1957) that variations in $\sigma_t$ closely follow the variations in salinity in British Columbia.
inlets. However, although salinity is usually more important than temperature in determining stability in upper waters, at times temperature is very important in the stability of Indian Arm waters, particularly at intermediate depths and in deeper water (Gilmartin, 1962).

For convenience, the monthly T-S diagrams and the distributions of temperature, salinity and density ($\sigma_t$) are discussed for intervals of three months.

January, February and March, 1960

A comparison of T-S diagrams in Figs. 3, 4, and 5 demonstrate that in Indian Arm, between January and March, 1960, there was a decrease in temperature and an increase in salinity at depths between 10 and 200 m. The T-S diagram for January, 1960 (Fig. 3), suggests a three-layered system; surface, brackish water from 0 - 5 m; transition water in which there is a moderate range of temperature and small range of salinity, from 10 - 50 m or more; and deep water with comparatively constant temperature and salinity, from about 75 - 200 m. By March (Fig. 5) there is a surface, brackish water from 0 - 5 m, characterized by relatively uniform temperature and a broad range of salinity, and subsurface water from 10 - 200 m, characterized by small ranges of low temperatures (7.1 to 8.0°C) and high salinities (26.9 to 27.3 °/oo). It appears that the properties of the waters at intermediate depths (approximately 10 - 50 m) have approached, and partially merged with those of the deep waters (75 - 200 m) to give an appearance of a two-layered system. However, some indication of the three-layered system remains in March in that there is a slight grouping and demarcation of water from 50 - 200 m from
that of 10 - 30 m.

The longitudinal sections (Figs. 3 - 5, inserts a and b; density, Fig. 18) indicate that the changes in the oceanographic properties in Indian Arm may have resulted from the entry and the subsequent movements of outside water.

A comparison between January (Fig. 3, insert a) and February (Fig. 4, insert a) indicates that the surface and intermediate-depth waters cooled (7.5 and 7.9°C isotherms) in February. By March, the temperature distribution indicates that a large body of cold water (7.1 to 7.8°C) was present at the southern end at depths between 10 and 200 m (Fig. 5, insert a). The 7.1, 7.2 and 7.5°C isotherms, which were not present in January and February, (or, as in the case of the 7.5°C isotherm, was limited to upper waters in February) together with the lowered temperature of the bottom water at Stations 6 and 9 (7.3°C as compared with 7.8 to 7.9°C) demonstrated the influence of this water.

Water of 27.0°/oo salinity was not observed in January (Fig. 3, insert b). However, in February salinities of 27°/oo and higher were present from 60 or 70 m and in March from 15 or 20 m downwards (Figs. 4 and 5, inserts b) and the salinity of bottom water at Stations 6 and 9 increased from 26.97°/oo in January to 27.28°/oo in February and to 27.30°/oo in March.

Three isopycnals (lines of equal density) have been selected: 19.5 \( \sigma_T \) for the upper waters, 20.75 \( \sigma_T \) for water at intermediate depths (transitional water) and 21.0 \( \sigma_T \) for the deep water. The isopycnal of 21.0 \( \sigma_T \) lay between 150 and 170 m in January; by February it had decreased in depth to between 50 and 60 m and by March to approximately 30 m (Fig. 18, a, b, c) indicating a progressive and substantial increase in the density of the
sub-surface waters. The isopycnal of 20.75 \( \sigma_t \) "accompanied" that of 21.0 \( \sigma_t \), decreasing in depth from 90 m in January, to 30 m in February, to 20 m in March. During the three months the isopycnal of 19.5 \( \sigma_t \) remained at about 10 m, indicating that density in the upper water was little influenced by the large changes occurring in the waters at intermediate and greater depths.

The evidence derived from a decrease in temperature and increases in salinity and density (\( \sigma_t \)) all point to one phenomenon, that cool, high-salinity water entered Indian Arm from outside. The only source of such comparatively highly saline water would be the Strait of Georgia, via Burrard Inlet. This water was of higher density than the resident water it displaced, and therefore entered into the deep basin of Indian Arm and strongly influenced the oceanographic conditions in February and especially in March, 1960. The entry of such water, in reality an intrusion of relatively massive proportions, may have extended over several weeks. By March a relative uniformity of the temperature and salinity had resulted between 10 and 200 m. The latter observation is related to the transformation of the three-layered system of January into a system approaching two layers in March.

April, June and July, 1960

The T-S diagram for April, 1960 (Fig. 6), suggests that a transition water, at depths between 10 and 50 m, had begun to differentiate from the low-temperature and high-salinity water which occupied depths between 10 and 200 m in March, 1960. By June, this transition water was strongly developed between 5 and 30 m, and by July, between 5 and 50 m (Figs. 7 and 8). Thus the three-layered system which had not been clearly evident in the preceding three months was strongly developed by June and July.
Comparison of the T-S diagrams (Figs. 6 - 8) for April, June and July, 1960, demonstrates a progressive increase in temperature and a decrease in salinity between 10 and 200 m. Seasonal warming of surface waters, freshwater runoff and tidal exchange, accompanied by vertical and horizontal mixing were probably responsible for this warming and dilution of the cold, highly saline waters which intruded in February and March, 1960.

In surface waters, also, seasonal changes of temperature and salinity were apparent between April and July, 1960. In April a maximum temperature of 8.3°C and a minimum salinity of 10.0‰ was recorded at the surface (Fig. 6); in June these values were 13.7°C and 8.8‰ (Fig. 7), and in July, 19.2°C and 18.0‰ (Fig. 8).

In the temperature distributions for April, June and July, 1960 (Figs. 6, 7 and 8 - insert a) the progressive deepening of the 7.5°C isotherm and the absence of water of 7.1 and 7.2°C suggests that the influence of the cold intruded water, particularly apparent in March, 1960, was decreasing. This was probably the result of a seasonal increase in heat input, as evident from the increase in the temperatures of upper waters. The increase in the temperature of bottom water at Stations 6 and 9, from a low of 7.3°C in April to 7.5°C in June and July (Figs. 6 - 8, insert a) may be indicative of the vertical extent of this warming trend. The horizontal appearance of the isotherms of 7.5, 7.6 and 7.8°C in July, as compared with their slope in April and June, suggests that up-inlet mixing between cool and warm waters was more or less completed and that oceanographic conditions in the deeper waters were relatively stable.
The deepening of the isohaline of 27.0°/o from 15 or 20 m in March to 45 - 60 m in April, to 75 m in June and to 90 m in July, 1960 (Figs. 5 - 8, insert b), also suggest that mixing between the high-salinity, deep water which had previously intruded into the basin and less-saline waters was occurring. The vertical extent of this mixing is indicated in the dilution of bottom waters at Station 6 and 9, where salinity decreased from 27.30°/o in March to 27.16°/o by July, 1960.

The gradual deepening of the isopycnal of 21.0°t from 30 m in March to 80 - 90 m in July, 1960, and of the isopycnal of 20.75°t from 20 m in March to 60 - 75 m in July (Fig. 18 c, d, e; Fig. 19 a), show there was a decrease in the density of subsurface waters. This would ensue on downward mixing of low-salinity, warmer water discussed above. The near surface isopycnal of 19.5°t also deepened, from 10 m in March and April, to 20 - 30 m in June, to 45 m in July, 1960 (Fig. 18 c, d, e; Fig. 19 a). This signified a decrease in the density of the near-surface waters, which is attributable to effects of seasonal warming at and near the surface and the spring and early summer runoff of freshwater.

September, October and December, 1960

The T-S diagram for September, 1960 (Fig.9), shows that the three-layered system of surface water, transition water (between 5 and 50 m) and relatively cold, high-salinity water between 75 and 200 m persisted but weakened. It continued during October (Fig.10), but there was a slight decrease in temperature and an appreciable increase in salinity at depths between 5 and 50 m;
this, coupled with the increase in temperature and salinity at 75 m extended the range of depth of transition water to between 5 and 75 m on the T-S diagram. By December, the temperatures between 5 and 75 m and salinities between 10 and 75 m indicated a substantial decrease in temperature and a further increase in salinity (Fig. 11); and with these changes, the transition water became continuous in salinity with the deeper water. Thus the distinct, three-layered system established in June and maintained until October, has become less well defined by December, 1960.

In surface water seasonal cooling and fluctuations in dilution from freshwater runoff are apparent (Figs. 9, 10 and 11). The maximum temperature and minimum salinity ranged from 15.2°C and 17°/oo in September, to 14.0°C and 19°/oo in October, to 10.4°C and 7°/oo in December. Clearly the effects of runoff on the surface water, increased sharply in December.

The distributions of temperature (Figs. 9, 10 and 11 - insert a) show that, at depths between 5 and 50 m, temperatures decreased from 13.0 - 10.0°C in September, to 12.0 - 10°C in October, to 10.0 - 9.0°C in December. In deeper waters, however, temperatures increased as shown by the deepening of the 8.0°C isotherm from 75 m in September to 90 m in October to 120 m in December. In bottom waters there was also a progressive increase of temperature, from 7.55°C in September to 7.6°C in October to 7.71°C in December (Figs. 9, 10 and 11 - insert a).

For salinity, the 26.75°/oo isohaline became shallower moving from 75 m in September to between 30 and 60 m in October and then to between 20 and 30 m in December, 1960 (Figs. 9, 10 and 11 - insert b). This is indicative of an increase in salinity
between 10 and 75 m during October and December. The downward slope in October of the isohalines of 26.0, 26.5, 26.75 and 27.0 o/oo from Station 23 towards Station 2, indicate that, for a given depth, salinities were decreasing towards the head of the inlet. By December, however, the positions of these isohalines indicated that, for a given depth, salinities were similar throughout the inlet.

The change of depth of the isopycnal of 20.75 o/t from 75 m in September and October to 30 - 45 m in December (Fig. 19 b, c, d) demonstrates an increase in density for intermediate-depth waters; this is also indicated by the increased separation of isopycnals of 20.75 o/t and 21.0 o/t which were about 15 m apart from February to October (Fig. 18 a-e and 19 b,c.), but had increased to 45 - 70 m apart by December, 1960 (Fig. 19 d). Towards the end of 1960 the isopycnal of 19.5 o/t became shallower, from 10 - 30 m in September to 5 - 10 m in October and December (Fig. 19 b, c, d), indicating an increase in density of waters between 5 and 30 m. The sustained position of the isopycnal of 21.0 (at 90 - 100 m) suggested that density was similar in the deeper waters from September through December (Fig. 19 b, c, d).

The general decrease in temperature at depths between 5 and 50 m in October and 5 and 75 m in December, 1960 (Figs. 10 and 11), could be attributed in part to the seasonal cooling of surface water and subsequent vertical mixing with the underlying water. However, the progressive increase in salinity of water between 10 and 75 m during these months, (as demonstrated by the shoaling of the 26.75% oo isohaline) is believed to have resulted from an intrusion of relatively high-salinity water from outside of Indian Arm. The downward slope in October of the
isohalines (Fig. 10 insert b), from Station 23 towards Station 2, also indicate this as does the increase in density in intermediate-depths in December (Fig. 19 d). It seems probable that the density of the outside water was similar to the Indian Arm water at the depths of these isohalines. If so, the intruded water flowed along them, but by December, (Fig. 11, insert b), their more or less horizontal position indicates that relatively stable conditions were again present in the inlet. This water may have been colder than the resident water, which would help to account, along with seasonal cooling, for the cooling between 5 and 75 m from October to December. Such an intrusion at intermediate-depth may also be implicated in the downward displacement of the 8.0°C isotherm from 75 m in September to 90 m in October to 120 m in December.

**January, February and March 1961**

The T-S diagrams for January, February and March, 1961 (Figs. 12, 13 and 14), suggest relatively stable conditions. This was unlike the situation reported for the same period in 1960 (Figs. 3, 4 and 5) when there was a "bunching" of the temperature-salinity points for depths between 10 and 200 m, particularly in March. In the first three months of 1961, much of the transition water, located between 10 and 50 m, was weakly demarcated from the deep water in the T-S diagrams but even so the water column appears as a three-layered system. The low temperatures of December persisted in the surface waters (Figs. 12, 13 and 14); and an abrupt decrease in the salinity in February probably reflects an increase in precipitation and freshwater runoff (Fig. 13).
The distribution of temperature for January (Figs. 12, insert a) shows a subsurface tongue of relatively warm water, delineated by the 8.5°C isotherm. This tongue occurred at intermediate depths and extended down-inlet from Station 2. It probably was a continuation of similar tongues of warmer water (delineated by 9.0 and 10.0°C isotherms) which were present in December, 1960, possibly as a remnant of warm water of the previous summer. By February and March (Figs. 13 and 14 - insert a) the 8.5°C tongue was restricted between Stations 2 and 6.

In March, 1961, other tongues, delineated by the isotherms of 7.75, 8.0 and 8.25°C, extended up-inlet. They are indicative of a decrease in temperature at depths between 10 and 60 m (Fig. 14, insert a).

Between December, 1960, and January, 1961, the isohalines of 26.75 and 27.0% deepened and the bottom water of 27.15°/oo disappeared. These changes indicate that the salinity decreased between approximately 15 and 200 m (Figs. 11 and 12 - insert b), probably because of extensive mixing between the less-saline resident waters and the waters which intruded in December. A gradual deepening of the isohaline for 26.75% from approximately 60 m in January to about 75 m in March, and of the isohaline of 27.0°/oo from 130 to 180 m in January to 180 m in March (Figs. 12, 13 and 14 - insert b) indicates a continuous decrease in salinity during the period.

The deepening of the isopycnal of 21.0 ρt, from between 90 and 100 m in January, to 90 - 120 m in February, to 150 m in March, 1961 (Figs. 19 e and 20 a, b), continues the trend which began in April, 1960. In January, February and March, 1961 the
isopycnal of 20.75 $\sigma_t$ returned to a depth range (60 to 75 m) similar to that in October, 1960, thus indicating that the influence on density of the intrusion of December, 1960 (Figs. 19, c, d, e and 20 a, b) was short-lived. In surface waters, the isopycnal of 19.5 $\sigma_t$ remained between 5 and 10 m, indicating that the density was relatively unchanged over the three months (Figs. 19 e and 20 a, b).

Oceanographic conditions between 10 and 200 m appeared to be relatively stable in January, February and March, 1961, with the result that the water column approximated a three-layered system. This was unlike the situation in the same period in 1960. The influence of the intrusion of December, 1960, appeared to be short-lived as shown by the return in January of the isohalines of 26.75 and 27.0% and the isopycnal of 20.75 $\sigma_t$ to depths similar to those prior to the intrusion. The decrease in temperature of waters between 10 and 60 m in March, 1961, as shown by the isotherms of 7.75, 8.0 and 8.25 extending up-inlet, suggest the possible entry into Indian Arm of cool waters from outside.

April, June and July-August, 1961

The T-S diagram for April, 1961 (Fig.15), shows continuance of the indistinct three-layered system of the preceding three months. However, during June and July-August (Figs. 16 and 17), the transition water, between 5 and 50 m was strongly developed and similar to the situation in June and July, 1960. Maximal temperatures in surface waters increased from 14.0°C in April to 19.8°C in July-August. The decrease of surface salinity from 14.0%/oo in April to 7.5%/oo in June is related to increasing
freshwater runoff, and the increased salinity in July-August to a decrease in this runoff.

In the distribution of temperature for April, 1961 (Fig. 15 - insert a), the warm-water tongue (8.5°C isotherm), apparent in previous months, is seen to persist only at depths between 60 and 90 m at Stations 2 and 6. In June and July-August, there was a seasonal increase in the temperature of waters between 0 and 50 m (Figs. 16 and 17 - insert a); the 8.5°C tongue which had progressively retreated towards the head of the inlet from January to April, 1961, has dissipated. The abrupt, upward slope of the 8.0°C isotherm from 150 m at Station 9 to 90 m at Station 2 in June, 1961, may be related to the concurrent changes in the distribution of salinity at these depths.

The 27°/oo isohaline is observed to shift surfaceward from 180 m in March, to 160 - 180 m in April, to 90 - 120 m in June (Figs. 14, 15 and 16 - insert b) indicating an increase in the salinity of the deeper waters. Concurrently, the salinity of the bottom waters at Stations 6 and 9 increased from 27.0°/oo in March to 27.18°/oo in June, 1961. In July-August, 1961, water of 27.0°/oo or greater salinity deepened (Figs. 16 and 17 - insert b), and its extent was reduced to a tongue lying at 120 - 150 m, between stations 2 and 9. Thus there was an overall decrease in the salinity of the deeper waters.

The isopycnal of 21.0 °t became shallower, from 150 m in March, to 135 m in April, to 90 - 115 m in June, 1961 (Fig. 20 b, c, d), indicating a progressive increase in the density of deep waters, corresponding with the increase in salinity for the same period. However, in July-August, 1961, water of 21.0 °t became restricted to a tongue between 135 and 180 m (Fig.20 e),
this decrease in density also corresponding with the decrease in salinity discussed above. The isopycnal of 19.5 °t deepened, from 10 m in April, to 45 m in June, to 45 - 60 m in July-August, 1961 (Fig. 20 c, d, e). As in the comparative period in 1960, this decrease of density in the upper waters reflects seasonal warming and the downward mixing of runoff.

There was a noticeable increase in the salinity and in the density of deeper waters (100 - 200 m) from April to June, 1961. The slopes of the isohalines did not suggest an inflow of high-salinity water into the inlet during this period, but such increases in salinity and density usually denote the entry of water from outside. The abrupt upward slope of the 8.0°C isotherm towards the head of the inlet in June suggests changes in the basin of the inlet, perhaps as a result of water intruding from outside. There was a decrease in the salinity and density of the deeper waters from June to July-August, 1961, which suggests that the influence of the intruded water was lessening, possibly because of mixing with resident waters.

From the above it seems probable that there was an intrusion of outside waters at some time between sampling in April and early June, 1961, which influenced the deeper waters in Indian Arm, and that the effects of such were lessening by July-August, 1961.
DISCUSSION OF TEMPERATURE, SALINITY AND DENSITY

The annual temperature-salinity (T-S) diagram for the period from September, 1960, to July-August, 1961 (Fig. 2), and the maximum and minimum temperatures, salinities and oxygen values for the period from January, 1960, to July-August, 1961 (Table 1), demonstrate a wide range of oceanographic conditions in Indian Arm.

During the period of the present study there were seasonal fluctuations in oceanographic conditions at depths between the surface and approximately 50 m (Figs. 2 - 20; inserts a and b). In general, temperatures decreased and salinities and density increased during January to April, 1960, and October, 1960 to April, 1961; these months are associated with cold air temperatures and with low runoff, as most precipitation is in the form of snow. Increased runoff led to lowered salinities at the surface in December, 1960, and February, 1961, resulting from heavy rain. The effects of the seasonal, climatic fluctuations on the increase of salinity and density between 10 and 75 m during October to December, 1960, were not clearly distinguishable from the similar influence on these properties of the intrusion of outside waters in these months.

In general, at depths between the surface and approximately 50 m, temperatures increased and salinities and density decreased during the warmer months of June to September, 1960, and June to July-August, 1961. During these months, and in particular from April to June, snow melts and the freshwater runoff is heavy.
From the two preceding paragraphs, it is apparent that there are broad, seasonal relationships between temperature, freshwater runoff, salinity and density in the upper waters of Indian Arm.

The oceanographic properties of the deep waters were relatively stable during non-intrusion periods ("normal" periods) and were not subject to the seasonal fluctuations of the upper waters. Following on intrusions, however, the temperature decreased and salinity and density increased at depths between 10 and 200 m in February and March, 1960 (Figs. 4, 5 and 18 b, c) and temperature was influenced and salinity and density increased between 100 and 200 m in April to June, 1961 (Figs. 15, 16 and 20 c, d). Subsequent to the intrusion of February - March, there was a general decrease in salinity (Figs. 6 - 17, insert b) and density (Figs. 18 - 20) in the deep waters from April, 1960, to July-August, 1961. These trends were indicative of the return of oceanographic conditions to the "normal" situation for Indian Arm, but they were interrupted by the increase in the salinity and density in deeper waters resulting from the intrusion between April and June, 1961 (Figs. 15, 16 and 20 c, d).

Gilmartin (1960, 1962) reported an intrusion into Indian Arm between January and March, 1957, when the resident waters apparently were displaced and flushed. In the present study, the intrusions consisted of a massive one in February - March, 1960, and two smaller ones between October and December, 1960, and April and June, 1961. The immediate source of the intruding water must have been Burrard Inlet, an extension of the Strait of Georgia. The large intrusion in February and March, 1960, was similar to that which occurred in 1957 (McHardy, 1961) and it
influenced temperature, salinity and density at depths between 10 and 200 m throughout Indian Arm (Fig. 4, 5 and 18 b, c). These intrusions probably result when water immediately outside Indian Arm and above its sill depth (26m) is, or becomes, denser than the water below this depth within the inlet. A density instability would arise and therefore water would flow into the inlet and, if the density were high enough, into the deep basin. The result would be an upward displacement of the resident waters which would flow out of the inlet at surface and sub-surface depths. Following this, the intruded water would gradually mix with the remaining less dense, resident waters. Tidal flow into and out of the inlet would probably assist in this mixing. An indication of the size and influence of the intrusion of February and March, 1960, is that it was some eleven months (April, 1960, to March, 1961) before the isopycnals of 20.75 $\sigma_t$ and 21.0 $\sigma_t$ returned to their pre-intrusion levels of January, 1960 (Figs. 18, 19 and 20).

The small intrusion between October and December, 1960, influenced salinity (and thereby density) but probably not temperature, at depths between 10 and 75 m (Figs. 10, 11 and 19 c,d). The intrusion between April and June, 1961, influenced salinity, density and perhaps temperature at depths between 100 and 200 m (Figs. 15, 16 and 20 c, d). The effects of these intrusions were limited not only in extent but in duration. Possibly they resulted from small amounts of outside water crossing the sill, rather than in a large replacement, as appeared to be the case in February-March, 1960. As shown by the salinity values for December, 1960, and June, 1961 (Figs. 11 and 16), the dilution
of surface waters by freshwater was high, indicating an increased outflow from the inlet. Therefore, small intrusions may have resulted from relatively high-salinity water from outside replacing the volume of water entrained from the inlet by the surface outflow (see p.13).

In the present study, it is convenient to regard the water column in Indian Arm as being basically a three-layered system. At depths between the surface and about 5m is a layer in which wide fluctuations of temperature and salinity occur. Between about 10 and 50 m is the transition water in which the temperature and salinity changes are intermediate between those at the surface and the small changes which occur in the deep waters. Lastly there is the deep water between about 75 and 200 m, where relatively low temperatures and high salinities prevailed and where fluctuations were slight.

Close examination indicates that although the water column was basically three-layered the amount of transition water at intermediate depths fluctuated. The T-S diagrams for summer and autumn (between June and October) indicate the presence of surface water, transition water (with a relatively wide range of temperature and salinity for this water), and deep water (Figs. 7 - 10, 16 and 17). For December to April, however, the transition water was characterized by small ranges in temperature and salinity and its properties approached more nearly to those of the deep water (Figs. 3 - 6, 11 - 15). Thus in Indian Arm the waters fluctuated between being distinctly three-layered during the summer and autumn and less distinctly three-layered
in the winter and spring. This interpretation differs from the
two-layered system of surface, brackish water and subsurface,
high salinity water discussed for Indian Arm by Gilmartin (1960).

The approach to a two-layered system, with little or no
transition water between the surface and deep waters, was found,
in particular, following intrusions of water originating outside
of Indian Arm. The relatively uniform temperatures and salinities
(and the approach to a two-layered system) between 10 and 200 m
in February and March, 1960, have been attributed to such an
intrusion. The intruded water was of higher salinity and lower
temperature than any water in the inlet (that is, during January,
1960). The effect as it entered and mixed with the resident
water was to increase the salinity and decrease the temperature
between 10 and 200 m. In the T-S diagrams for these months, a
merging of the transition water at intermediate depths and deep
water occurred with a two-layered system (consisting of surface,
brackish water and subsurface, high salinity water) as a conse-
quence. This is particularly evident in the T-S diagram for
March, 1960 (Fig. 5).

The continuing presence of transition water interconnect-
ing the surface and deep waters in January, February and March,
1961 (Figs. 12 - 14) is in contrast to the condition which
developed during these months in 1960. It is probably attribut-
able to the absence of detectable intrusions of outside water
during this period.
An intrusion of relatively high-salinity water which entered Indian Arm at intermediate depths between October and December, 1960, increased the salinities between 10 and 75 m. The result is most apparent in the T-S diagram for December (Fig. 11), in which the salinity values for water from these intermediate-depths again tend to merge with those for deep water, again producing almost uniform salinities for depths between 10 and 200 m. However, on the basis of temperature differences between the water at intermediate depths (9.0 to 10.2°C) and deep water (7.7 to 8.5°C) it is possible to differentiate the transition water, even though its salinity is similar to that of deep water.

Transition water at intermediate depths was becoming differentiated again in April and was well developed by June, 1961 (Fig. 15 and 16). In these months outside water again intruded into Indian Arm, but it influenced the water of the deep basin between 100 and 200 m. Possibly because of this, the seasonal formation of transition water at the intermediate depths was not precluded.

The regions of maximum temperature and salinity change (i.e., thermocline and halocline) were present in the waters from the surface to approximately 5 - 10 m in depth. (Fig. 2). In general, the salinity gradient in these waters was maximal (a range of 1.5 - 3.2 °/oo/m, from 0 to 5 m ) in the periods of increased runoff of freshwater, during April to June, 1961, and December, 1960, to February, 1961, and was minimal (a range of 0.7 - 1.0 °/oo/m, from 0 to 5 m ) in their periods of low runoff,
during September and October, 1960, and March and July-August, 1961. The temperature gradient in these waters was maximal (a range of 1.0 - 1.2 °C/m) during June and July-August, 1961, in periods of warming, and was minimal (a range of 0.08 - 0.6 °C/m) from September, 1960, to April, 1961, in periods of cooling. The influence of the thermocline and halocline on the vertical distribution and migration of zooplankton is of considerable importance in the following studies of euphausiids in Indian Arm and in the laboratory,
IV. TEMPERATURE, SALINITY AND THE OCCURRENCES OF EUPHAUSIIDS

The changing conditions of temperature and salinity in Indian Arm, in whatever manner they originate, are indicative of a variable environment encountered by plankton in the inlet. In particular, intrusions of outside waters, in that they induce relatively large and rapid changes, may be expected to influence occurrences, distribution and abundance of species in the inlet. In addition, seasonal fluctuations in the temperature and salinity of the surface water, and the formation of transition water at intermediate depths may be important considerations in the vertical distribution of the zooplankton species.

In recent years, a technique has been developed (Pickford, 1946, 1952) in which occurrences of plankton are presented in a diagram in direct relation to the temperature and salinity of the water at the time and place at which the organisms were collected. These correlation diagrams have been further developed by Bary; he refers to them as temperature-salinity-plankton (T-S-P) diagrams (Bary, 1959). The diagrams relate species to temperature and salinity condition *per se*, and to "bodies" of water (Bary, 1963 a, c and d, 1964) as these are delineated by their temperatures and salinities (Helland-Hansen, 1916) (see Sverdrup et al, 1942).

In the present study, concurrent data on temperature and salinity and the occurrences of euphausiids in Indian Arm are presented in monthly and annual T-S-P diagrams. These have been used to indicate the reactions to their environment, and to
changes in it, of the adults of four species (Euphausia pacifica, Thyanoessa spinifera, Thysanoessa longipes and Thysanoessa raschii), and the developmental stages of E. pacifica, by means of changes in occurrences and fluctuations in abundance of the species and stages.

The "annual" T-S-P diagrams (Figs. 21 - 27) delineate gross relationships of the species and developmental stages, based on presence or absence, to total ranges of temperature and salinity, over the period from September, 1960, to July-August, 1961. The solid or dotted line enclosing a number of points indicates the range of temperature and salinity over which a particular species or developmental stage was collected; the points outside of these areas represent conditions in which no specimens were collected. The geographical distributions for the corresponding period are presented in longitudinal sections of Indian Arm (Figs. 28 and 29). The hatched areas in these reproduce in another way the enclosed areas in the appropriate T-S-P diagrams.

Monthly T-S-P diagrams are presented for adult specimens of the four species from January, 1960, to July-August, 1961 (Figs. 30 - 44, 83 - 97, 99 - 111 and 113 - 117), and for the developmental stages of E. pacifica from September, 1960, to July-August, 1961 (Figs. 46 - 82). In contrast to the "annual" T-S-P diagrams, these concern short periods. The reactions of organisms to short-term changes and seasonal fluctuations in temperature and salinity, become apparent by comparing a series of such diagrams. Depth intervals, in metres, indicate the
vertical range from which groups of temperature-salinity points and organisms were obtained at the six stations in Indian Arm. The occurrences of euphausiids are presented as the numbers collected per unit volume of seawater filtered (Tables 2 and 3). The blocked in and open circles indicate the presence of specimens during night and day respectively; half-blocked circles indicate that specimens were collected during both night and day. Relative abundance is indicated by the diameter of the circle; the small points represent temperatures and salinities at which specimens were not collected. Inserts on some diagrams show occurrences and abundance in deeper waters on an enlarged scale. The monthly occurrences and relative abundance of species are also shown in longitudinal sections of Indian Arm (Figs. 45, 46 - 82, 98 and 112 - 117). These provide geographical orientation for the occurrences as presented in the corresponding T-S-P diagrams.

**Euphausia pacifica**

**Adults**

From September, 1960, to July-August, 1961, *Euphausia pacifica* occurred, as shown by the several enclosed areas in Fig. 21 over temperatures ranging from 5.3 to 13.8°C and salinities from 7.0 to 27.15°/oo. The largest area represents the temperature-salinity conditions of subsurface waters (7.6 to 13.8°C; 23.5 to 27.15 °/oo) in which specimens were collected in maximum abundance. The several small areas (over the ranges of 5.3 to 7.5°C and 7.0 to 21.0 °/oo) represent the conditions
in surface water in which small numbers of specimens were collected in December, 1960, and January, February and March, 1961. It is also apparent that there were associated conditions of temperature and salinity from which specimens were not collected.

Geographically *E. pacifica* (Fig. 28 a) was collected during the 12 months at all stations and in surface, intermediate-depth and deeper waters. Specimens were noticeably absent below 120 m at Station 9 and in bottom waters at Station 6. Such absence from the deepest waters is an important, consistent feature of the occurrences of *E. pacifica*.

Specimens were collected at night in surface waters from January to April, 1960 (Figs. 30 - 33), and from December, 1960, to March, 1961 (Figs. 38 - 41). The numbers were low, 0.1 to 7.8 animals/m³, and coincided with and may be related to, the seasonal cooling of surface waters in Indian Arm. Temperatures ranged from 5.3 to 8.5°C, approaching that of subsurface waters (7.2 to 9.8°C). The small collection at the surface in February, 1961 (Fig. 40), was made in water of 5.3°C and 7.0 °/oo, values which were minimal for collections during the entire sampling programme (Table 4). Of the surface collections, specimens were most abundant (4.1 and 7.8/m³) in March, 1961 (Fig.41) when the water was cool (5.5 to 7.8°C) and of moderately high salinity (18.9 to 22.4 °/oo).

Specimens were not collected in surface waters from June to October, 1960 (Figs. 34 - 37), or from April to July-August, 1961 (Figs. 42 - 44). The failure to collect specimens in the
relatively cool, surface waters (9.0 to 10.1°C) in April, 1961 (Fig. 42), may have resulted from the absence of plankton tows during the night in this month. Except for April, 1961, the temperature at the surface ranged from 12.0 to 20.0°C for the months during which no specimens were collected.

Specimens were collected in subsurface waters throughout the sampling period. Numbers were often high, up to 37.9/m³. *Euphausia pacifica* demonstrated a diel vertical migration; in general, occurrences vertically appear to be defined into night (0 to 60 m) and day (30 to 180 m) levels, with overlap at intermediate depths (Fig. 45 a-o).

During January, February and March, 1960 (Figs. 30, 31 and 32), there was a progressive decrease in temperature and increase in salinity of the subsurface waters, but despite these changes, *E. pacifica* continued to be present. Thus, in January (Fig. 31), specimens were collected at temperatures of 8.1 to 9.0°C and salinities of 26.4 to 26.9 °/oo and by March (Fig. 32) in temperatures of 7.2 to 7.8°C and salinities of 27.0 to 27.3 °/oo (but not at depths of 150 and 180 m).

From the geographical occurrences of specimens (Fig. 45 a, b, c) it is apparent that from January to March, 1960, there was a general decrease in the numbers present. This amounted to 19%. By April, 1960 (Figs. 33 and 45 d), numbers /m³ were the lowest recorded. A comparison of the abundances at Station 12, 9 and 6 for January and April indicates this decrease approximated 73%; only at Station 2, (Fig. 1) near the head of the inlet was the abundance maintained.
During April, June and July, 1960 (Figs. 33, 34 and 35), temperature increased and salinity decreased in waters at the surface and at intermediate depths. The occurrences of specimens at 30 and 60 m, however, indicate that *E. pacific* accommodated to these changes. For example, specimens were collected at 30 m in water with temperatures and salinities of about 7.9°C and 26.4 °/oo in April (Fig. 33), 9.5 and 25.0 °/oo in June (Fig. 34) and 11.0°C and 24.8 °/oo in July (Fig. 35). Specimens were not collected at 150 and 180 m except once in June.

The geographical occurrences indicate that in April, June and July, 1960 (Figs. 45 d, e, f), specimens were collected at the same depths (30, 60, 90 and 120 m) as in previous months. They were absent from the deeper waters, excepting the small collection in June of 0.1 specimens/m³, made at 180 m at Station 9.

There was a four-fold increase in the overall abundance of specimens from April to July. In June (Fig. 45e) there was an increase in the relative abundance at 30 and 60 m at Stations 15, 12 and 9, towards the mouth of the inlet, and a decrease at Station 2, towards its head. By July (Fig. 45 f) specimens were relatively abundant at 30, 60 and 90 m, between Stations 15 and 2.

The T-S-P diagrams for September, October and December, 1960 (Figs. 36, 37 and 38) show that during the process in which transition water "merged" with the deep waters (p. 33), specimens at 30 and 60 m remained at these depths despite the ensuing decrease in temperature and the increase in salinity. For example, at 30 m specimens were collected at temperatures and salinities
of about 11.5°C and 25.9 °/oo in September (Fig. 36), 11.0°C and 26.5 °/oo in October (Fig. 37), and 9.7°C and 26.8 °/oo in December (Fig. 38), 1960.

The geographic profiles illustrate that during September, October and December, 1960 (Figs. 45 g, h, i) there were dissimilarities in the distribution and abundance of specimens. In September, specimens were most abundant and evenly distributed at 30, 60 and 90 m from Station 15 to 2, but except for one collection at 120 m, at Station 9, they were absent below 90 m. In October, there was a decrease in the relative abundance at Stations 15, 12 and 9. The population appeared to be concentrated towards the head of the inlet at Stations 6 and 2, and at greater depths (90 and 120 m) than usual; no specimens were collected below 120 m. By December, specimens were concentrated at Station 2, and in the deeper waters at Stations 6 and 9; the collections at 90 m and in bottom water at Station 2 represented the maximum abundance of specimens, up to 37.9/m$^3$; recorded during the sampling programme. Except for the small collection (0.3 animals/m$^3$) at 180 m, specimens were not collected below 120 m in December. From September to December, however, there was an increase in the relative abundance of specimens at 120 m, and in December, the numbers collected at that depth were considerably larger than in any of the preceding months. Thus the occurrences of *E. pacifica* moved towards the head and into the deeper waters of the inlet during the period from October to December, 1960.
Small changes in subsurface waters in the distribution of temperature and salinity, and significant changes in the occurrences of specimens took place between December, 1960, and January, 1961 (Figs. 38 and 39). The temperature between 30 and 180 m ranged from 7.6 to 9.7°C in December and from 7.7 to 8.7°C in January; salinity ranged from 26.7 to 27.15 °/oo in December, to 26.3 to 27.0 °/oo in January. Unlike the situation in December when *E. pacifica* occurred towards the head of the inlet and in the deeper waters there (Fig. 45 i), in January specimens were distributed more evenly between Stations 15 and 2 and were absent below 90 m (Fig. 45 j). The distribution in January, 1961, thus closely resembled that during September, 1960.

In the T-S-P diagrams for January to April, 1961 (Figs. 39 - 42), occurrences of *E. pacifica* are shown for a period when relatively stable conditions of temperature (7.7 to 8.7°C) and salinity (26.0 - 27.0 °/oo) prevailed in waters between 30 and 180 m.

Geographically, from January to April, 1961 (Fig. 45 j, k, l, m) specimens were more or less evenly distributed at depths less than 90 to 120 m (the occurrences for April were limited to day collections), and in general, for the standard sampling depths (30, 60 and 90 m), the abundance was similar from month to month. These results differ considerably from the substantial decrease in abundance reported for January to April, 1960. Specimens were distributed to a maximum depth of 90 m in January, 120 m in February and March, and 90 m in April, 1961. There was an increase in the relative abundance at 90
and 120 m from February to March, 1961; in April, there was a small decrease at 90 m, foreshadowing a larger decrease at this depth in June, 1961.

The T-S-P diagrams for June and July-August, 1961 (Figs. 43 and 44) show (as happened during June and July, 1960) that occurrences of *E. pacifica* were not affected by the changes in the temperature and salinity of transition waters at intermediate depths. For example specimens were collected at 15 m in water with temperatures and salinities ranging from about 8.3°C and 25.8 °/oo in April (Fig. 42), to 11.0°C and 24.3 °/oo in June (Fig. 43), to 13.0°C and 24.7 °/oo in July-August (Fig.44). One collection, from 8 m in July-August, was from water of 13.8°C, the maximum at which adults were found (Table 4).

Between April and June, 1961, there was a decrease in relative abundance at 90 m (Fig. 45 m, n) but between June and July-August, there was considerable increase at 60, 75 and 90 m (Fig. 45 n, o). Specimens were not collected below 90 m in April and June, but one collection of 7.7 animals/m³ was made at 120 m in July-August.

Discussion of adults of *Euphausia pacifica*

Temperature-salinity diagrams and geographical distributions of temperature, salinity and density for waters in Indian Arm show that within the annual ranges, conditions fluctuated monthly and seasonally, or were disrupted by intrusions of outside waters. The temperature-salinity-plankton diagrams show the ranges of properties from which adult specimens of *E. pacifica* were collected annually (Fig. 21) and month by month.
Within the total range occupied, certain consistent features are apparent.

Firstly, *E. pacifica* occurred over a wide range of temperature and salinity. It was collected only exceptionally from surface waters (January to April, 1960, and December, 1960, to March, 1961) or the deepest waters (June and December, 1960), features best illustrated by the monthly, geographical distributions of specimens (Fig. 45 a to o). All occurrences in the surface waters were in winter and coincided with low temperatures then; and the abundance of specimens increased as the salinity increased (e.g., March, 1961). The waters from about 90 to 200 m varied only slightly in temperature and salinity from month to month and yet specimens were not generally collected below 120 m. Occurrences therefore were in waters designated "transition" and "deep" by means of the T-S diagrams, but it is clear that only the upper part of the deep water was occupied (with rare exceptions).

Secondly, changes in properties of the transition and deep waters may have one of two effects. If the change resulted from only seasonal fluctuations in temperature and/or salinity, neither the numbers of specimens, nor their occurrences (and hence distribution), were greatly affected. If, on the other hand, the changes resulted from intrusions into the inlet of outside waters their numbers may be reduced and/or the distribution altered. Thus during, and closely following, the major intrusion in February and March, 1960 (pp.18, 29 and 30 ), when much of the water column was affected, the numbers of
specimens were greatly reduced throughout the inlet, particularly during March at the maximum extent of the intrusion, and in April. It is probable that substantial numbers of specimens were transported out of the inlet along with the volume displacement and removal of resident water by intruded water (p. 30). Only at Station 2, close to the head of the inlet and furthest removed from the influence of the intruding waters, was the abundance of specimens maintained. In the relatively small intrusion which occurred between April and June, 1961 (pp. 27 and 30) and influenced waters between 100 and 200 m, the number of specimens was noticeably reduced at 90 m and none was collected below this depth. In July-August, 1961, coincident with the decreasing influence of the intruded water (p. 27), specimens were collected at 120 m and numbers increased at 90 m (the distribution, with respect to the deeper waters, thus resembled that during March, 1961, prior to the intrusion).

Intrusions also shifted the centre of population of *E. pacifica*. Thus the intrusion which influenced waters between about 10 and 75 m during October to December, 1960 (pp. 22 and 23) only slightly reduced the abundance, but specimens concentrated at 90 and 120 m at Stations 2 and 6 below and remote from the intruding waters. By January, 1961, specimens were again distributed evenly throughout the inlet and were not collected below 90 m, coincident with the decreasing influence of the intruded water (pp. 24 and 25).

It is important to note that the changes in temperatures and salinities during 1960 and 1961 (apart from the seasonal
fluctuations at the surface) were relatively slight, and always within the range that *E. pacifica* had been shown to tolerate in the T-S-P diagrams of Indian Arm (and in later studies in the laboratory). From this, and the points discussed above, it is reasonable to infer that fluctuations in the abundance and distribution of *E. pacifica* in Indian Arm may be related to firstly, the volume displacement and mass transport of resident water and specimens out of the inlet as a result of the intrusion of outside waters, and secondly, to the influence of environmental conditions other than, or in addition to, temperature and salinity and associated with intruded water. This is particularly evident when considering the effects of intrusions into Indian Arm of outside waters, which while instrumental in producing relatively minor changes in temperature and salinity, often resulted in major fluctuations and shifts in the occurrences of the resident population of *E. pacifica*. The situation becomes the more interesting in that *E. pacifica* occurs in the Strait of Georgia, the source of the waters intruding into Indian Arm. Despite this the resident population of Indian Arm reacted adversely to the intrusions, a point returned to in the design of the laboratory experiments.
Developmental stages of *Euphausia pacifica*

Eggs

Eggs of *E. pacifica* were collected in Indian Arm from March to July-August, 1961, from waters with temperatures of 7.7 to 16.8°C and salinities of 14.0 to 27.1 °/oo (Fig. 22; Table 4). Geographically, they were present at all stations and from the surface to 150 m (Fig. 29 a).

Eggs were not observed in samples from September, 1960, to February, 1961, from Indian Arm. Small numbers (0.1 to 0.4 eggs/m³) were collected at intermediate depths in March, 1961 (Fig. 46). Their abundance increased in April (Fig. 47) and June (Fig. 48) when 86 eggs/m³ (the maximum recorded) were collected at 30 m at Station 12; numbers continued to be relatively high (0.2 to 35/m³) in July-August, 1961 (Fig. 49).

In surface waters eggs were not collected in March, but were present at most stations in April and also at Station 23 in June (Figs. 46 – 48). By July-August (Fig. 49) they were again absent from surface waters. At intermediate depths and in deep waters, eggs were more or less evenly distributed from Station 15 to 2 in March and July-August and from Station 23 to 2 in April and June. The maximum depths at which they were collected was 60 m in March and 150 m in April, June and July-August, but in general, they appeared to be most abundant between about 15 and 60 m (Figs. 46 – 48).
Nauplius I

Specimens of the first nauplius stage were collected in water with temperatures of 8.0 to 11.0°C and salinities of 24.7 to 27.1 °/oo (Fig. 22; Table 4). Geographically, specimens occurred at all stations between 15 - 30 and 150 m in Indian Arm (Fig. 29 b). In general, they were more restricted with respect to temperature and salinity (and geographical range) than the eggs.

The first nauplius stage was collected in Indian Arm only during April, June and July-August of 1961 (Figs. 50-52 and inserts). In April (Fig. 50) they were present at all stations, in relatively cool (8.0 to 8.7°C), high-salinity (26.0 to 27.0 °/oo) water between 15 and 120 m. In June specimens were absent from the warm, low-salinity waters between 0 and 30 m, but were concentrated in the cooler (8.0 to 8.8°C), high-salinity (26.0 to 27.15 °/oo) waters from 45 to 150 m (Fig. 51); occurrences were restricted to Stations 2, 9 and 12, with specimens apparently concentrated at Station 9.

In July-August (Fig. 52) the majority of specimens were collected from water with temperatures of 8.0 to 8.8°C and salinities of 26.0 to 27.1 °/oo; small numbers, however, were present in water of 9.0 to 11.0°C and 24.7 to 25.9 °/oo. The geographical insert shows that with the exception of one collection at 30 m at Station 6, specimens were not collected nearer the surface than 50 - 60 m during July-August. In contrast with the restricted distribution in June, specimens were collected from Stations 2 to 15.
The abundance of specimens at the sampling locations in April, June and July-August, 1961, ranged from 0.1 to 9.0 specimens/m³. This represents a large reduction in abundance (approximately 90%) from that of the eggs.

Nauplius II

Specimens of the second nauplius stage were collected at temperatures of 7.85 to 10.3°C and salinities of 25.6 to 27.18 °/oo, but predominantly in the range of 7.85 to 8.7°C and 25.8 to 27.18 °/oo (i.e., the deeper waters —Fig.23, dotted lines). The geographical presentation (Fig. 29 c) indicates that, over the course of several months, specimens occurred at all stations, between 15 and 180 m in Indian Arm. A noticeable feature of the geographical occurrences is the absence of specimens from 0 to 75 - 90 m at Station 6 and 9, from which it appears that the tendency to occur in deeper water shown by the first nauplius stage has continued.

In the period from September, 1960, to July-August, 1961, the second nauplius stage was collected in Indian Arm only during April, June and July-August, 1961. The T-S-P diagrams (Figs. 53 - 55) indicate that specimens occurred in cool, high-salinity waters within limited ranges of temperatures (7.85 to 8.7°C) and salinities (25.8 to 27.18 °/oo) during these months. One exception was the small collection in water of 10.3°C and 25.6 °/oo in July-August (Fig.55). In April specimens were collected between 15 and 180 m, but not in any samples at Station 6 or between 0 and 90 m at Station 9. During June and July-August specimens were not collected from the warmer, low-salinity waters
between 0 and 50 m, but were present in the cooler high-salinity, deeper waters (Figs. 54 and 55); in June, they appeared to be concentrated between 75 and 180 m at Station 9, and in July-August, between 90 and 150 m at Stations 12, 9 and 2.

The abundance of specimens ranged from 0.3 to 1440 specimens/m$^3$. This represents an increase (approximately 36%) over that of the first nauplius stage for the same months.

Metanauplius

Specimens of the final naupliar stage, the metanauplius, were collected at temperatures of 7.85 to 9.4°C and salinities of 25.6 to 27.18°/oo (Fig. 23; Table 4). They occurred most frequently, however, (Figs. 56 - 58), at temperatures of 7.85 to 8.5°C and salinities of 26.0 to 27.18 °/oo. Geographically (Fig. 29 d and 56 - 58) metanauplii were more limited in their horizontal and vertical occurrences than either of the preceding stages. Specimens were not collected at Station 23 and in general, not from waters above 50 m in Indian Arm; nor were they collected from much of the water column (between 0 and 90 to 120 m) at Stations 2, 6 and 9. Thus, the deepening trend in the vertical distribution of specimens, first observed in the first nauplius stage (as opposed to the distribution of eggs) and continued in the second nauplius stage, is most apparent in the occurrences of metanauplii.

The abundance of metanauplii ranged from 0.1 to 8.0 specimens/m$^3$. This was similar to the abundance of the first nauplius stage but represented a decrease of approximately 43% from that of the second nauplius stage for the same period.
Calyptopus I, II and III

Specimens of the first, second and third calyptopus stages, as a group, occurred in water with temperatures of 8.0 to 12.5°C and salinities of 23.4 to 27.18 °/oo (Fig.24). The calyptopus are thus the first developmental stages in which the relationship to temperature and salinity approximates that of adult E. pacifica for the same period (Figs. 21, 36, 37 and 42 - 44). The individual stages were collected (Table 4) in similar ranges of temperature and salinity. The "annual" T-S-P diagram and the geographical occurrences demonstrate a significant broadening of the distributional range of calyptopus, with respect to temperature, salinity and depth, over that of the preceding naupliar stages.

Calyptopus were collected in Indian Arm during September and October, 1960, and from April to July-August, 1961. They occurred in minimal numbers during September and October (Figs. 59, 63 and 67) were absent from collections in December through March, re-appeared in April (Figs. 60, 64 and 68) were most abundant in June (Figs. 61, 65 and 69) and continued in high numbers into July-August (Figs. 62, 66 and 70). The third calyptopus stage, unlike the first and second stages, was not collected in September, but was present in October. The abundance of specimens was similar for the three stages, ranging from 0.1 to 11 - 12/m³; the abundance of the first calyptopus stage represented an increase of approximately 27% over that of the metanauplius.
The monthly T-S-P diagrams and geographical occurrences for the first calyptopis stage (Figs. 59 - 62) show that specimens were collected from waters with a broad range of temperature and salinity, between 8 and 180 m. Excepting for surface waters, specimens occurred throughout the inlet in June, 1961 (Fig. 60) which is a broad distribution when compared with the limited occurrences of the metanauplius.

The monthly T-S-P diagrams for the second calyptopis stage (Figs. 63 - 66) indicated that specimens were not collected from waters which the inserted geographical profiles show were deeper than 120 m. The absence of specimens at 150 and 180 m in June and July-August (Figs. 65 and 66) contrasts with the occurrences of the first calyptopis stage at these depths. From this, it appears that the second calyptopis stage is the first larval stage which begins to approximate the vertical distribution of adult specimens of *Euphausia pacifica* in Indian Arm.

The third calyptopis stage (Figs. 67 - 70) was collected in waters with a relatively wide range of temperature and salinity, between 8 and 100 m. Specimens were not collected at 120 m and, as with the second calyptopis stage, were also absent at 150 and 180 m. The small collections of the third calyptopis stage at 30 m at night and at 60 m during daylight in October, 1960 (Fig. 67), provided the first suggestion of a diel vertical migration of a developmental stage.
Furculia I, III and VI

The distribution and relationships to temperature and salinity of the first, third and sixth furculia stages were selected as being representative of the seven stages in this developmental sequence of *Euphausia pacifica*.

In general, the annual T-S-P diagram (Fig. 25) and the geographical occurrences of the furculia stages (Fig. 29 f) were similar to those for the adult (Figs. 21 and 28 a) *E. pacifica*. They were collected from water with temperatures of 8.0 to 13.8°C and salinities of 23.3 to 27.18 °/oo (Fig. 25) with one exception, an isolated occurrence of the third and sixth furculia stages in surface water of 18.5°C and 22.0 °/oo in July-August, 1961 (Figs. 78 and 82). Other than this exception, Table 4 shows that the three furculia stages occurred in similar ranges of temperature and salinity. Geographically, furculia were collected at all stations and in waters between 8 and 180 m (Fig. 29 f), plus the exceptional occurrence in surface waters at Station 12 reported above; they were not collected in waters below 90 m at Station 9.

The first and third stages were collected in small numbers in September, 1960 (Figs. 71 and 75), were absent from collections in October through March, were most abundant in June (Figs. 73 and 77) and continued into July-August, 1961 (Figs. 74 and 78). The sixth furculia stage was not collected in September 1960, but was present in small numbers in October (Fig. 80); this stage was not collected from December through April, reappeared in relatively large numbers in June (Fig. 81) and
continued into July-August, 1961 (Fig. 82). The general abundance of specimens was similar for all the furcilia stages, ranging from 0.1 to 37 specimens/m³. The latter number represents a substantial increase per unit volume over the maximal numbers recorded for the preceding third calyptopis stage.

The monthly, T-S-P diagrams and geographical occurrences for the first furcilia stage (Figs. 71 - 74) indicate that specimens occurred over a wide range of temperature and salinity in waters between 8 and 90 m. They were absent in collections from surface water and from a group of samples at 120, 150 and 180 m. Their vertical distribution thus closely resembles that of the third calyptopis stage. Diel vertical migration in the first furcilia stage was strongly suggested by changes in depth in September (Fig. 71) from 30 m at night to 60 m during daylight, and in July-August (Fig. 73) from 15 to 30 m at night to between 30 and 90 m during daylight.

The third furcilia stage (Figs. 75 - 78) was collected in a wide range of conditions between 0 and 180 m, but the majority of specimens occurred between 8 and 90 m. Diel vertical migration of specimens is strongly suggested in June (Fig. 76) and takes place in July-August (Fig. 78) and September (Fig. 75).

The sixth furcilia stage (Figs. 79 - 82) was also collected from a wide range of environmental conditions, between 0 and 150 m, but as with the third furcilia stage the majority occurred between 8 and 90 m. Diel vertical migration appears to be firmly established in the occurrences of the sixth
furcilia stage, as demonstrated by occurrences being clearly defined into night and day levels in June and July-August (Figs. 81 and 82).

It is of interest that with few exceptions the furcilia stages were not collected below 90 m, a situation that is similar to the distributions of the second and third calyptopis stages and adults of *Euphausia pacifica*.

Discussion of the developmental stages of *Euphausia pacifica*

There are variations in distribution among the developmental stages of *E. pacifica*. Geographically, and in relation to temperature and salinity, the eggs displayed a distribution similar to that of the adults. Among the naupliar stages, however, there is a tendency for specimens to be distributed deeper in the water. This is apparent first with the first nauplius stage, continues with the second nauplius stage, and culminates with the metanauplius. The naupliar stages, while free-swimming (cephalic locomotion), lack the stronger swimming appendages (abdominal pleopods and thoracic appendages) and compound eyes which begin to develop strongly in the calyptopii and furcilia. The possibility arises, therefore, that the naupliar stages may sink and become concentrated at deeper levels because of poor swimming capabilities. The absence of diel migration would ensure that specimens remained in the deeper water until such time as eyes developed that were capable of perceiving light stimuli and the organism could respond to the stimuli. Observations in the field indicate diel migrations commenced in the third calyptopis and first furcilia stages.
Alternatively the naupliar stages may have concentrated in the deep waters because conditions there were "preferred".

The concentration of the naupliar stages contrasts with the distributions of calyptopii and furcilia. In general, these later developmental stages were similar to the adults in that they were concentrated at intermediate depths, between 8 and 90 m, with relatively few or no occurrences in deeper waters. In view of the wide range of temperature and salinity encountered by calyptopii and furcilia in the transition waters which were present at intermediate depths, it seems improbable that the small differences in temperature and salinity between these and deeper waters were instrumental in preventing movements into the deeper waters. It seems more likely that other environmental factors in these waters were responsible for the general failure to collect calyptopii and furcilia (and adults) there.

The intrusion of outside water which influenced environmental conditions between 100 and 200 m in the inlet between April and June, 1961, may have provided barriers for the entry of the second and third calyptopis stages and furcilia into the deep waters. This possibility has been previously discussed with respect to the vertical distribution of adult specimens in April and June, 1961. In contrast, the naupliar stages were concentrated during these months in a depth range which closely coincided with the influence of the intruding waters (pp. 27 and 29).
Diel vertical migration was suggested in the third calyptopis stage, strongly indicated in the first and second furcilia stages and firmly established in the sixth furcilia stage; this corresponds with the progressive development in morphology and in particular, swimming appendages and compound eyes. The increased mobility also accorded with changes in distribution, but as already shown, not in all waters of the inlet -- i.e., specimens were "selecting" their environment.
**Thysanoessa spinifera**

The occurrences of *T. spinifera* relative to temperature and salinity in Indian Arm, from September 1960, to July-August 1961, are shown in the T-S-P diagram of Fig. 26. The enclosed area, indicating the total range of temperature (7.6 to 13.7°C) and salinity (23.7 to 27.15 °/oo) occupied by specimens, coincides with intermediate-depth (transition) and deep waters. Geographically, specimens occurred (Fig. 28b) from Station 15 to 2, between 8 and 180 m, during the above period.

Figures 83 - 97 are monthly T-S-P diagrams showing the occurrences and relative abundance of adult *T. spinifera* from January, 1960, to July-August, 1961; the associated geographical distributions are presented in Fig. 98 a-o. Adults were collected in all months except April, 1961 (Fig. 95, 98 m). Numbers ranged from 1 to 30.3 specimens/10m$^3$ (Table 3), but more often were between 1 and 6 specimens/10m$^3$. This was considerably less than that recorded for *E. pacifica* (p,39).

*Thysanoessa spinifera*, appears to undergo diel vertical migration, occurring above 90 m at night and as deep as 180 m during the day. Unlike *E. pacifica*, a complete developmental sequence of *T. spinifera* was not observed in Indian Arm. Collections were limited to adults, immature adults and a very few of the late furcilia stages.

The isolated collections of *T. spinifera* made in surface waters in February and March, 1960 (Figs. 84, 85 and 98 b,c) were from cool, low-salinity waters. In February the temperature was 6.6°C and the salinity 14.3 °/oo, the minimal values at which *T. spinifera* was collected (Table 5).
Thysanoessa spinifera was collected from waters of intermediate and greater depth in January, February and March, 1960 (Figs. 83 - 85) during the period of general decrease in temperature and increase in salinity associated with the major intrusion of outside waters which entered Indian Arm in February and March (pp. 18, 19, 29 and 30). There was an increase, amounting to 80%, in the abundance of specimens from January to February, 1960 (Fig. 98 a, b). This increase was most evident at Stations 12 and 15, and in the deeper waters at Stations 2, 6 and 9. Although the geographical occurrences of specimens were not as wide-spread in March (Fig. 98 c) as in February, there was an increase in relative abundance at intermediate depths in March which resulted in the total abundance being similar in the two months.

In April, 1960, specimens almost disappeared from Indian Arm (Figs. 86, 98 d); only two small collections were made at Stations 9 and 12. The T-S (Figs. 5 and 6) and T-S-P (Figs. 85 and 86) diagrams show that temperature increased and salinity decreased at intermediate depths from March to April, 1960, (e.g., at 30 m, values were around 7.7°C and 27.1 °/oo in March and 7.9°C and 26.4 °/oo in April) but it seems unlikely that the small changes which occurred were directly responsible for the large decrease in abundance of T. spinifera. The temperatures and salinities of the waters from which specimens were not collected in April were within the range occupied in preceding and subsequent months.

The T-S-P diagram for June, 1960 (Fig. 87), shows a
continuance of the trend of increasing temperature and decreasing salinity in waters at intermediate depths, and a large increase over April (approximately twenty-fold) in the abundance of specimens in the inlet. Whereas at 30 m no specimens were collected in water of 7.9°C and 26.4 °/oo in April (Fig. 86), numerous specimens were present at this depth in water of 9.5°C and 25.0 °/oo in June (Fig. 87).

Geographically, specimens occurred in June, 1960 (Fig. 98 e), at 30 and 60 m, between Stations 15 and 6; the maximum numbers, up to 30.3 specimens/10m³, were collected at 30 m at Stations 12, 9 and 6. The increase in abundance in June, combined with the occurrences being confined to "intermediate water" (Fig. 87), suggests that a population of T. spinifera from outside Indian Arm may have entered at the intermediate-depths. The substantial volumes of surface runoff leaving Indian Arm and a compensating inflow at intermediate levels in June (pp. 12 and 3) would provide the necessary means of transport for such an influx. The distributions of temperature and salinity for June did not indicate such an inflow (pp. 19 and 20) but the possibility remains that subsurface water from outside entered the inlet and, because temperatures and salinities were similar to those in Indian Arm, or perhaps because of mixing with resident water, it was not detected.

The decrease in abundance from June to July, 1960, was approximately 80%. In July (Fig. 98 f), specimens were evenly distributed between Stations 12 and 2, predominantly in waters between 60 and 90 m. The reduced numbers in waters above 60 m
coincides with increased temperatures in the shallower waters; e.g., the temperature at 30 m ranged from 9 to 10.5°C in June to 9.8 to 12.7°C in July, 1960 (Figs. 87 and 88). Subsequent occurrences in June and July-August, 1961 indicate, however, that even 12.7°C is within the range "tolerated" by *T. spinifera* in Indian Arm.

The trend of decreasing abundance continued into September and October, 1960. Accompanying the decrease was a shift of specimens towards the head of the inlet from Stations 15 to 2 in June and Stations 12 to 2 in July (Fig. 98 e, f) to between Stations 9 and 2 in September and Stations 6 and 2 in October, 1960 (Fig. 98 g, h).

In the period from June to October, 1960, the range of temperature between 30 and 180 m did not vary appreciably from month to month (Figs. 87-90). However, the T-S (Figs. 8-10) and T-S-P (Figs. 88-90) diagrams for July, September and October indicate an increase in salinity at intermediate depths. At 30 m the salinity was about 24.8 °/oo in July, 25.9°/oo in September and 26.5 °/oo in October (Figs. 88-90), but such an increase is within the range shown (Fig. 26) to be "tolerated" by *T. spinifera* in Indian Arm.

There was a five-fold increase in the abundance of *T. spinifera* by December, 1960, compared with October. This increase coincided with the period during which the temperature and salinity of transition water at intermediate depths and deep water "merged" (p.33) a process attributed to relatively cool, high-salinity water intruding from outside.

Geographically, *T. spinifera* was collected only at 90 m
at up-inlet stations in October, but in December it occurred from Station 12 to 2, between 30 and 180 m (Fig. 98 h, i). This change of distribution, coupled with the increase in abundance during December strongly indicates an influx of specimens accompanying the intrusion of outside waters in this month. The small collections at 150 and 180 m at Station 6 in December, 1960, represented one of the few occurrences of *T. spinifera* in waters deeper than 120 m in Indian Arm (Fig. 98 i). By January, 1961, there was a decrease in abundance by approximately 60 % (Fig. 92), accompanied by a shift of the remaining population toward the head of the inlet (Fig. 98 j) where occurrences were limited to Stations 9, 6 and 2 between 30 and 90 m. This decrease appears to ensue on or accompany mixing between the resident and the intruded water of December (pp. 23 and 24) and presumably results from a decreasing influence of this water.

The abundance of specimens in February, 1961 (Fig. 93) was unchanged from January, but geographically, occurrences were concentrated centrally in the inlet, at Station 9 (Fig. 98 k). The small collection at 150 m at Station 9 represents the fourth and last occurrence of specimens in waters below 120 m. An increase of approximately 20 % in abundance by March, 1961 (Fig. 94), was restricted to waters 15 to 90 m in depth (Fig. 98 l) over the length of the inlet. A small intrusion of outside water may have entered Indian Arm, between approximately 10 and 60 m (p.25) during this time.
No specimens were collected in April, 1961 (Figs. 95 and 98). Thus there was a large reduction between March and April of 1961 which was similar to that recorded for the same months of 1960. *Thysanoessa spinifera* re-appeared in collections from Indian Arm in June, 1961 (Fig. 96). The majority were present at 15 m at Station 15 (Fig. 98 n) near the mouth, suggesting specimens may have been entering from outside waters and between June and July-August, 1961 (Fig. 97) there was a ten-fold increase. The situation in these months resembles that of June, 1960, when the circulation pattern of surface outflow and subsurface inflow in Indian Arm provided a possible explanation for a large influx of specimens.

Discussion of *Thysanoessa spinifera*

*Thysanoessa spinifera* occurred over a relatively wide range of temperature and salinity in Indian Arm, but only occasionally below 120 m (February, September and December, 1960; and February, 1961) and rarely in surface water (February and March, 1960). From the T-S-P diagrams (Figs. 26, 83 - 97) it is apparent that from month to month the waters from about 90 to 200 m displayed only small ranges in temperature and salinity so that the near-absence of specimens below 120 m would not appear to result from changes in these properties.

By and large, therefore, occurrences were confined to intermediate depths and to upper levels of the deep waters. The near-absence of specimens in surface waters possibly can be attributed to the low salinities and extremes of temperature
there. This situation contrasts with the occurrences of *Euphausia pacifica* at the surface in low-salinity water during periods of seasonal cooling (p. 38). For the few collections of *T. spinifera* from surface waters (made at night in February and March, 1960 (Figs. 84, 85 and 98 b, c) the minimal temperature was 6.6°C, slightly higher than the 5.3°C for *E. pacifica*, and the minimal salinity was 14.3 °/oo, compared with 7.0 °/oo for *E. pacifica* (Table 5). It is possible therefore, that *T. spinifera* may be less "tolerant" to temperature and salinity extremes in surface waters than *E. pacifica*.

It seems that *T. spinifera* may have been recruited into Indian Arm during periods when outside waters were entering. In general, when temperatures and salinities indicated the presence or possible presence, of intruding waters (February, March and December, 1960, March and June, 1961) or when the circulation pattern was seasonally predisposed to subsurface inflows into the inlet because of high runoff of freshwater (June and July, 1960, June and July-August, 1961) there were associated increases in the abundance of *T. spinifera*. The geographical occurrences demonstrated that these increases were most apparent at stations in proximity to the mouth of the inlet (Fig. 98 b, c, e, i, n, o). During periods in which intruding waters were not observed or when their influence was decreasing, and when seasonal, subsurface inflows into the inlet were reduced (January, April, September and October, 1960, January, February and April, 1961), there was a corresponding,
general decrease in the abundance of *T. spinifera*, a decrease which initially was most apparent near the mouth. The abundance of specimens in January, February and March, 1960 (when a major intrusion of outside water is believed to have influenced conditions in Indian Arm between 10 and 200 m), compared with the few that were present in January, February and March, 1961 (during a period when relatively stable conditions prevailed), is a strong indication of the association between intruded water and the presence of *T. spinifera* in Indian Arm. Furthermore, the isolated occurrences of specimens at the surface were coincident with the large intrusion in February and March, 1960. In January, 1960, prior to this intrusion, and in subsequent months in which intruding waters were of less importance or were not observed, specimens were not observed in surface waters.

The T-S diagrams and the distributions of temperature and salinity have shown previously (pp. 16 and 17, 20 and 21, 26, 29 - 31) that the intrusions of outside waters in general produced lower temperatures and in particular, higher salinities in Indian Arm. This leads to the preliminary suggestion that the increases of *T. spinifera*, coincident with these intrusions, may be related therefore to the temperature and salinity of the intruding water. The annual and monthly T-S-P diagrams indicate, however, that the ranges of temperature and salinity of subsurface waters during periods when intrusions were not detected (e. g., between 10 and 200 m, from February to March, 1961, ranges were 7.77 - 8.0 °C and 25.2 - 27.0 °/oo -- Figs. 13 and 14) were not substantially different from those in
months in which there were intrusions (between 10 and 200 m from February to March, 1960, ranges were 7.1 to 8.2°C and 26.0 to 27.3 °oo -- Figs. 4 and 5). In either case the temperatures and salinities of the subsurface waters were within the ranges over which specimens were collected (Fig. 26), i.e. within the limits "tolerated".

The evidence presented suggests that the presence or absence, and abundance of T. spinifera in intermediate-depth and deep waters in Indian Arm is associated with the concurrent presence or absence of intruding waters and is not dependent on the temperature or salinity of water, either within the inlet or entering. Once this species is within the inlet, it is necessary to postulate that some undetermined property or properties, present in the intruding water and/or present in the resident water, may control its presence and abundance.

Thyanoessa spinifera is probably an expatriate species (Ekman, 1953) at or near the limit of its range of distribution in Indian Arm. There are three reasons. Firstly, T. spinifera occurred at approximately 10% of the numbers of E. pacifica and on occasion was not collected (e.g., in April, 1961); secondly, the greater part of the developmental sequence of this species was not collected in the inlet, suggesting that it does not reproduce there; and thirdly, specimens appeared to be recruited into the inlet along with intrusions of outside water. Because T. spinifera appears to be an expatriate species it can be regarded as a reasonably good biological
indicator (a plankton indicator species) of oceanographic events in Indian Arm, particularly the detection by means of its presence of outside waters entering the inlet.
**Thysanoessa longipes**

The occurrences of adults of *Thysanoessa longipes* relative to temperatures and salinities in Indian Arm are shown in the T-S-P diagram for the period from September, 1960, to July-August, 1961, (Fig. 27). The two areas enclosed by solid lines indicate the total ranges of temperature (7.6 to 10.3°C) and salinity (24.5 to 27.15 °/oo) from which specimens were collected (Table 5). Of these two areas the small one is of a single collection from 30 m in June, 1961; the larger one represents temperature-salinity conditions of deeper waters, from which maximum numbers were collected. Geographically (Fig. 28c), *T. longipes* occurred between Station 15 and 2 from depths between 30 and 90 m to 200 m; specimens were not collected from surface water and only occasionally from waters at intermediate depths.

Figures 99-111 are the monthly T-S-P diagrams for *T. longipes*, from January, 1960, to July-August, 1961 and Fig. 112 a-o presents the geographical occurrences for these months. *Thysanoessa longipes* was collected in Indian Arm during January, February and from April to December, 1960, and from April to July-August, 1961; specimens were not collected during March, 1960, nor during January, February and March, 1961. Numbers ranged from 1 to 5/10m\(^3\) (Table 3), but more usually were 1 to 3/10m\(^3\). The occurrences therefore were sporadic and abundance very low in comparison with *Euphausia pacifica*. Collections of *T. longipes* (unlike *E. pacifica* and *T. spinifera*) did not
suggest that diel vertical migration occurred. Juveniles (immature adults) and adults of *T. longipes* were collected, but not earlier developmental stages, which was similar to the occurrences of *T. spinifera*, but differed considerably from the collections of all stages of *E. pacifica*.

The T-S-P diagrams for January, February and March, 1960 (Figs. 99 - 101) show the relationship between temperature and salinity and the occurrences of *T. longipes* during the period of the major intrusion of outside water which influenced waters between 10 and 200 m in Indian Arm (pp. 18 29 and 30) The geographical occurrences (Fig. 112 a, b, c) show that specimens were collected at 60, 90 and 120 m at Station 6 in January, at 60 m at Station 9 in February and were absent at all stations in March, 1960. This suggests that *T. longipes* did not accompany the entry of outside waters in February and March, as did *T. spinifera* (pp. 59 and 64).

*Thysanoessa longipes* reappeared in one sample from 60 m in April, 1960 at Station 2 (Figs. 102, 112 d). By June, 1960 (Fig. 103), specimens had substantially increased in abundance and were extending up-inlet at 50-60 m from Station 23 to Station 9 (Fig. 112 e). The small collection at 20 m at Station 23, in waters of 10.3°C and 25.0 °/oo represents the minimum depth at which *T. longipes* was observed.

The circulation pattern during this period (pp. 12 and 13) would provide the necessary means for transport of *T.*
**T. longipes** into Indian Arm, a situation comparable to that reported for *T. spinifera* (p. 60) for June, 1960. By July, 1960 (Figs. 104, 112 f), **T. longipes** was more abundant than in June and was centered in two pockets, one up-inlet at Stations 6 and 2 and the other at Stations 15 and 12. This distribution could have resulted from a movement towards the head of the inlet of those specimens that had entered in June, combined with a continuing entry of specimens into the inlet.

In September and October, 1960, **T. longipes** was reduced to single collections of specimens (Figs. 105 and 106) which were deep and towards the head of the inlet (Fig. 112 g, h). The T-S and T-S-P diagrams for September (Figs. 9 and 105) indicate that the temperatures and salinities between 30 and 200 m were little changed from July (Figs. 8 and 104), and thus the decrease in specimens from July to September does not appear to be related to these factors. The low numbers in September and October do correspond, however, with the seasonal decrease in surface runoff and thus a low subsurface inflow of outside water (p. 13).

The T-S-P diagram for December, 1960 (Fig. 107) shows a large increase in the abundance of **T. longipes** over October. This increase (as with **T. spinifera** (p. 61)) was associated with the intrusion which influenced water between 10 and 75 m (pp. 22, 23 and 30). Geographically, specimens were collected during December in the deeper water (60-180 m) at Stations 12, 9 and 6 (Fig. 112 i). The small collections at 150 and 200 m
represent the only occurrences of *T. longipes* in waters below 120 m.

By January, 1961, despite the influx of *T. longipes* in December, no specimens were collected (Fig. 108, 112 j). This situation continued during February and March, 1961 (Fig. 112 k, l). The absence of specimens between January and March was associated with a decreasing influence of the intrusion of December (pp. 24 and 30) and relatively stable conditions of temperature and salinity (p. 25).

One small collection was made at 50 m at Station 15 in April 1961 (Fig. 112 m), but by June, specimens occurred at Station 15, 12 and 9, between 30 and 120 m (Fig. 112 n). This increase coincided with an inflow of outside water at intermediate and greater depths, in part compensating for the maximal outflow of runoff at the surface (pp. 12 and 13) and in part resulting from an intrusion which influenced the inlet waters between 100 and 200 m (pp. 27, 29 and 33). The proximity of the occurrences of *T. longipes* to the mouth of the inlet (Stations 15 and 12) suggests that the specimens accompanied these outside waters. By July-August, 1961, there had been a substantial decrease in the abundance of *T. longipes* and an up-inlet shift in the distribution of specimens (Figs. 111, 112 o), probably resulting from the decreasing influence of outside waters during July-August (p. 27).
Discussion of Thysanoessa longipes

Waters intruding into Indian Arm via Burrard Inlet, and presumably originating in the Strait of Georgia, appear to be important in transporting *T. longipes* into the inlet. If so, they must be considered in relation to the occurrences and distribution of this species. During periods in which the temperatures and salinities indicated intrusions of outside water (e.g., December, 1960 and June, 1961), and in periods in which the circulation pattern was seasonally predisposed to subsurface inflows of outside waters (e.g., June and July, 1960 and June, 1961), there was a corresponding increase in the abundance of *T. longipes*, particularly at stations located towards the mouth of the inlet. In general, also, during periods in which the influence of intruded waters was decreasing, the species was rapidly reduced in numbers or was not observed in the inlet (e.g., April, September and October, 1960, January to April and July-August, 1961).

Even though a primary pre-requisite for the entry of *T. longipes* into Indian Arm was the corresponding entry of outside waters, there was one notable exception, the near-absence of specimens during the major intrusion of February and March, 1960. A second and obvious pre-requisite for the entry of *T. longipes* into Indian Arm is its presence in waters adjacent to the inlet. A comparison of collections of *T. longipes* obtained from cruises in Indian Arm and extended into nearly Strait of Georgia in March and July-
August, 1961, bears on this aspect. In vertical hauls from 0-240 m in central and southern locations in the Strait of Georgia the number of specimens collected ranged from nil to 6 in March, and from 10 to 63 in July-August. Perhaps a reflection of this was that specimens were not collected in Indian Arm during March but were present in small numbers in July-August, 1961. Although the periods under discussion are not the same (March, 1960; March and July-August, 1961) the absence of specimens in Indian Arm during March, 1960, may be attributable to an absence of this species in waters adjacent to Indian Arm, similar to the case in March, 1961.

Thysanoessa longipes usually occurred between 60 and 120 m, in a relatively narrow range of temperature and salinity. Exceptions were the collections made at 20-30 m (June and July, 1960, and June, 1961) and at 150 and 200 m in December, 1960. Outside waters are believed to have entered Indian Arm during these months.

On the basis of the field study, the scarcity of specimens in waters above 60 m may be related to the extremes of temperature and salinity in the upper waters. In that T. longipes was usually absent above 60 m indicates it was less "tolerant" to these extremes than either T. spinifera of E. pacifica (Table 5).

Thysanoessa longipes, as with T. spinifera and E. pacifica, was infrequently collected below 120 m. Exceptions were the collections at 150 and 200 m in December, 1960, when an intrusion of outside waters entered Indian Arm at depths
between 10 and 75 m. The T-S-P diagrams show that on a month by month basis the fluctuations in the temperature and salinity of waters between 60 and 200 m in the inlet were relatively slight over the two-year period, and as such would not appear to account for the fluctuations of *T. longipes*. The above points indicate that the various influxes of specimens and their brief survival in Indian Arm may be related to environmental conditions other than temperature and salinity.

Because, firstly no specimens were collected over several months and when present they were in low abundance (approximately 2% that of the resident species, *E. pacifica*), secondly, the absence of a developmental sequence of the species in the inlet, and thirdly, the association of specimens with the entry of outside waters, *T. longipes* is regarded as an expatriate species in Indian Arm and probably at or near the limits of its distributional range. As such this species, when present, is useful as a biological indicator, particularly of those outside waters which may have entered recently, or be entering the inlet.
Thysanoessa raschii

The occurrences of adults of *Thysanoessa raschii* are shown in relation to temperatures and salinities in Indian Arm, from September, 1960, to July-August, 1961 (Fig. 27). In this T-S-P diagram, four areas enclosed by dotted lines indicate the total ranges of temperature (8.8 to 11.7 °C) and salinity (25.7 to 26.8 °/oo) in waters of intermediate depth from which specimens were collected. The developmental stages of *T. raschii* were not observed in Indian Arm. Geographically (Fig. 28 d) *T. raschii* was collected at Station 15 and 12, between 30 and 50 m, and at Stations 6 and 2 at 60 m. Specimens were not collected above 30 m, or deeper than 60 m.

Figures 113 - 117 are monthly T-S-P diagrams, with accompanying inserts of the geographical distribution of specimens, showing the occurrences and relative abundance of *T. raschii* in Indian Arm between January, 1960, and July-August, 1961. Numbers ranged from 1 to 6/10 m³ (Table 3), but more usually were 1 to 2/10 m³. This is the lowest abundance among the four species of euphausiid collected; *T. raschii* also was the most sporadic in its occurrences. The highest numbers (4 to 6/10 m³) were present towards the mouth of the inlet in July and September, 1960, and in July-August, 1961 (Figs. 113, 114 and 117). Other small, isolated collections were made at Station 2 in October and at Station 6 in December, 1960 (Figs. 115 and 116); specimens were not observed
in the inlet from January to June of 1960 and 1961. From this it appears that \textit{T. raschii} entered from outside waters in the summer and early autumn, shifted towards the head of the inlet and decreased in numbers in late autumn and early winter, and was absent for the remaining winter months and spring.

Discussion of \textit{Thysanoessa raschii}

Substantial movements of water, such as intrusions of outside water, were not detected in the inlet during July to September of 1960 and July-August, 1961, when \textit{T. raschii} was most abundant. Furthermore, seasonal runoff at the surface and compensating inflows of subsurface water (pp. 12 and 13) were decreasing in July and were minimal in August and September. Thus the means of transport, shown to be associated with the entry of \textit{T. spinifera} (pp. 60 and 64) and \textit{T. longipes} (p. 68) into Indian Arm, either were not apparent or were reduced for the periods during which \textit{T. raschii} entered.

The oceanographic conditions, and the occurrences of \textit{T. raschii}, in waters adjacent to Indian Arm, may provide some explanation for the occurrences of this species within the inlet. Waldichuck (1957) reported that a warm, high-salinity water at intermediate depths intrudes into the Strait of Georgia from Juan de Fuca Strait in late summer (August to September), and by late autumn has formed intermediate and deep waters with different characteristics from those which occur in winter (Waldichuck, 1957). There are
indications, too that *T. raschii* is most abundant in the Strait of Georgia during the summer months. For example, in 1965, in a series of collections in the southern Strait of Georgia, the average number/tow was 24.7 in March, 4.8 in April and 46.2 in July (personal communication, Pacific Oceanographic Group). Similarly, in 1962, in collections from Saanich Inlet, an inlet adjacent to the Strait of Georgia, the numbers/plankton tow averaged 34 specimens in January, 2.3 in May and 1,562 in July (unpublished data, Institute of Oceanography, University of B. C.).

Over the two years of the present study in Indian Arm, approximately 85% of the specimens were collected during July, August and September. This coincides in a general way with the increased abundance of specimens in outside waters in July and, in turn, with the summer intrusion of "oceanic" water into the Strait of Georgia. That is, presence of *T. raschii* in Indian Arm during the summer and absence during the winter accords with the seasonal changes in the water masses of the Strait of Georgia - Juan de Fuca Strait system. The plankton data, while sparse, suggests that *T. raschii*, a species inhabiting oceanic-coastal mixed waters, probably accompanied the summer intrusion of "oceanic" water into the Strait of Georgia, and thence into Indian Arm. On the other hand, the decrease to apparent absence of specimens in Indian Arm in the winter and spring coincides with a decrease in the influence of the "oceanic" intrusion and a return to winter conditions in the Strait of Georgia.
The occurrences of *T. raschii* were in a narrow range of depth, between 30 and 60 m in Indian Arm. This may be an indication that the specimens remained within the confines of small and undetected volumes of outside water entering at particular density levels. The integrity of this water eventually would be destroyed through mixing with resident water in Indian Arm.

The failure to collect *T. raschii* in waters above 30 m may be related to the extremes of temperature and salinity in the upper waters of Indian Arm. In particular, the diluted surface waters during periods of runoff would subject specimens to salinities considerably lower than those encountered in outside waters. The maximum depth at which specimens occurred (60 m) in Indian Arm, however, does not appear to be related to temperature and salinity. The waters below 60 m are characterized by relatively low temperatures and high salinities and have considerably less variation in temperature and salinity than the waters (30 to 60 m) in which *T. raschii* was collected. Furthermore, the temperature and salinity of deeper waters would be closer to those of outside waters from which specimens originated. Thus, with regard to temperature and salinity, it would appear that the waters below 60 m were as suitable as the waters between 30 and 60 m, for an oceanic-coastal species such as *T. raschii*.

The most notable feature was the presence of *T. raschii* in Indian Arm during July and September, 1960 and July-August, 1961 and its rarity or absence in all other months. Neither
temperature nor salinity appeared to be a causative factor in these fluctuations. For example, from June (no specimens collected) to July (4 specimens/10m$^3$) and from September (as high as 6 specimens/10m$^3$) to October (one specimen/10m$^3$) the ranges in these properties (Figs. 7-10) were well within the "range tolerated" by $T$. raschii as shown in the annual T-S-P diagram. It appears, therefore, that the sporadic occurrences of $T$. raschii were not associated with changes in temperature and salinity. It is suggested that the occurrences between July and December and their not being collected during January to June were related to other undetermined environmental conditions.

On the basis of the rare occurrences and limited distribution of specimens in Indian Arm, the absence of a developmental sequence of the species in the inlet, and the suggestions that the presence of specimens is associated with oceanographic changes in the Strait of Georgia, $T$. raschii is regarded as an expatriate species in Indian Arm and probably at or near the limits of its distributional range in the inlet. As with $T$. spinifera and $T$. longipes this species may be potentially useful as a biological indicator.
V. VERTICAL MIGRATION OF EUPHAUSIA PACIFICA
IN RELATION TO TEMPERATURE AND SALINITY:
PRELIMINARY OBSERVATIONS FROM INDIAN ARM

Daily changes in vertical distribution of planktonic organisms result from vertical migrations of specimens, by which they ascend into the upper waters at night and return to the deeper waters during daylight. It is, therefore, only during the night that migrating animals could encounter the regions of maximum temperature and salinity change (i.e., the thermocline and halocline) characteristic of upper waters in Indian Arm (p. 33). Field observations provided the first indications that temperature and salinity may exert important effects on the vertical migration of Euphausia pacifica in Indian Arm.

Figures 118, 119 and 120 consist of temperature-depth and salinity-depth curves in relation to the numbers of E. pacifica collected during selected months. Collections were obtained from 0, 8, 15, 30 and 45 m in upper waters and from 60, 75, 90, 120, 150 and 180 m. In February, 1961 (Fig. 118) only a few specimens (2/10m³) were collected at the surface. A strong halocline (6.8 - 25.4 °/oo, from 0 to 5 m) was present, resulting in a mean salinity gradient of 3.7 °/oo/m in the upper waters. In March, 1961 (Fig. 119) an increased collection (12/10m³) was made at the surface at night, associated with a moderate halocline (19.5 - 26.0 °/oo, from 0 to 10 m) and a weak thermocline (7.3 - 8.4°C, from
0 to 10 m). In June, 1961 (Fig. 120) *E. pacifica* was not collected in surface waters. At this time there was a strong halocline (12.7 - 23.2 °/oo, from 0 to 5 m) and a pronounced thermocline (19.2 - 12.3°C, from 0 to 5 m) resulting in a mean temperature gradient of 1.4°C/m in the upper waters. Additionally, (Figs. 118, 119 and 120) the maximum concentration of *E. pacifica* in each of February, March and June, 1961 (29, 30 and 78 animals/10m³, respectively) occurred immediately below the regions of maximum temperature and salinity change, during the night tows.

It appears therefore, that the thermocline and halocline restricted upward migration. Few specimens were able to reach the surface; they appear to have concentrated at, or immediately below, the thermocline and/or halocline.
PART B:
LABORATORY PROGRAMME

The objects of the laboratory programme were to determine if the variations in euphausiid distributions in Indian Arm were the result of reactions to ranges of temperature, salinity and temperature-salinity combinations, or to some other property or properties acting within the temperature-salinity ranges of the waters.

The procedures were directed to assessing the following:

1. the effects of separate temperature and salinity structures on the vertical migration of specimens,
2. the effects of combined temperature and salinity structures on the vertical migration of specimens, a condition comparable to that found in the field,
3. the effects of "home" and "foreign" waters, where temperature and salinity were not limiting, on the vertical migration of specimens, and
4. the effects of "home" and "foreign" waters (where temperature and salinity variations were eliminated) on the survival of specimens.

*Euphausia pacifica* is the dominant euphausiid in Indian Arm and the above tests mainly concerned the adults of this species. Other tests were made to determine the effects of temperature on the vertical migration of *Thysanoessa spinifera* and of salinity on the vertical
migration of *Thysanoessa spinifera* and *Thysanoessa longipes*. Tests on the developmental stages of *E. pacifica* were limited to the effects of salinity on the vertical migration of furcilia.
VI. MATERIALS AND METHODS

COLLECTIONS OF SPECIMENS AND WATER

Between April, 1964, and April, 1966, live specimens and seawater were collected from one station in each of Indian Arm, Strait of Georgia and Juan de Fuca Strait (Fig. 1 b7 A, C, D); seawater also was collected once from Malaspina Strait, (Fig. 1 b-B) in the northeast Strait of Georgia.

To compare with results of the preceding study of the distribution of euphausiids in Indian Arm the greater part of the laboratory study was concerned with specimens from the inlet. The collections were made at a central location (Station 9 - Fig. 1 a) in the inlet.

Vertical plankton hauls were made with a one-metre ring net from 150 m to the surface at the three selected locations in Indian Arm, Strait of Georgia and Juan de Fuca Strait. Precautions were taken to minimize the possibility of mechanical and/or physiological damage to specimens. A towing speed of approximately two knots (1 m/sec) was selected as being slow enough to limit mechanical damage to specimens and yet to catch the faster-moving adults. The short, wide standard metal bucket, was replaced by one of 7.5 cm internal diameter and 62 cm long, of poly-vinyl-chloride. This should further reduce the mechanical damage by reducing turbulent action within the bucket while towing, and the possibility of physiological damage by reducing the amount of mixing within the bucket during the ascent from high-
salinity to low-salinity waters.

The latter point was substantiated by analyses of salinity following a tow from 150 m to the surface in Indian Arm during June, 1964, a period when warming and maximum dilution of surface water may be expected (pp.12 and 13). The salinity of water in the bucket was 23.17 °/oo compared with 26.96 °/oo at 150 m and 10.8 °/oo at the surface; in the Strait of Georgia in July, 1964, the salinity in the bucket was 27.71 °/oo compared with 29.96 °/oo at 150 m and 17.8 °/oo at the surface. Studies both in the field and the laboratory indicated that salinities of 23.17 and 27.17 °/oo were tolerable to adult *E. pacifica*. In any event, specimens were immediately transferred with a dip-tube from the bucket into two-litre isothermal (vacuum) flasks containing seawater collected at the location and approximate depth from which specimens were collected. For example, in Indian Arm the majority of specimens of *E. pacifica* during daylight were located between approximately 60 and 90 m. Specimens, therefore, were placed in seawater from 75 m.

Seawater was collected with a Van Dorn Water Sampler (16 litre) from 75 m in Indian Arm, 100 m in the Strait of Georgia, 150 m in Juan de Fuca Strait and 50 m in Malaspina Strait. The oxygen content was 2-4 ml/l at these locations and depths (Institute of Oceanography, University of British Columbia, Data Reports, 1960, 1961, 1964) which was not limiting to survival. On ship-board the seawater was filtered
through nylon bolting cloth with a mesh of 0.07 mm and put in 5-gal. polyethylene carboys and a series of isothermal flasks.

Specimens and seawater from Indian Arm were taken to the laboratory within three to four hours and in up to six hours from the Strait of Georgia and Juan de Fuca Strait. The number of specimens was limited to 10 - 15/2 litres in the isothermal flasks. The temperature of the seawater in these flasks fluctuated little during transit and remained within the range occupied by specimens collected in the field.

In the laboratory, the seawater was filtered through a millipore filter of pore size 0.45 μ and placed in 4-litre beakers, or in 5-gal. carboys and stored at 10° C. Ten specimens were transferred with a dip-tube from the isothermal flasks into each of the beakers. These were placed in an incubator at a temperature (10° C) similar to that (8.3 - 9.0°C) in the field at the depth of collection of specimens, and in complete darkness. The beakers were loosely covered to prevent excessive evaporation.

TERMS USED IN DESCRIBING EXPERIMENTAL OBSERVATIONS

The various test-conditions of temperature and salinity in the experimental column of water are conveniently described in terms of structure and mean gradient. Structure is defined as gradations in a property of seawater (e.g., temperature or salinity) with respect to depth in the experimental vessel. Mean gradient refers to the average change in value of any property of seawater per unit of depth over
a given vertical distance. In the present study all gradients are vertical, with temperature increasing and salinity decreasing towards the surface in the experimental column. In the various temperature structures, however, the increase was not linear in relation to depth and calculation of a mean temperature gradient was based not on the full range of depth, but only on that part of the particular temperature structure over which there was a decrease in the migration of euphausiids. The increase in salinity towards the surface was generally linear with depth, but increased in steps of either 1.3 or 3.0 °/oo from layer to layer in a given structure. The mean salinity gradient (the average change per unit of depth) was calculated from the total range and depth.

The terms limiting temperature and limiting salinity refer to those highest values of temperature or lowest values of salinity beyond which no migrations occurred, in a particular set of test conditions in the laboratory.

There were several sources of seawater, namely, Indian Arm, Strait of Georgia, Juan de Fuca Strait and Malaspina Strait, which were used in the tests of survival of Euphausia pacifica in the laboratory. Seawater collected at the same location as experimental organisms is referred to as "home" water; that collected at a different location, as "foreign" water.
VERTICAL MIGRATION IN THE LABORATORY

The principal apparatus used for tests (Figs. 121 and 122) consisted of an inner, cylindrical column within an outer jacket, both of clear, colourless perspex; measurements were 57 cm high by 24.5 cm diameter (outer jacket) and 19.5 cm diameter (inner column). The capacity of the inner cylinder (the "experimental column" when containing seawater and specimens) was approximately 17.5 litres. A continuous flow of freshwater was maintained within the outer jacket; its temperature was 9 - 10°C. The purpose of this flow was to cool the water of the experimental column (and entry tube - see below) approximately to the temperature usual in the field, and to maintain the temperature as nearly constant as possible in the column and thus reduce the possibility of temperature changes affecting the vertical migration of specimens. In practice the temperature range did not exceed 1.2°C between top and bottom of the experimental column which, for convenience, is referred to as the condition of "constant temperature".

A series of taps (2.5cm apart - Fig.122) permanently inserted through the outer jacket and into the experimental column, enabled water samples to be withdrawn for salinity determinations. An entry tube, 2.5 cm in diameter, was used to introduce specimens into the experimental column.

Lance (1962) used a 40-W lamp to induce decapod larvae and adult copepods to swim upward in columns of seawater. Preliminary tests in the present study showed
that euphausiids would swim toward artificial illumination; a 100-W lamp, placed 20 cm above the experimental vessel, was found to be more effective than lower light intensities in inducing specimens to migrate upwards. The light intensity used (100-W) throughout the temperature and salinity tests was not intended to simulate conditions in the field, but rather to provide maximal inducement for specimens to migrate vertically. A sheet of perspex, 0.5 cm thick, was placed on top of the vessel as a heat screen. The entire apparatus was placed in an enclosure, consisting of plywood painted flat black, which prevented extraneous light from entering through the back or sides of the vessel.

Migration in salinity structures

In order to obtain a salinity structure (at nearly constant temperature) layers of water of decreasing salinity were successively introduced into the inner cylinder. The result was to form a series in which each layer was approximately 1.3 °/oo lower in salinity than the previous one, with the lowest salinity at the surface. Water for each layer was siphoned slowly from a container onto the centre of a free-floating plywood disc, 18 cm in diameter, whence it flowed outwards and over the preceding layer. The disc eliminated mixing as layers were being formed. A slot in the disc enabled the entry tube to be fitted as necessary (Figs. 121 and 122) At completion of the layering, the disc was removed from the surface of the column. Alternate layers, dyed with non-toxic food colouring(Fig.123),
demonstrated that the layers could be maintained for up to 24 hours under conditions of constant temperature.

The water for each layer was prepared by diluting the seawater collected with the specimens with distilled water to a pre-determined salinity. It was aerated for 10 min and the pH determined using a Beckman pH Meter. The pH of undiluted seawater from the various locations ranged from 7.5 to 7.8; that of the distilled water was around 6.0. The dilution of seawater, however, could not have affected migration tests by changing the pH as the buffering action of seawater prevented large reductions in pH. For example, the minimum pH observed was 7.3, for a mixture of 8 parts of distilled water and 2 parts of seawater from Indian Arm. Samples of the various layers were taken for analysis prior to their introduction into the column and were withdrawn from the column (by means of the taps) on completing a test. Salinity determinations were made with an inductively-coupled salinometer.

The lower-end of the entry tube was inserted into the bottom, high-salinity layer, at approximately 52 cm, prior to adding the subsequent layers. Thus the water within the entry tube was continuous with that in the bottom layer and of the same salinity and temperature (and similar to the temperature and salinity in the field at the depth of collection and the same as those at which specimens were maintained in the incubator). The temperature in the experimental column and entry tube was maintained by the cooling jacket within a range of about 1.2°C from bottom to top, in the
several tests.

Specimens were transferred with a dip-tube from the incubator to the entry tube and the majority guided into the bottom layer in the experimental column. The over-head light was turned on and the specimens were observed over one hour, migrating from the bottom water into the waters of decreasing salinity towards the surface. In each test the number of migrations which stopped in each of the salinity layers was counted and then expressed as a percentage of the total number of migrations observed in the test. The specimens in the entry tube in which temperature and salinity as ecological factors had been eliminated provided a control, subject to the same conditions of lighting as the experimental column. Differences between the vertical migrations in the controlled conditions and in the experimental column could be attributed to effects of the salinity changes in the latter.

Migration in temperature structures

For the tests of vertical migration in temperature structures of constant salinity (approximately 26.7 °/oo), the layers of water of increasing temperature and the specimens were introduced into the experimental column in a manner similar to that used for the salinity tests. The outer cooling jacket was not used. The temperature of the bottom layer of water in the experimental column, into which specimens first entered, was similar (9-10°C) to that at the depth at which euphausiids were collected.
and were maintained in the laboratory. The subsequent layers of water were heated prior to being added to the experimental column. Temperatures of the layers were obtained using a thermistor probe prior to and immediately after being added, and at completion of a test. Some heat transfer occurred between the layers of water in the column and therefore it was not possible to accurately predetermine a given temperature structure; temperature increased towards the surface, but the increase was not linear with depth. To reduce the influence of transfer of heat during the tests, these were limited to a duration of 30 minutes.

The number of migrations which stopped at the various temperatures in a given structure was expressed as a percentage of the total number of migrations observed in the particular test.

A control was established in a vessel separate from the experimental column. This vessel contained undiluted seawater of approximately 26.7 °/oo from Indian Arm and was maintained at a temperature as nearly constant as possible (the vertical range approximated a maximum of 1.2 °C from bottom to top). This sort of control differed from the "inbuilt" control (the entry tube) used in the salinity tests.

The technique, however, effectively eliminated temperature and salinity as ecological factors in the control which was also subjected to the same conditions of lighting as the experimental column. A comparison of
vertical migration in the control with that in the experimental vessel would indicate whether the temperature structure was affecting the migration.

Migration in combined temperature and salinity structures

In the combined temperature and salinity structures, layers of water of increasing temperature and decreasing salinity were introduced into the experimental column in a manner similar to that used for the individual temperature and salinity tests. Two tests were set up in which the mean salinity gradients were 0.39 and 0.42 °/oo/cm and the mean temperature tradients were 0.40 and 0.58 °/cm, respectively. While these gradients were designed to simulate halocline and thermocline conditions in Indian Arm, it is important to note that they were considerably steeper than the maximal gradients, 3.7°/oo/m (0.04°/oo/cm) and 1.4 °/m (0.01 °/cm), discussed for the field (p. 79). Each test was of 20 specimens. Records were kept of the total number of migrations in the course of one hour, the number of migrations which stopped at intermediate levels in the experimental column, and of the temperature and salinity at which specimens stopped. The number migrating to particular temperature/salinity ranges was then expressed as a percentage of the total number of migrations. Data obtained from previous tests in a salinity structure of nearly constant temperature (0.08 °/cm between 12 and 3 cm in the experimental column) and a temperature structure with constant salinity (26.7 °/oo) constituted controls.
Migration in "home" and "foreign" waters

In the tests of the vertical migration of *E. pacifica* in "home" and "foreign" waters differences in temperature and salinity between the waters were kept to a minimum in order that possible effects on migration of other factors in the water could be observed.

Specimens and seawater from Indian Arm and Juan de Fuca Strait were used in two series of tests. Each series consisted of three columns of water (Figs. 139 and 140): (a), a control of "home" water of constant salinity; (b), a column of "home" water with a small salinity decrease separating lower and upper regions; and (c), a column in which "home" water in the lower part was separated from "foreign" water in the upper part by a small salinity decrease, sufficient to provide stability and prevent all but minimal mixing. The range of salinities in columns b and c of the two series was 26.76 to 25.12 °/oo. The salinity in the controls was 26.76 and 26.06 °/00. Previous migration tests in salinity structures showed that unrestricted migration of *E. pacifica* occurred in the salinities used. Temperatures in the columns were similar and the vertical range approximated a maximum of 1.2 C° from bottom to top.

Fifteen adult *E. pacifica* were tested for 20 minutes in each of the three light intensities used in each column of a series of tests. The columns for the two series were lighted in turn by 100-W and 6-W lamps placed 20 cm above
the surface, and in indirect room illumination. The latter two intensities were additional to the single intensity (100-W) used in the temperature and salinity structures. The number of migrations and the positions in the columns to which specimens migrated were recorded.

The above procedures provided comparable conditions of temperature and lighting in the "home" water in columns a and b, but a small salinity decrease in column b, separating lower and upper parts. Any effects on the migrations in column b could be attributable to this salinity decrease. For columns b and c, there were comparable conditions of temperature, lighting and change of salinity, but in column c "home" water in the lower part was separated from "foreign" in the upper part. Differences in the migrations between column b and c could be attributable therefore to factors associated with "home" and "foreign" waters.

SURVIVAL IN THE LABORATORY

The survival tests were limited to one species, E. pacifica. In general the preliminary procedures for these tests was reported on p.85. Distilled water was used as a diluent where adjustment of salinity was required. The distillation vessel was a Barnstead Water Still; all surfaces coming in contact with water and vapours are heavily clad with pure block tin. In the series of tests where dilution was required, tests were included which would indicate the effects, if any, of distilled water. Prior to the introduction of specimens, the water in the 4-litre
beakers was aerated for 15 min and then checked for pH. Specimens were removed from the storage beakers with a dip-tube, released carefully on to a nylon mesh so as to remove water, and then put into the test beakers. The removal of water was particularly important when specimens were being transferred from "home" into "foreign" waters.

Specimens were fed a culture of *Isochrysis galbana* Parke, a green flagellate. The culture was suspended, centrifuged and resuspended twice in the same water as that in which euphausiids were being tested in order to remove as much of the culture medium as possible.

Survival in diluted seawater

Two tests were carried out on the survival of *E. pacifica* from Indian Arm in dilutions of water from Indian Arm. Specimens were transferred at two-day intervals into progressively more diluted waters held in 4-litre beakers; the transfers were continued until there was no survival. Survival in these tests was compared with that in accompanying controls containing undiluted seawater (26.9 °/oo) from Indian Arm. In the first test the total range of salinity in the series of test beakers was 26.9 to 16.0 °/oo over 8 days, and in the second, 26.9 to 13.5 °/oo over 12 days. The number of specimens was 10 in the first test and in the control and 17 in the second test and control. Food consisted of 1 cc of *Isochrysis* /2 days mixed into the water of the control and test beakers. Data recorded were the % of speci-
mens which survived each transfer to diluted water and the % surviving at each time in the control.

Observations from the above tests indicated that dilution which most affected survival not only by the actual percentage that died but also by means of the "rate" at which specimens died. These data were prerequisite to subsequent tests of the survival of *E. pacifica* in "home" and "foreign" waters whenever it was necessary to adjust the salinities to similar values by dilution.

Survival in "home" and "foreign" waters

In the survival tests of *E. pacifica* in "home" and "foreign" waters, three populations of specimens (p. 83) and seawater from four locations (p. 84) were used. Analyses of water samples collected throughout the study from the selected depths indicated salinity values ranging from 26.4 to 26.9 °/oo for Indian Arm, 29.96 to 30.8 °/oo for the Strait of Georgia, 32.8 to 34.08 °/oo for Juan de Fuca Strait and 29.6 °/oo for Malaspina Strait. The salinities were adjusted to a total range of 26.3 - 26.9 °/oo, which were well within the range inhabited by *E. pacifica* in Indian Arm and in which specimens survived during the tests using water from Indian Arm.

Special tests were run on two occasions in which undiluted (33.1 and 32.8 °/oo) and diluted seawaters (26.9 °/oo) from Juan de Fuca Strait were used. In the first, the survival of specimens from Indian Arm at a salinity above
those encountered in Indian Arm was tested; and in the second, the tests were to determine whether there were differences in survival of specimens from Juan de Fuca Strait in undiluted and diluted Juan de Fuca waters (p. 94).

For the tests of "home" and "foreign" waters the range of pH, approximately 7.5 - 7.8, of undiluted seawater from the various locations was considered to be negligible and no adjustments were made. In waters where salinity was decreased with distilled water, the maximum dilution used was approximately 22%. Determination of pH indicated that even at this dilution the distilled water was sufficiently buffered by the accompanying seawater (p. 89) and consequently no adjustments were made.

The oxygen concentration in all waters ranged between 2 - 4 ml/litre and was not limiting to survival (p. 84). All waters were aerated prior to the survival tests in the laboratory.

The initial concentration of specimens in the tests was 10/4-litre beaker (an exception to this was 20/4 litres in two tests — Fig. 144b). The beakers were loosely covered and kept at a temperature of 10°C; 5 cc of Isochrysis was introduced into each beaker at weekly intervals.

In each series of tests specimens were placed in a beaker of "home" water and in one or more beakers containing the "foreign" waters, or mixtures of "home" and "foreign" waters. The "home" water acted as a control in which conditions of temperature, salinity, pH, oxygen content, concen-
tration of specimens, darkness and food were the same as those of the "foreign" waters. From the procedure adopted, it is believed that differences in survival of *E. pacifica* in "home" and "foreign" waters, could be attributed to factors other than those listed above.
VERTICAL MIGRATION OF EUPHAUSIIDS IN RELATION TO SALINITY: EXPERIMENTAL OBSERVATIONS

Results obtained from three species of euphausiids, and one developmental stage, demonstrate that a salinity structure, composed of layers of successively lower salinities towards the surface in an experimental vessel, affects the vertical migration of euphausiids in the laboratory (Figs. 124 to 129). The effect is particularly evident where the salinity structure includes an extreme range. In the series of tests, the total number of migrations of 20 animals, in the course of one hour, ranged from 17 to 45. The mean number of migrations per test was 26.

Behaviour during migrations:

a. in constant temperature and salinity (control).

Euphausiids in the control (entry) tube (p.87) of the experimental vessel displayed no difficulty in migrating directly, at a sustained speed, towards the light source (100-W lamp) at the surface. Individuals often remained at the surface with no detectable, adverse reaction for periods of up to one hour of maximum illumination.

b. in a salinity structure, at constant temperature.

An active, vertical migration of specimens towards the overhead light followed their introduction into the experimental vessel at a depth of approximately 52 cm. In the
high-salinity layers, their swimming behaviour was similar to that in the control tube. In the successive layers, however, the number of euphausiids able to migrate upwards (referred to subsequently as the "number of migrations" decreased and ultimately none extended beyond some low-salinity layer in the series, the limiting salinity.

There were three types of swimming behaviour in the vertical migration of euphausiids in salinity structures. The most frequent type produced a straight, upward migration, characterized by a progressively slower vertical swimming speed as successive salinity layers were encountered. At some dilution, specimens would reverse direction in a slow, deliberate movement and would return to the high-salinity waters below. The second type consisted of a straight, upward migration followed, when low salinities were met, by a slow circling in the vertical plane, the circles progressively enlarging in an upwards direction. Apparently this enabled a gradual penetration into water of lower and lower salinity. In this way some migrations were vertically extended to include low-salinity layers not previously entered during migrations of the usual, direct type. Eventually the circling animals would enter a layer with a limiting salinity. Subsequently the circling behaviour continued, but directed downwards away from the limiting salinity, until at some higher salinity the majority of specimens discontinued the circling and descended directly into the deeper waters. In the third type of swimming, specimens migrated rapidly at
first (approximately 7 to 8 cm/sec), but when the limiting
salinity was reached they reacted in an erratic and evasive
manner. Following this the specimens sank passively, some-
times with feeble, twitching movements, to the bottom of the
experimental vessel. After a short period in the high-
salinity bottom waters, these specimens recovered and the
same animals often made additional migrations.

All three types of swimming behaviour were observed
in any one salinity test. Euphausiids in the first and
second types characteristically swam slowly during the
migrations, which possibly enabled some physiological adjust-
ment to be made to the low-salinity waters. In the third
type, the apparent "collapse" of specimens appeared to
result from the rapid ascent into the low-salinity waters
of the experimental vessel.

Specimens congregated between migrations, or when the
overhead light was off, towards or at the bottom of the exper-
imental vessel in salinities approximating the range from
which they were collected in the field.

Vertical migration of Euphausia pacifica:
a. in a salinity structure at constant temperature.

In Fig. 124 the results are presented of the vertical
migrations in a series of salinity layers of adult E. pacif-
ica from Indian Arm. The mean salinity gradient was 0.4°/oo/
cm (differences of 1.3 °/oo between layers) and the tempera-
ture constant. (and see p. 87 ). Five tests were carried out
in water from Indian Arm, two in water from Juan de Fuca Strait and one in Strait of Georgia water. Symbols are used to differentiate individual tests in the three waters; also the mean percentage migration is shown for Indian Arm water (five tests) and combined for Juan de Fuca Strait (two tests) and Strait of Georgia (one test) waters.

As shown by the mean percentage curves (Fig. 124) migrations in general were not influenced by dilution until the salinity approached about 16.5 °/oo in Indian Arm and 21.0 °/oo in Juan de Fuca Strait and Strait of Georgia waters. There was an abrupt decrease in the percentage of migrations passing into the layers of lower salinities in all three waters. Ultimately no specimens succeeded in swimming beyond a particular salinity layer. For Indian Arm water this limiting salinity was approximately 8.5 °/oo, and for Juan de Fuca Strait and Strait of Georgia waters, approximately 13.0 °/oo. The animals therefore "tolerated" approximately 4 - 5 °/oo lower salinity in Indian Arm water (i.e., their "home" water) than in similar salinity structures composed of Juan de Fuca Strait and Strait of Georgia waters (i.e., "foreign" waters). This is an important feature.

A comparison of the two migration-salinity curves in Fig. 125 indicates no significant differences in migration behaviour between the adults and a late furcilia of *E. pacifica*. The salinity corresponding to the initial decrease in migration (21.3 °/oo) and the limiting-salinity (7.5 °/oo) were the same for both.
In Fig. 126 the percentage migrations of *E. pacifica* are compared for salinity structures in which the decrease was approximately 1.3 °/oo and 3.0 °/oo per layer. In the structure with the lesser rate of change between layers, migrations were unaffected between 26.5 and 16.8 °/oo, but were reduced at lesser salinities until the limiting salinity was reached between 9.5 and 8 °/oo (Fig. 126 A). When the salinity difference between layers approximated 3.0 °/oo, migrations began to decrease at less than 21.7 °/oo and ceased between 15.2 and 11.1 °/oo (Fig. 126 B). These data indicate that migrations become restricted to higher salinities when the difference between successive layers is increased from 1.3 to 3.0 °/oo.

b. Migrations in relation to maximal and minimal salinities.

Whereas the salinity range in the previous tests (Figs. 124, 125 and 126) was designed to include the maximal and minimal salinities encountered by specimens in Indian Arm (7.0 to 27.4 °/oo), there was some interest in observing the migration of *E. pacifica* in salinities higher and lower than those usually encountered in Indian Arm. Tests were run of 20 adult *E. pacifica* from Indian Arm, migrating in a salinity range of 1.1 to 39.8 °/oo; results are presented in Fig. 127. For salinities of 1.1 to 26.7 °/oo, the mean percentage migration for five tests is given; for the range of 28.5 to 39.8 °/oo, the percentage migration is for one test. Specimens had no difficulty migrating vertically through a total
range of 16.5 to 33.6 °/oo. Progressively fewer migrations were observed into layers above and below this range, and at extremes of the range, below 8.5 °/oo and above 35.0 °/oo, animals did not enter. These results indicate that both high and low extremes of salinity limited the vertical migration of *E. pacifica* in the laboratory.

**Vertical migration of Euphausia pacifica, Thysanoessa spinifera and Thysanoessa longipes in a salinity structure.**

In Fig. 128 results are shown of tests of the vertical migration of *E. pacifica* and *T. spinifera* in a salinity structure with gradations approximating 3.0 °/oo between layers. Specimens and seawater were collected in Indian Arm. Only one test with each species was possible. Results indicate that vertical migration of *E. pacifica* occurred over a salinity range of 26.5 to 15.2 °/oo, with the initial decrease at 17.8 °/oo; migration of *T. spinifera* was observed between 26.5 and 17.8 °/oo, with the initial decrease at 21.7 °/oo.

In Fig. 129 results are shown of the vertical migration of *T. longipes* in layers with increments of 1.3 °/oo. Few specimens of *T. longipes* were collected in Indian Arm at any time and because of this, animals and water for this test were collected in the Strait of Georgia. Migrations occurred over a salinity range of 29.5 to 15.0 °/oo, with the initial decrease at 25.1 °/oo.

Comparison of results obtained in a similar salinity
structure (increments of 1.3 °/oo) with *E. pacifica* (Fig. 126A) and *T. longipes* (Fig. 129) is questionable because the source of the waters and animals for the tests differed. Despite this qualification, it is apparent that *E. pacifica* from Indian Arm, in a salinity structure composed of Indian Arm water, was substantially more "tolerant" towards changing salinity than *T. longipes* from the Strait of Georgia, in a salinity structure composed of Strait of Georgia water. Because the gradations of salinity were greater (3.0 °/oo) in the test with *T. spinifera* (Fig. 128) comparison between the migration of this species and *T. longipes* is not valid; tests using *E. pacifica* (Fig. 126) have shown previously the differing results obtained with salinity structures with increments of 1.3 and 3.0 °/oo.

**VERTICAL MIGRATION OF EUPHAUSIIDS IN RELATION TO TEMPERATURE: EXPERIMENTAL OBSERVATIONS**

Results obtained from two species demonstrate that a temperature structure, increasing towards the surface, influences the vertical migration of euphausiids in the laboratory (Figs. 130, 131, and 132). The strongest effects occurred when temperatures reached relatively high values, i.e., extreme temperatures, when compared with conditions normally met by specimens in Indian Arm.
Behaviour during migrations:

a. in constant temperature and salinity

Euphausiids displayed little difficulty in migrating to the surface of a control vessel (in which the salinity of the water was constant at 26.7 °/oo and was maintained at as nearly a constant temperature as possible -- total range approximating 1.2°C from bottom to top), when stimulated by an overhead light. Migrations were straight and direct, and moved at a uniform speed upwards towards the light. Individuals often remained at the surface, displaying no apparent adverse reaction to the light for the duration of the tests, namely up to 30 minutes. The results of one typical test in a control vessel are shown in Fig. 130 (triangles); 42 migrations of 20 E. pacifica during 30 min. are represented in the percentage values superimposed upon the temperature-depth curve.

b. in changing temperature and constant salinity.

Euphausiids displayed one type of swimming behaviour during migrations in the experimental vessel when temperature increased towards the surface, but salinity was constant. It was characterized by a straight, rapid ascent at the lower temperatures, followed by a progressively slower speed as higher temperatures were encountered. Ultimately no specimens migrated beyond a particular temperature (the limiting temperature). The
subsequent behaviour consisted of a slow, deliberate reversal in the direction of swimming and a straight descent to lower temperatures in the water below.

In the various tests in a column of water with changing temperature, the total number of migrations of 20 euphausiids over 30 min ranged from 30 to 51, with a mean of 44 per test.

Vertical migration of Euphausia pacifica and Thysanoessa spinifera in a temperature structure with constant salinity.

These tests were concerned solely with the effects of temperature on migration of E. pacifica and T. spinifera. Therefore salinity was kept constant at 26.7 °/oo, approximately the value in Indian Arm at the time and depth at which experimental animals were collected.

Figure 130 presents the percentage of migrations of E. pacifica reaching various depths in the control and in one test in which the mean temperature gradient was 0.39°C/cm (between depths of 46 and 12 cm) and a second in which it was 0.68 °C/cm (between depths of 46 and 36 cm). In the control, 94 °/o of the migrations reached the surface of the vessel. In the two tests, the percentage of migrations began to decrease at approximately 14°C, continued to decrease between 14° and 25°C and ceased between 25 and 26°C.

There appears to be an effect on migration attributable not only to high values of temperature but also to the steepness of the mean temperature gradient. The decrease in
percentage migration (Fig. 130) was more pronounced when the gradient was 0.68 °C/cm, than when 0.39 °C/cm, with the most pronounced effect occurring between the range of 16.0 and 22.5°C. Thus for the gradient of 0.68 °C/cm, between these temperatures, migration decreased from 80 to 8 %, and for 0.39 °C/cm from 85 to 44 %. Further support is seen in Fig. 131 (which includes data from Fig. 130) wherein results are presented of the vertical migration of *E. pacifica* in four temperature structures in which mean gradients ranged from 0.38 to 0.68 °C/cm. The general trend among the curves is for a decrease in the percentage migration with increasing steepness of the mean temperature gradient.

The results of a test on the effects of a temperature structure, with a mean temperature gradient of 0.68 °C/cm, on the vertical migration of *T. spinifera* are shown in Fig. 132. The percentage migration again decreased progressively with increasing temperature beginning at about 14°C and continuing up to 25°C, which was the limiting temperature.

**VERTICAL MIGRATION OF EUPHAUSIA PACIFICA IN RELATION TO COMBINED TEMPERATURE AND SALINITY:**

a. Experimental

Results of tests of the effects of combined temperature and salinity structures on the vertical migration of *E. pacifica* are shown in Figs. 133 to 138 and are summarized in Tables 6 and 7.

The results in Fig. 133 are from tests of *E. pacifica*
in a salinity structure with a mean gradient of 0.38 °/oo/cm combined with a mean temperature gradient of 0.08 C°/cm. The temperature gradient was present at depths (between 12 and 3 cm) which were shallower than those at which the decrease in migration occurred (between 39 and 9 cm - Fig. 133), and in any case, was negligible. The results in Fig. 133 there, fore, provide a control against which effects of the combined temperature and salinity structures can be measured.

Figures 134 and 135 show the results of tests in which mean gradients of salinity (0.39 and 0.42 °/oo/cm) were similar to that in Fig. 133 (0.38 °/oo/cm) but in which the temperature gradients were steeper, namely 0.40 C°/cm (Fig. 134) over the depth range of 42 to 14 cm, and 0.58 C°/cm (Fig. 135) over the depth range of 46 to 26 cm. In these, unrestricted migration (Table 6) was limited at the progressively higher salinities of 21.3, 22.2 and 24.0 °/oo) as the mean temperature gradient increased from 0.08 to 0.40 to 0.58 C°/cm (and Figs. 133, 134 and 135). In the same tests, the ranges of salinities over which migrations decreased were 19.7 - 8.5, 20.8 - 10.1, and 22.9 - 14.8 °/oo, with limiting salinities of 8.5, 10.0 and 14.8 °/oo, respectively (Table 6). Together these data indicate that in similar salinity structures the more pronounced the superimposed, mean temperature gradient, the more restricted will be the vertical migration of *E. pacifica* with respect to waters of reduced salinity.

The results of tests presented in Fig. 136 indicate
that conversely, change of salinity can modify the effects of temperature on the experimentally induced migrations of *E. pacifica*. The two curves for the percentage migration in combined temperature-salinity structures (Fig. 136 b and c) show that animals migrated into water of lower temperature than when there was a temperature structure without a superimposed salinity structure (Fig. 136 a). The main features of these temperature-migration curves are summarized in Table 7; in temperature structures with similar mean gradients of 0.41 (a) and 0.40 °C/cm (b), the 100% level of migration was restricted to a temperature of 14.7 °C when the salinity was constant (a), but to 13.6°C when associated with a mean salinity gradient of 0.39 ‰/cm(b). In the same tests, the limiting temperatures were 25.5°C (a) and 23.0°C (b). From these data, it appears that, in tests with similar temperature structures, the effect of a high temperature on the vertical migration of *E. pacifica* is more pronounced when a salinity structure is present than when it is absent.

b. Comparison of laboratory results and field observations.

The results of the effects that temperatures and salinities have on the vertical migration of *E. pacifica* in the laboratory have been summarized in Figs. 137 and 138, and are compared with the range of conditions in which the species occurred in the field (in Indian Arm). In Fig. 137, contour-lines representing percentages of migration (100, 75,
50, 25 and nil per cent) in the laboratory have been drawn relative to a salinity structure with constant temperature (open circles), a temperature structure with constant salinity (closed circles), and combined temperature-salinity structures (triangles and squares).

A general feature of the experimental results is a progressive decrease in percentage of migrations with increasing temperature (ordinate) and decreasing salinity (abscissas). In a salinity structure with constant temperature (Figs. 133, 137), migration was almost unrestricted (98 to 100%) over a salinity range of 26.5 to 16.5 °/oo, but decreased below 16.5 °/oo until the limiting salinity was encountered, at about 8.5 °/oo. In a temperature structure with constant salinity (Figs. 136 a, 137), migration was unrestricted (100%) over a temperature range of 9.0 to 14.7 °C but began to decrease above 14.7°C until a limiting temperature was encountered at about 25.5 °C. In the combined structures (Figs. 134, 135 and 137), migration was unrestricted over 9.0 to 13.0 - 13.6 °C and 26.9 to 24.0 - 22.2 °/oo; a decrease in migration began at higher temperatures and at lower salinities, with limiting values occurring at 22.3 and 23.0 °C and at 14.8 and 10.0 °/oo.

The "flattened" contour-lines for 100, 75 and to a lesser degree 50 % migration (Fig. 137) illustrate that in combined temperature and salinity structures migration is reduced at lower temperatures and higher salinities over the
migration occurring when there is a salinity structure with a constant temperature or a temperature structure with a constant salinity. That is, the combined structures are more restrictive of migration than either temperature or salinity structures alone. In turn, this suggests that in combined structures, temperature and salinity "reinforce" each other and that this is reflected in the reduced numbers migrating.

On the other hand, the right-angle contours at 25% and nil percentage, and the tendency for the 50% contour to be intermediate in shape between these and the 75 and 100% contours indicate that the effects on migration of "reinforcement" may become less when either temperature or salinity approaches a limiting value. For example, the limiting value (nil percentage) in the temperature structure alone (solid circles) was 25.5°C and in the salinity structure alone (open circles) was 8.5°/oo and these approximate 23.0°C and 10.0°/oo for one of the combined temperature-salinity structures (Fig. 137). Apparently, in the presence of an extreme condition in one variable there may be only a slight additional response in *E. pacifica* to the extreme in the co-variable in a combined structure.

The ranges of temperature and salinity over which *E. pacifica* was collected in Indian Arm during one year have been included in Fig. 137. The maximum temperature (13.8°C) and minimum salinity (23.5°/oo) at which specimens occurred for April to October (Fig. 137), a period when both thermocline and halocline were strongly evident -- Fig. 2, closely
agree with the maximum temperature and minimum salinity values intersected by the contour of 100% of migrations in combined temperature-salinity structures in the laboratory (13.0 to 13.6°C and 24.0 to 22.2 °/oo). From December to March (Figs. 2 and 137), conditions in the field were characterized by an isothermal structure combined with a wide range of salinity. The minimal salinity (7.0 °/oo) coinciding with the absence of specimens of *E. pacifica* in Indian Arm during this period is similar to the minimal salinity (8.5 °/oo) intersected by the line of nil per cent of migrations in a salinity structure in which temperature was constant (i.e., isothermal) in the laboratory. Thus, here again there appears to be close agreement between field and laboratory data.

However, there are also dissimilarities between the laboratory and field data. In Fig. 138 (top) the total ranges of temperature and salinity over which *E. pacifica* was collected in Indian Arm during one year have been subdivided into two parts; firstly, a range of properties in which specimens were abundant (zone 1); and secondly, a range in which specimens were few or rare (zone 2). A third area delimits the range of properties from which no specimens were collected (zone 3). In Fig. 138 (bottom) the range of temperature and salinity through which *E. pacifica* migrated vertically in the laboratory also has been subdivided into two parts; firstly, a range of properties within which unrestricted migration was observed (zone A); and
secondly, a range in which there was decreasing migration (zone B). A third area delimits the range of properties into which no specimens migrated (zone C).

A comparison of zone 1 and A in the two diagrams indicates that maximal numbers of *E. pacifica* were collected in a smaller range of salinity in Indian Arm (27.1 to 23.5 °/oo) than was observed for virtually unrestricted migration (98 - 100 %) of specimens in the laboratory (26.9 to 16.5 °/oo). In a similar way, zones 2 and B (Fig. 138) indicate that while the temperature-salinity conditions in which specimens were few or rare in the field were characterized by a large range of salinity and relatively isothermal temperatures, the comparable zone of decreasing migration in the laboratory was represented by a relatively wide range of both temperature and salinity. Finally, comparison of zones 3 and B demonstrated that in Indian Arm *E. pacifica* does not enter a wide range of temperatures and salinities, but in the laboratory specimens migrated into similar ranges to these and into gradients much steeper than those encountered in the field (p. 92), and although the number of migrations decreased, they did not cease entirely.
VERTICAL MIGRATION OF *EUPHAUSIA PACIFICA* IN "HOME" AND "FOREIGN" WATERS:

EXPERIMENTAL OBSERVATIONS

Because previous results indicated that *E. pacifica* from Indian Arm migrated more freely in a salinity structure composed of Indian Arm (i.e., "home") water than in similar structures composed of "foreign" waters (Fig. 124), an additional series of tests was carried out to test the premise that this species may be reacting to water properties other than temperature and salinity.

Vertical migration of *E. pacifica* from Indian Arm and from Juan de Fuca Strait was observed in:

- a. columns of "home" water with no salinity decrease towards the surface (these situations were used as controls),
- b. columns of "home" water in which a small decrease in salinity separated upper from lower parts of the column,
- c. columns containing "home" water in the lower part and "foreign" water in the upper part, separated by a small decrease in salinity.

While specimens migrated towards the surface of the columns in all light intensities (100-W and 6-W lamps and indirect room illumination) in a series of tests, the number of migrations was greater in the column with the 100-W lamp (Figs. 139 and 140). This may be related to procedures
whereby the tests were commenced 24 hours after capture of the animals, and during this period the specimens were kept in darkness in the isothermal coolers and in the incubator. This would infer that the specimens were most active when the change in light was the greatest, for example, from darkness to an intensity of 100-W.

Results of the tests on the vertical migration of *E. pacifica*, collected in Indian Arm and migrating in Indian Arm ("home") and Juan de Fuca Strait ("foreign") waters are presented in Fig. 139, in which open circle designate the positions to which animals migrated. Migration in "home" water with no salinity decrease (column a, control) is shown to be similar to that in a column of "home" water with a salinity decrease of 1.32 °/oo (column b) separating lower and upper parts. Only 3 of 27 migrations (11.1 °/oo) stopped in or below the salinity decrease in column b. However, in column c, 15 of 30 (50 %) of the vertical migrations did not extend above the transition zone between the "home" and "foreign" waters between which there was a salinity decrease of only 1.07 °/oo. Thus vertical migration into the upper part of the columns was substantially decreased when the water there was "foreign" instead of "home" water, even when the salinity decrease in column c was less than in column b and, therefore, less of a potential barrier to vertical migration.

Similar tests were carried out using specimens of *E. pacifica* collected in Juan de Fuca Strait and migrating
into water from there ("home" water) and from Indian Arm
("foreign" water). Results are presented in Fig. 140. Column a is Juan de Fuca water with no salinity decrease
(control); column b is Juan de Fuca water with a zone in
which salinity decreases by 0.94 °/oo ; and column c con­
sists of Juan de Fuca water in the lower part separated
from Indian Arm water by a transition zone with a salinity
decrease of 0.26 °/oo. In the control, 5 of 36 (13.9 °/oo)
migrations did not extend above depths between 22 and 18 cm,
the depth of the salinity decrease in column b. In column
b, however, 8 of 29 migrations (27.6 °/oo) ended in or below
this position. It appears, therefore, that migrations were
being restricted to some extent in the presence of the
small salinity decrease (0.94 °/oo) in "home" water. Never­
theless, in column c, 17 of 31 migrations (54.8 °/oo) did
not extend above the transition zone between "home" and
"foreign" waters (salinity decrease was only 0.26 °/oo). Here
again the results indicate that E. pacifica from Juan de Fuca
Strait entered less freely into "foreign" than into its
"home" water. Bearing on this, is the procedure whereby the
dilution with distilled water of "home" water (from
32.8 °/oo to 25.12 °/oo) in the upper part of column b was
substantially greater than that (from 26.9 °/oo to 25.8°/oo)
of the "foreign" water in the upper part of column c (Fig.
140). From this, it appears that the use of an increased
volume of distilled water as a diluent for "home" water,
over that used for "foreign" water, did not influence the
specimens' preference for "home" water (p. 94).

In both series of tests specimens migrated into their "home" water in greater numbers than into the "foreign" water. As temperature was constant, and as salinity changes were minimal and well within the "tolerances" for E. pacifica already shown from field and laboratory results, this difference can be attributed to specimens showing a preference for that water from which they were collected, i.e., their "home" water, and reacting against the "foreign" water.
SURVIVAL OF EUPHAUSIA PACIFICA IN THE LABORATORY IN DILUTIONS OF INDIAN ARM WATER

Previous tests of *E. pacifica* in salinity structures in the laboratory have indicated that water of salinity as low as 8.5 °/oo may be occupied temporarily by some specimens during their vertical migrations (Fig. 133, Table 6). It was desirable to determine whether specimens could in fact survive in such low salinity, or if not, then at what dilutions of seawater did lowering the salinity affect survival. This latter consideration was pre-requisite to subsequent tests of the survival of *E. pacifica* in "home" and "foreign" waters.

In the first test 10 specimens were placed in a control, (26.9 °/oo) of Indian Arm water and in the water to be diluted, and in the second test, 17 specimens were similarly treated. The results presented in Fig. 141 indicate that at salinities below 22.9 °/oo there was a progressive decrease in survival over that in the control. The results of the second test (Fig. 142) indicate a progressive decrease in survival at salinities below 24.2 °/oo; however, the percentage survival did not fall below that for the control until the water had been diluted to 18.9 °/oo.

In general these tests indicated that *E. pacifica* would survive reasonably well in water with a minimal salinity of approximately 23 - 24 °/oo for periods of at least two days. A comparison of this salinity range with those
used in the migration tests (Table 6), indicates that while specimens may be capable of migrating into water with salinities as low as 8.5 °/oo, they were not able to survive in low-salinity water when placed in such conditions for extended periods. On the other hand, the minimal range for high survival in the laboratory was comparable with the minimal salinity (23.5 °/oo) at which maximal numbers of *E. pacifica* were collected in Indian Arm (p. 112) and with the minimal salinity of water (approximately 21.3 °/oo) in which migration was unrestricted in salinity structures with near-constant temperature (Table 6) in the laboratory.

**SURVIVAL OF EUPHAUSIA PACIFICA IN THE LABORATORY IN "HOME" AND "FOREIGN" WATERS**

The results presented in Figs. 143 - 147 and summarized in Tables 8, 9 and 10 derive from tests of survival in the laboratory of *E. pacifica* in "home" and in "foreign" waters in conditions of constant temperature and similar salinities.

a. **Survival in "home" water (Indian Arm) and in waters from Strait of Georgia, Juan de Fuca Strait and Malaspina Strait.**

Figures 143 - 145 present the percentage survival of specimens of *E. pacifica* collected in Indian Arm and placed in filtered "home" and "foreign" waters. Results are summarized in Table 8; they are tabulated either as the percentage surviving at the end of the test, or as the duration of
the test when there was no survival. A general feature was that larger numbers of specimens of *E. pacifica* from Indian Arm survived for longer periods in their "home" water (control) than in waters from the Strait of Georgia, Juan de Fuca Strait and Malaspina Strait; values ranged from 57 % to 100 % at termination of the several tests (33 to 52 days) in "home" water. Survival in "foreign" waters, and in mixtures of "home" and "foreign" waters, varied from nil to 50 % at termination of the various tests (3 to 47 days) (Table 8).

In one of a series of two tests (Fig. 143 b and Table 8) survival was 100 % after 43 days in Indian Arm ("home") water, 50 % after 43 days in Strait of Georgia water and nil after 9 days in water from Juan de Fuca Strait. In the other (Fig. 144 a and Table 8) the survival, after 47 days, was 60 % in Indian Arm water, 30 % in Strait of Georgia water and nil in water from Juan de Fuca Strait. These results suggest a "preferential sequence" for survival of Indian Arm—Strait of Georgia—Juan de Fuca Strait waters. Thus there appears to be a relationship of decreasing survival with increasing distance between the locations of the "home" (Indian Arm) and the "foreign" waters (see Fig. 1 b for geographical location of various waters).

In another series of tests, carried out between June 16 and August 6, 1965 (Fig. 143 a), survival of specimens from Indian Arm was 80 % after 52 days in the "home" water, 50 % after 42 days in water from Juan de Fuca Strait and nil after only 9 days in Strait of Georgia water (Table 8).
These results indicated a "preferential sequence" of Indian Arm → Juan de Fuca Strait → Strait of Georgia water.

In a third series, water from Malaspina Strait (Fig. 1b) was substituted for that from the more centrally-located area in the Strait of Georgia. Survival (Fig. 144 b; Table 8) ranged from 60 % after 33 days in "home" water from Indian Arm, 10 % after 33 days in water from Juan de Fuca Strait, and nil after only 6 days in water from Malaspina Strait. In this series, therefore, the "preferential sequence" for *E. pacifica* from Indian Arm was Indian Arm → Juan de Fuca Strait → Malaspina Strait water.

The survival of *E. pacifica* from Indian Arm was tested in "home" water, in diluted (26.6 °/oo) and undiluted (33.1 °/oo) waters from Juan de Fuca Strait and in a mixture of equal parts of water from Indian Arm and Juan de Fuca Strait. The results (Fig. 145 a; Table 8), after 47 days, was 57 % survival in water from Indian Arm, 13 % in the diluted water from Juan de Fuca Strait, and nil in the undiluted water from Juan de Fuca Strait. Survival was nil in the mixture of Indian Arm and Juan de Fuca Strait waters and, as well, the rate at which specimens died was highest. A comparison of the curves of survival (Fig. 145 a) of *E. pacifica* from Indian Arm in the diluted and undiluted waters from Juan de Fuca Strait, indicates little or no difference attributable to the use of distilled water as a diluent or to the higher salinity, even though salinities in Indian Arm have not been observed to exceed approximately 27.4 °/oo.
In a series of tests of Indian Arm specimens in mixtures of waters from Indian Arm and Malaspina Strait, survival (Fig. 145 b; Table 8) was 57% after 47 days in Indian Arm water, nil to 10% after 6 to 37 days in the various mixtures of waters, and nil after 3 days in water entirely from Malaspina Strait. Comparison of the survival curves demonstrated that *E. pacifica* from Indian Arm survived in larger numbers and for longer periods in the "preferential sequence" of Indian Arm water \( \rightarrow \) a mixture containing 25% of water from Malaspina Strait \( \rightarrow \) 33% Malaspina Strait water \( \rightarrow \) 50% Malaspina Strait water \( \rightarrow \) 100% Malaspina Strait water. Thus with an increasing proportion of water from Malaspina Strait, survival of specimens from Indian Arm was progressively lowered.

b. Survival in "home" water (Juan de Fuca Strait) and in waters from Strait of Georgia and Indian Arm.

A second procedure was adopted in order to determine whether specimens from a different "home" water (from Juan de Fuca Strait) reacted in "preferential sequences" equivalent to those of the Indian Arm specimens. Accordingly the survival of specimens of *E. pacifica* collected in Juan de Fuca Strait was tested in filtered seawater from Juan de Fuca Strait ("home" water), the Strait of Georgia and Indian Arm. Results are summarized in Fig. 146 a, b, and Table 9. Survival in one test (Fig. 146 a; Table 9) lasting 43 days was 100% in diluted (26.5 °/oo salinity) and 80% in
undiluted (32.8 °/oo) "home" water; 80 % in water from Indian Arm, and 50 % in water from the Strait of Georgia. In a second test (Fig. 146 b; Table 9) survival, after 31 days, was 60 % in the "home" water diluted to 26.8 °/oo, 30 % in water from Indian Arm and 20 % in water from the Strait of Georgia.

From the results of these two tests it appears that there was a "preferential sequence" in the survival of *E. pacifica* from Juan de Fuca Strait in the order: Juan de Fuca Strait → Indian Arm → Strait of Georgia. Although salinities in Juan de Fuca Strait range from 31 to 34 °/oo, survival of *E. Pacifica* (Fig. 146 a, Table 9) from there was greater in diluted (26.5 °/oo) than in undiluted (32.8 °/oo) waters from the Strait. This suggests the absence of any harmful effects attributable to a decrease in salinity (below that encountered in the field) or to the use of distilled water as a diluent in the laboratory tests.

c. Survival in "home" water (Strait of Georgia) and in water from Indian Arm.

Figure 147 and Table 10 present the percentage survival of specimens of *E. pacifica* collected in the Strait of Georgia and placed in seawater from Strait of Georgia and Indian Arm. A general feature was the similarity in survival of the species in the two waters. There was nil survival (Fig. 147 a) after 34 days in water from the Strait of Georgia and after 37 days in water from Indian Arm. Results presented in Fig. 147 b show a survival, after 37 days, of 50 % in water from the Strait of Georgia, and 40% in water.
from Indian Arm.

In these tests the survival of specimens from the Strait of Georgia in their "home" water was lower than in the equivalent tests of the survival of *E. pacifica* from Indian Arm and Juan de Fuca Strait in their "home" waters.
DISCUSSION OF SURVIVAL IN THE LABORATORY

In the tests of survival of *Euphausia pacifica*, the "home" and "foreign" waters were subjected to the same conditions of darkness, concentration of specimens, additions of food, pH and oxygen content. Particular attention was given to eliminating any but minor differences in salinity among the samples and temperature was constant at 10°C which was similar to that at the locations and depths at which specimens were collected in the field.

Tests with *E. pacifica* from Indian Arm indicated that survival was similar in diluted (26.5 °/oo) and undiluted (33.1 °/oo) water from Juan de Fuca Strait, although salinities in Indian Arm were not observed to exceed approximately 27.4 °/oo. In a second test survival of specimens from Juan de Fuca Strait was slightly greater in diluted (26.5 °/oo) than in undiluted (32.8 °/oo) water from Juan de Fuca Strait, although salinities there ranged from approximately 31 - 34 °/oo. Thus, there was no decrease in the survival in salinities which differed substantially from those encountered in the field. Another important point in the above is the absence of any harmful effects attributable to the use of distilled water as a diluent (p. 94).

Although *E. pacifica* survived comparatively well over a wide range of salinities (23 or 24 to 33.1 °/oo) in the laboratory, nevertheless, in order to remove differences in salinity as a possible factor in the survival of specimens
in "home" and "foreign" waters, salinities of waters used were adjusted to similar values (a total range of 26.3 - 26.9 °/oo).

The experiments with _E. pacifica_ demonstrated that, in general, specimens survived better in their "home" waters than in "foreign" waters, or in mixtures of these waters. It is suggested that such differences resulted from the influence of environmental factors other than temperature and salinity which, in some way are associated with the "home" and "foreign" waters. Bary (1963 a, 1964) developed the premise that different water bodies contain factors that are in some sense unique, the "unique properties", and that each species (or the population of a species in the present study) reacts to these properties in an individual manner. On this basis, the survival of _E. pacifica_ in the laboratory requires to be considered in relation to firstly, an oceanographic factor - the unique properties of waters collected from several locations; and secondly, a biological factor - the reactions of specimens collected at different locations to these properties. It follows that survival of _E. pacifica_ would be dependent on the tolerance of specimens towards the unique properties of waters collected at different geographical locations.

The survival of _E. pacifica_ from Indian Arm indicated that specimens were considerably more tolerant towards "home" water than towards "foreign" waters. The comparatively poor survival in "foreign" waters may have resulted from a deficiency in these waters of some essential property or properties
present in the "home" water, or (and perhaps as well as) that other properties present in the "foreign" waters were in some way deleterious to survival. Although the nature of these properties is unknown, the preference for "home" over "foreign" waters was a consistent feature in all tests, over a one-year period. For particular waters, there were fluctuations in survival. For example, in Juan de Fuca Strait water survival ranged from nil to 50% over periods varying from 9 to 47 days; and even in "home" water, survival ranged from 52 to 100% over 33 to 57 days. These fluctuations were obtained in experimental conditions that were similar for all tests and were closely controlled. They indicate, therefore, that the properties of "home" and "foreign" water affecting survival probably were being modified, thereby influencing the reaction of specimens.

Not only were there fluctuations in survival within a water from a particular location, but the relative merits of a series of waters varied from time to time. This was indicated by changes in the "preferential sequence" in the survival of specimens. In one sequence, specimens from Indian Arm survived best in water from Indian Arm, less so for water from the Strait of Georgia, and least for water from Juan de Fuca Strait (tests of December 9, 1965 - January 20, 1966, and January 26 - March 14, 1966), but this changed to survival being best in water from Indian Arm, less so in water from Juan de Fuca Strait and least in Strait of Georgia water (test of June 16 - August 6, 1965).
first sequence suggests that survival decreased with increasing (geographical) distance between the locations of the "home" and the "foreign" waters (Fig. 1 b). This leads to the speculation that Indian Arm water included a property essential to the survival of *E. pacifica* from Indian Arm, and that specimens became increasingly adversely affected by some change (perhaps in the concentration of the property) in the "foreign" waters, the further these were from the "home" water. The reversal in the second sequence of the "foreign" waters may have been influenced by the use of unfiltered seawater in the survival tests of June 16 - August 6, 1965. Survival was poor (nil after 9 days) in unfiltered water from the Strait of Georgia when compared with that (30 to 50% over 43 - 47 days) for filtered water from the same location in the tests of December, 1965 to March, 1966.

Alternatively, runoff is maximal during late June to mid-July and the Strait of Georgia water used in the survival tests was collected in the central part of the Strait, which is strongly influenced by the discharge of the Fraser River. This runoff, although generally regarded as affecting the surface and near-surface waters, could possibly have caused fluctuations in the properties of water at 100 m and have contributed to the poor survival of specimens collected in June, 1965. Some support for this alternative is given by Waldichuk (1957) who describes the deep water which flows into the basin of the Strait of Georgia as being not a "pure" water but rather a mixture of seawater and Fraser River water.
of a certain age. It is possible therefore, that the influence of Strait of Georgia water on the survival of specimens may be modified, (perhaps fairly rapidly) through mixing with Fraser River water.

If the lower survival of *E. pacifica* in "foreign" waters could be attributed to a deficiency of essential properties and/or the presence of deleterious properties, then it would be of interest to observe whether the addition of "home" water to it would improve survival. Survival of specimens from Indian Arm in waters from Indian Arm, Malaspina Strait and mixtures of the two indicated, firstly, a better survival in "home" than in "foreign" water, and, secondly, increases in survival in mixtures in which the proportion of "home" water was progressively increased. Presumably, any deficiency of essential properties and/or properties deleterious to survival in Malaspina Strait water were alleviated, at least to some extent, through mixture with "home" water. However, even at the greatest dilution of Malaspina Strait water with Indian Arm water, the survival of *E. pacifica* indicated that specimens were considerably less "tolerant" towards the mixture than to the "pure" Indian Arm water and that considerably more "home" water than "foreign" water would be required in a mixture of the two in order to approach the survival of specimens in water of entirely "home" origin.

Why Malaspina Strait water should contribute to the poor survival (nil after 3 - 6 days) of specimens from
Indian Arm is unknown. The location (off the mouth of Jervis Inlet) and the relatively shallow depth (50 m) from which water was collected in Malaspina Strait may be implicated. This area receives the combined influence of runoff from the northern inlets and the Fraser River (Waldichuk, 1957) which presumably, could have modified some property or properties essential to, or perhaps introduced some property or properties detrimental to, the survival of the specimens from Indian Arm.

Survival of E. pacifica from Indian Arm indicated that specimens were considerably more tolerant of "home" water than of water from Juan de Fuca Strait or of a 1:1 mixture of the two waters. Apparently, the low tolerance of specimens from a coastal inlet towards an "oceanic-coastal" water, such as collected in Juan de Fuca Strait, persisted with the introduction of "home" water, at least in the 1:1 mixture.

The survival of E. pacifica from Juan de Fuca Strait demonstrated, as with specimens from Indian Arm, a greater tolerance towards "home" water than towards "foreign" waters. Survival in the "foreign" waters further demonstrated, however, that specimens from Juan de Fuca Strait were more tolerant of Indian Arm water (30 to 80 % survival, over 31 - 43 days) than were specimens from Indian Arm (p.128 ) of water from Juan de Fuca Strait (nil to 50 % survival, over 9 - 47 days). In other words specimens from an "oceanic-coastal" population of E. pacifica as collected in Juan de
Fuca Strait, were more tolerant towards inlet water than were specimens of an inlet population of the same species towards "oceanic-coastal" water.

The survival of specimens from Juan de Fuca Strait and Indian Arm was similar in Strait of Georgia water, although substantially below that observed in "home" waters. Survival in water from the Strait of Georgia ranged from 20 to 50 %, over 31 - 43 days for specimens from Juan de Fuca Strait, and 30 - 50 %, over 43 - 47 days, for specimens from Indian Arm. (The one exception to this was the abrupt decrease in survival (nil after 9 days) of specimens from Indian Arm in unfiltered water from the Strait of Georgia during June, 1965). From the above it might be inferred that E. pacifica collected from "oceanic-coastal" and inlet waters have a low but a similar degree of tolerance towards Strait of Georgia water.

In contrast to E. pacifica from Indian Arm and Juan de Fuca Strait, the survival of specimens from the Strait of Georgia was comparatively low, and also similar, in both "home" and "foreign" waters. It must be emphasized, however, that there were only a few tests and that these were made using unfiltered water. Survival ranged from 0 to 50 %, over 34 - 37 days in Strait of Georgia water, and from 0 to 40 %, over the same period, in water from Indian Arm. This suggests that the specimens were "tolerant" to a similar degree towards both waters.

The survival of E. pacifica from the Strait of Georgia demonstrated that specimens were more tolerant of Indian Arm
water (nil to 40 % survival, over 34 - 37 days, in unfiltered water) than were specimens from Indian Arm towards water from the Strait of Georgia (nil survival after 9 days, in unfiltered water). On this basis specimens of a "coastal" population of *E. pacifica*, such as collected in the Strait of Georgia, appear to have been more tolerant of inlet water than were specimens of an inlet population of the same species towards "coastal" water. This situation is similar to that discussed earlier (p. 131) for specimens from Juan de Fuca Strait.
The ranges of temperature and salinity in Indian Arm during the period from January, 1960, to July-August, 1961, have been shown in temperature-salinity (T-S) diagrams. These diagrams and geographical distributions of temperature, salinity and density ($\sigma_t$) also show that within these ranges, conditions fluctuated seasonally and were periodically disrupted by intrusions of outside water from the Strait of Georgia through Burrard Inlet (see discussion pp. 29-33).

Temperature-salinity-plankton (T-S-P) diagrams and geographical distributions of euphausiids have been used to indicate their occurrences and reactions to their environment, and changes in it, of the adults of four species (*Euphausia pacifica*, *Thysanoessa spinifera*, *Thysanoessa longipes* and *Thysanoessa raschii*) and the developmental stages of *E. pacifica*. The occurrences of large numbers of adult specimens of *E. pacifica* in a wide range of distribution and in all months in Indian Arm, coupled with the presence of a complete developmental sequence, indicated that this species was resident in the inlet and as such was tolerant to a high degree towards the properties, in particular temperature and salinity, of inlet waters. On the other hand, the occurrences (often sporadic), of relatively small numbers and in limited distributions of adult specimens of *T. spinifera*, *T. longipes* and *T. raschii*, and the
absence of most or all of the developmental stages of these species, indicated that they were expatriates in Indian Arm. This, together with their usually rapid disappearance from the inlet suggests they were considerably less tolerant of the properties of inlet water than *E. pacifica*.

Wide variations in distribution, and perhaps tolerances to temperature and salinity, occurred not only among the four species, but also within the one developmental sequence studied, that of *E. pacifica*. The earlier developmental stages (the first and second nauplius stages and the metanauplius stage) were markedly restricted in their distributions to deeper waters, within a relatively narrow range of temperature and salinity, when compared with the eggs, later developmental stages (calyptopii and furcilia) and the adults (see discussion pp.55-57). These accord, in general terms, with results from other workers who have reported that a species may occur at a certain depth when adult, but while young it may have a different vertical distribution. In particular, Fraser (1936) reported that whereas eggs, nauplii and metanauplii of *Euphausia superba* were found at deep levels, the later developmental stages (calyptopii and furcilia) migrated to shallower depths. In a previous study in Indian Arm (Shan, 1962) adult copepods were found at depths different from those of the developmental stages. It has been suggested in reviews by Kinne (1963, 1964) that the range of temperature and salinity tolerance, and thereby distribution, may be narrower during
early development.

Although the occurrences and distribution of the various species and developmental stages were related by temperature and salinity (Tables 4 and 5) to environmental conditions in Indian Arm, there was a question as to whether the temperatures and salinities were the "regulatory" factors controlling the distributions, or whether other, as yet undetermined, properties, and the reactions of specimens towards these, were operative (see discussions: *E. pacifica* (pp. 45 - 46), *T. spinifera* (p. 65a), *T. longipes* (pp. 71 - 73) and *T. raschii* (pp. 77 - 78).

There are indications that temperature and salinity may be, at least in part, regulatory factors particularly in the highly modified waters between about 10 m and the surface. The first indications were that the rapid changes in temperature and salinity appeared to restrict the vertical migration of *E. pacifica* into these near-surface waters. This species is widely distributed in transitional water at intermediate depths and in deeper waters and did not appear to be influenced by the ranges and fluctuations of temperature and salinity in these waters. On the other hand, the occasional occurrences of small numbers in, or more usually the complete absence of specimens from, surface waters appeared to result largely from their reactions towards the zone of maximum change in the temperature and salinity (i.e., the thermocline and halocline) characteristic of the upper waters. During December-April, in periods of seasonal cooling
isothermal (but not isohaline) conditions prevailed and small numbers of *E. pacifica* were collected in surface waters in which minimal temperatures and salinities were as low as 5.3°C and 7.0 °/oo. Between June and October, during the period of seasonal warming, the temperature of upper waters was up to 20.2°C and salinity was low; both the halocline and thermocline were present. Specimens did not occur in the upper waters in these conditions. These data suggested there was more influence on migration when temperature and salinity changes were pronounced and occurred together.

The results of that portion of the laboratory study concerned with the migration of *E. pacifica* in temperature, salinity and combined temperature-salinity structures demonstrated relationships similar to those in the field. In conditions simulating those of thermocline and halocline in the field the numbers migrating decreased as the temperature increased or salinity decreased towards the surface; the effects were more pronounced when the rate of change of temperature (pp.107 - 108) or salinity (p.103) was greatest and when temperature and salinity structures were combined (for discussion, see pp.111 - 112). Although there appeared to be some agreement between field and laboratory findings in the effects of thermoclines and haloclines on *E. pacifica*, occurrences in relation to temperature and salinity in the field suggested that reactions of specimens towards temperature and salinity were stronger than in the laboratory (pp.113 - 114) despite the much steeper gradients.
obtained in the laboratory (p. 92).

The field studies indicate that, except on rare occasions, the expatriate species were not collected either in the surface water (T. spinifera) or above 30 m (T. raschii) and 60 m (T. longipes). It is possible these distributions may be related, at least in part, to the large fluctuations in the temperature and salinity of upper waters. The very few tests in the laboratory of the migration of T. spinifera and T. longipes suggested, however, that these species may be considerably more tolerant of high temperatures and low salinities than the field studies indicated. For example, a few specimens of T. spinifera migrated in the laboratory into waters with a maximal temperature of 25.0°C and a minimal salinity of 17.8 °/oo, whereas in Indian Arm, with only two exceptions over two years, the maximum temperature at which T. spinifera was collected was 13.7°C and the minimal salinity was 23.7 °/oo. Similarly, specimens of T. longipes migrated in the laboratory into waters with a minimal salinity of 15.0 °/oo, but in Indian Arm were collected at the minimal salinity of 24.5 °/oo.

It appears, therefore, that in general there was a more limited distribution of E. pacifica, T. spinifera and T. longipes with respect to changes in temperature and salinity in the upper waters in Indian Arm than temperature and salinity structures in the laboratory would indicate was feasible; and this, despite the steeper gradients used
in the laboratory. An inference to be drawn is that other environmental properties, as yet undetermined, were superimposed upon those of temperature and salinity and were exerting an influence on the distribution of these species in Indian Arm.

A possible explanation is that the disparity between the distributions as observed in the field, and the potential distributions suggested by laboratory findings may lie in the different properties of natural fresh waters and distilled water, and in the processes ensuing on dilution of seawater in natural conditions. Dilution of upper waters in Indian Arm is predominantly by freshwater runoff at the surface and subsequent entrainment and mixing between this and saline waters immediately below. In contrast, in the laboratory, distilled water was used as a diluent for seawater, which was collected consistently from one, deep source (75m) in Indian Arm and which probably was relatively free from the dilution processes present in the upper waters. Although the temperature and salinity of this deep water was adjusted in the laboratory to simulate conditions in "natural" upper waters, it may have been quite different in other properties with the result that reactions of specimens differed from those in the field.

In general, occurrences of the expatriate species in Indian Arm were associated with the inflow (from various causes) of outside waters into the inlet. In these situations, *T. spinifera* (p. 64) and *T. longipes* (p. 71) occurred in
maximal numbers and usually towards the mouth of the inlet. When the influence of outside waters was decreasing through mixing with resident water or was not apparent, these species decreased in abundance and were often absent from collections. On the other hand, the resident species, *E. pacifica*, decreased in numbers and/or shifted in distribution in a direction removed from the influence of outside waters entering Indian Arm (pp. 44 - 45). During periods when oceanographic conditions were relatively stable in the inlet, with no detectable inflow of outside waters, *E. pacifica* increased in abundance and became more or less evenly distributed throughout waters at intermediate and deeper levels.

The sporadic occurrences in Indian Arm of *T. raschii*, another expatriate species, were not associated with detectable movements of outside water into the inlet. Thus the means of transport associated with the entry of the other expatriate species into Indian Arm, either were not apparent or were reduced for the periods in which *T. raschii* entered. The implications of this are discussed on pp.75 - 76).

The short-lived occurrences of this species, and its narrow range of distribution on occasions when it was present, suggest that this species was reacting against Indian Arm waters.

Although the entry of outside waters was detectable for the most part in the distributions of temperature and salinity of intermediate and deep waters, the changes in these properties were relatively minor and well within the
range that the distributions of the various species have shown they were able to tolerate in Indian Arm. Nevertheless, these intrusions of outside water often were to be associated with the presence and/or an increase in the abundance of expatriate species and in major fluctuations in the abundance and/or distribution of the resident species (E. pacifica) in the inlet. It is believed that the intruding waters transported expatriate species into Indian Arm, and also flushed resident water and species out of the inlet and/or altered their distribution within the inlet.

For specimens within the inlet the above evidence leads to a questioning of the concept that temperature and salinity were the primary regulatory factors in the occurrences, abundance and distributions of euphausiids in intermediate and deep waters. It suggests, instead, that other properties associated with intruding and resident waters, and the reactions of specimens to these were more important. The nature of these properties (analogous to the "biological differences" between natural sea waters of Wilson et al. (1951, 1952, 1954), the "unique properties" of Bary (1963a, 1964); and to the seawater "qualities" of Johnston (1962, 1964) is unknown. They may be attributable to: "ectocrines" or "external metabolites" released into the water by marine organisms and beneficial or harmful to others of the same or different species (Lucas, 1947, 1949; Srinivasagam, 1966), dissolved organic substances acting as growth factors and supplementing the diet (Shiraishi and Provasoli, 1959;
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Johnston, 1962), non-living particulate material also supplementing the diet (Conover, 1964), the type of good organism in the water (Mullin, 1963), dissolved inorganic materials (Lucas, 1947; Lewis, 1967, and unpublished, Institute of Oceanography, University of British Columbia), or perhaps interactions of organic and inorganic materials such as chelation of trace metals by naturally occurring dissolved organic substances (Johnston, 1964).

Regardless of their nature, these undetermined properties apparently "regulate" the reactions of specimens and do this, it would seem, by means of physiological responses to the properties -- the species "tolerance". Thus, expatriate species appear to tolerate the "unique properties" of outside water, as indicated by their entry into Indian Arm in association with these waters, but the decrease in their numbers and often short-lived residence which ensued on the mixing between outside and resident waters indicates a degree of intolerance of the "unique properties" of Indian Arm water.

In order to explain these reactions the interaction of properties between the resident and intruding waters and the effects on the species must be considered. Essential properties present in intruding water would become diluted during the process of mixing with the resident water; with sufficient dilution the concentration of such properties could become limiting to the expatriate species, resulting in a decrease in their abundance, and eventually in their elimination from the waters in the inlet. Conversely, an increasing concentration of properties present in resident water and
deleterious to expatriate species would provide similar results. This sort of mechanism may also "explain" the reactions of the resident species (E. pacifica). That E. pacifica is resident (and reproduces) in Indian Arm water means that it is "tolerant" of the properties of this water. But that the abundance of E. pacifica is reduced and the distribution altered by intruding water shows that some property of the intruding water, or perhaps the dilution of some essential property of resident water, produces an adverse effect on specimens. Thus the specimens of all species are reacting favourably towards (i.e., they tolerate) the "unique properties" or "essential factors" within the water in which they are resident (the "home" waters) and against (i.e., they are intolerant towards) the properties of the water in which they are not resident. This two-way type of reaction appears to be essential to an understanding of the occurrences of all species of euphausiids in Indian Arm.

This same two-way reaction helps to understand the vertical distributions of E. pacifica, T. spinifera and T. longipes in Indian Arm. From the T-S-P diagrams it was apparent that from month to month the waters from about 90 to 200 m displayed only small ranges of temperature and salinity. For E. pacifica, these ranges were subsequently shown in the laboratory tests of migration and survival not to cause adverse reactions in this species. Moreover, the temperature and salinity of waters below 120 m, from which all species were mostly absent, would be closer to the
outside waters in which such species as *T. spinifera* and *T. longipes* are believed to have entered Indian Arm. Accordingly, if only temperature and salinity were regulating occurrences these species could be expected to concentrate in those deeper waters. Such was not the case, with only rare exceptions. Again, it would appear that a deficiency of some essential property or properties or perhaps the presence of some deleterious property or properties inhibited distribution into these deep waters. It is interesting to note, however, that nauplius I and II and the metanauplius of *E. pacifica* occurred in the deep waters.

Occurrences of *Thysanoessa raschii*, between 30 and 60m in Indian Arm, did not appear to be related to temperature and salinity. The waters below 60 m were characterized by relatively low temperatures and high salinities, with considerably less range of variation than the water from which *T. raschii* was collected, and nearer the properties of the outside waters, from which the specimens originated. It would appear, therefore, that the waters below 60 m should have been as suitable (or even more so) as the waters between 30 and 60 m for a species such as *T. raschii* which normally inhabits mixtures of oceanic and coastal water.

It is a possibility, to judge from its occurrences in a narrow range of geographical distribution in the inlet that the few specimens of *T. raschii* which entered did so within the confines of small and undetected volumes of outside water. This water would eventually be dissipated through mixing and
dilution with the resident waters in Indian Arm. As with other expatriate species (T. spinifera and T. longipes), the dilution of essential properties introduced by outside waters and/or the presence of detrimental properties in the resident water would have contributed to the failure of T. raschii to survive for prolonged periods in Indian Arm.

Euphausia pacifica occurs commonly in much of the North Pacific (Brinton, 1962) and also extends, very often in large numbers, into the most secluded of coastal areas, e.g., Indian Arm. This sort of distribution is not common among zooplanktonic species. It is presumed to be maintained in two ways, by recruitment into coastal areas from the oceanic stock, and by specimens becoming more or less permanent, breeding populations within particular locations. Both means probably apply in British Columbia coastal waters. The expatriate species enter Indian Arm and there is no reason to believe the E. pacifica does not enter along with them; on the other hand, E. pacifica undergoes a complete life-history in Indian Arm whereas the other species apparently do not breed there at all, and as already discussed, occur there only spasmodically, in association with intrusions of outside waters.

A large range in environmental conditions ensues on mixing of oceanic into coastal waters and E. pacifica occurs throughout this range. It seemed that this single species provided an opportunity to test whether its occurrences were related to the changing temperatures and salinities between oceanic and coastal areas, or whether other properties were
involved, and whether specimens became "adapted" to waters such as found in Indian Arm. Accordingly, the laboratory series of experiments were carried out.

Specimens clearly reacted to changes of temperatures and salinity in the laboratory (Figs. 137 and 138) but usually not until temperatures were higher or salinities lower than were "usual" in the species environment; and this, despite the steeper gradients used in the laboratory. The only natural situation where such reactions were likely was in the thermocline and halocline where ranges (but not gradients) comparable to those in experimental situations were present. Even though these reactions were present, evidence suggested that a response to another condition was superimposed in the field.

In laboratory experiments in which specimens of *E. pacifica* from one locality and water ("home" water) were tested for their reactions (migration or survival) in water from another area ("foreign" water) specimens showed notably less adverse reactions in the "home" than in the "foreign" water. Migration in salinity structures composed of waters collected from several geographical locations (p. 102) indicated that, while migrations decreased in low-salinity waters, the specimens "tolerated" approximately 4 - 5 °/oo lower salinity (Fig. 124) in Indian Arm water (i.e., their "home" water) than in identical salinity structures composed of Strait of Georgia and Juan de Fuca waters (i.e., "foreign" waters). This was the first indication in the laboratory
that in addition to the reaction of specimens towards decreasing salinity, they were also reacting towards some factor(s) associated with other properties of "home" and "foreign" waters. Subsequent tests of migration, in water columns with nearly constant temperature and small differences in salinity separating the two waters, further demonstrated that *E. pacifica* was considerably more tolerant of the properties of "home" water than of those of "foreign" waters (Figs. 139, 140 and pp.116 -118). Again the influence of properties, other than temperature and salinity, apparently was (being) instrumental in determining the vertical migration of specimens. Finally, the survival of *E. pacifica* collected from several geographical locations and placed in various waters under controlled conditions demonstrated that populations in general were more tolerant towards the properties of their "home" water than towards the "foreign" waters or mixtures of the two. The evidence again suggests, as with the field studies, that the relatively poor survival of specimens in "foreign" waters, and in mixtures containing such water, resulted from a deficiency of some essential property or properties or (and perhaps as well as) that some other property or properties were present and were in some way deleterious to survival (see discussion, pp.127 - 133).

The evidence from occurrences and reactions of euphausiids in the field and from results of experiments, appears to be mutually supporting. From the above it is
apparent that species do react against gradients of temperature and salinity in the field, for example by concentrating below structures such as the thermocline and halocline, and in laboratory experiments. Nevertheless, in experiments specimens from one water ("home") reacted similarly, but at different values, to the same gradients of temperature and salinity set up in another water ("foreign"). *Euphausia pacifica* as a resident species in Indian Arm apparently reacts against and becomes distributed at the furthest point away from intruding water that is associated with the presence of other species (*Thysanoessa* spp.). None of the four species entered the deeper water of Indian Arm, except very rarely. Neither of these situations was dependent on changes of salinity or temperature since the changes involved are inclusive in the ranges inhabited by the species in the field and were subsequently shown to be well within the ranges "tolerated" by species in laboratory experiments. The situation has two parallels in the laboratory experiments. Firstly, specimens of *E. pacifica* migrated less freely from their "home" into "foreign" water, than from "home" into "home" water. And secondly, specimens of *E. pacifica* survived better in their "home" waters than in any "foreign" water.

There seems to be little doubt that these several pieces of evidence are mutually supporting. Together they appear to point to a situation wherein neither temperature nor salinity play primary roles in the occurrences of
specimens and therefore in the distributions of the species, (except in the conditions of thermocline and halocline in upper waters), or of populations within the distribution of a single species. In the absence of primary regulatory roles for temperature and salinity, other properties must be invoked, as has been discussed above, and at length by Bary (1963a, 1964). What these properties are and how they operate is not known, but they appear to have their parallel in such concepts as "biological differences" of seawater (Wilson, 1951; Wilson and Armstrong, 1952, 1954) and "qualities" of seawater (Johnston, 1962, 1964).

The present study indicates that the operative properties act directly on the specimens. The inference therefore is that these properties are an integral part of the water. On the other hand, the properties of water from one area differ from those of other, even geographically fairly close, areas. Since, however, there is a continuity between waters of say, the Strait of Georgia and Indian Arm, it would seem reasonable to assume continuity of these special properties. If so, then the regulatory processes are exerted not necessarily by different properties, but presumably by differing proportions of properties common to all of the waters. There is the additional possibility that in particular situations other, distinct properties may be added by, for example, fresh water runoff.

Since there is continuity in space and in time in the properties, demonstrated by the similar sorts of reactions
in the field and laboratory, over a period of two years, the properties must be a relatively permanent feature, even though clearly their "proportions" may be modified, perhaps rapidly. This would suggest they are not solely dependent on being excreted or otherwise obtained as a result of seasonal fluctuations of phytoplankton or other activities of organisms, (Lucas 1947, 1949; Srinivasagam, 1966) but rather that the influence of these and other organic derivatives on the "unique properties" of a water body may be secondary to the role of inorganic materials. (Johnston, 1964).

Of equal importance is the question of how specimens, and species, react to these properties. It is clear that species react to the properties individually i.e., their tolerances differ — although these may be in general similar among several species, as exemplified by the expatriates in Indian Arm. It is equally clear that among populations of a single species (E. pacifica) associated with different bodies of water, tolerances differ from population to population. In laboratory experiments involving migration, reactions to a "foreign" water were immediate in that specimens either did not enter the water at all or, if so, then in fewer numbers than in "home" water. In the experiments involving survival over extended periods, reactions to "foreign" water varied with the location from which the water was collected and in time with a particular water; nevertheless, survival was less than in the accompanying experiments with "home" water. It is more difficult to determine how quickly specimens of a
species react in the field, in part because stations were separated by one or a few miles and the period between sampling in one set of conditions and another was a month or longer. Bary (1964) thought that reactions were chiefly at the boundaries between different water bodies, and the impression from the field data is that this may be the case in Indian Arm.

If specimens are reacting immediately or slowly to properties, "unique" to bodies of water, they must be able to detect not only the property, favourable or otherwise, but also a gradient in the concentration of the property. Presumably detection of the properties is physiological and expressed in behaviour, but how it is accomplished is not known. The aggregation of *E. pacifica* away from water intruding into Indian Arm would suggest specimens escaped by swimming and this may be a usual reaction where it is feasible. On the other hand, the considerable reduction in overall numbers collected, towards the mouth of the inlet in particular, indicate that specimens may have been eliminated by the entering water, or possibly they were flushed out of the inlet; in either case fewer specimens would be left, except perhaps in the up-inlet location.

Among the problems the present study opens up is that exemplified by the differing reactions of populations of *Euphausia pacifica* to their "home" and to a series of "foreign" waters. The evidence can be interpreted in two ways. A group of specimens entering B. C. coastal waters may have among themselves a variety of tolerances which could
enable some specimens to inhabit one set of conditions, and others to inhabit another. This would be feasible if in fact the properties to which they were reacting in different waters were common ones and modified only to the extent, for example, that proportions changed in different waters. Alternatively, the specimens entering coastal areas could be similar in tolerance and subsequently inhabit differing waters by adapting to their properties possibly in one generation or more probably over several. Unfortunately, the data from the present study do not indicate which of these alternatives apply.

The usual taxonomic characters used in the identification of *Euphausia pacifica* (eyes large and spherical, lack of rostrum on carapace, strong denticle near middle of carapace, abdomen without denticles or keels and the structure of the male copulatory organ --- Banner, 1950; Boden, Johnson and Brinton, 1955) were present in specimens of this species collected in Indian Arm, Strait of Georgia and Juan de Fuca Strait. On this basis, they were regarded as local populations, and not subspecies, of a species. If it is assumed that the populations are physiologically adapted (see above) to different, but adjoining, habitats perhaps they may be referred to as "ecological races" of a species. In either case, it is interesting to speculate on the properties of the different waters, and the reactions of specimens to these, which resulted in specimens preferring "home" water over "foreign" waters. This is especially so in view of the
continuity of the various waters.

From the survey above it is apparent that the present study strongly suggests the presence of properties other than (or as well as) temperature and salinity acting as a means of regulating occurrences of some pelagic zooplanktonic species. It is clear also, that many problems have been indicated. There seems little doubt, however, that the relationships between species and waters outlined and the physiological problems implied in these are important to the understanding of the ecology of pelagic organisms.
IX. SUMMARY AND CONCLUSIONS

Temperature-salinity (T-S) diagrams and the geographical distributions of temperature, salinity and density (\(\sigma_t\)) have shown the ranges of temperature and salinity in Indian Arm over a two year period including changes associated with seasonal fluctuations and periodic intrusions of outside water entering the inlet from outside, presumably from the Strait of Georgia through Burrard Inlet.

The adults of four species of euphausiids (\textit{Euphausia pacifica}, \textit{Thysanoessa spinifera}, \textit{Thysanoessa longipes} and \textit{Thysanoessa raschii}) and the developmental stages of \textit{E. pacifica} have been related to environmental conditions in Indian Arm by means of Temperature-Salinity-Plankton (T-S-P) diagrams and by profiles of the inlet showing occurrences in relation to isotherms, isohalines and isopycnals. Of the four species, \textit{E. pacifica} is a resident species and is the most tolerant towards environmental conditions in Indian Arm, followed by the expatriate species \textit{T. spinifera}, \textit{T. longipes} and \textit{T. raschii} in order of decreasing tolerance. All species, whether resident or expatriate, were useful as biological indicators of oceanographic changes in Indian Arm, particularly with reference to the detection of outside waters entering the inlet.

Wide variations in distribution occurred not only amongst species but also within the developmental sequence of the resident species, \textit{E. pacifica}; the earlier develop-
mental stages (nauplii, metanauplii) were markedly restricted in their distribution to deeper water when compared with the broad vertical distribution of the eggs, later developmental stages (calypтопii, furcilia) and the adults.

Indications were that temperature and salinity may have been, at least in part, "regulatory factors", particularly for waters between about 10 m and the surface. The general absence of the expatriate species and the occurrences of only small numbers, or more often the absence, of *E. pacifica* in these upper waters may have been dependent on the reactions of specimens towards the maximum temperature and salinity changes (i.e., thermocline and halocline) characteristic of the upper waters. That portion of the laboratory study concerned with the migration of euphausiids in temperature, salinity and combined temperature-salinity structures demonstrated relationships similar to those for the upper waters in Indian Arm. In the laboratory the migration of specimens decreased as the temperature increased and salinity decreased towards the surface, the effect becoming more pronounced in tests where the rate of change of temperature and salinity were increased and in tests where temperature and salinity structures were combined. These tests indicated, however, that at least some of the specimens were considerably more tolerant of high temperatures and low salinities than was generally indicated by the field studies; and this despite the steeper gradients used in the laboratory. From this it is suggested that even in upper waters in Indian
Arm other properties in addition to temperature and salinity, may also have been instrumental in determining the distribution of euphausiids.

It is believed that while expatriate species were transported into Indian Arm in association with intruding waters, the resident species, at least to some extent, was flushed out of the inlet along with the subsequent volume displacement and transport of resident water. For expatriate specimens which have entered the inlet and for resident specimens which have remained within the inlet, their occurrences and distribution in intermediate-depth and deeper waters indicated the probable presence of regulatory factors other than temperature and salinity. This was subsequently demonstrated in the migration and survival of *E. pacifica* in the laboratory. It is postulated that properties "unique" in some way to different waters, and the reactions of specimens towards these, were important.

From the field study it appeared firstly, that the expatriates transported by intruding waters into Indian Arm were intolerant of the properties of Indian Arm water, and secondly, that the resident species (at least those which were not flushed out of the inlet) while tolerant of the properties of Indian Arm water reacted adversely towards the properties of intruded waters. Furthermore, general absence of *E. pacifica, T. spinifera* and *T. longipes* from the deep waters, below 120 m, and of *T. raschii* from waters below 60m did not appear to be associated with temperature and salinity
but rather to an adverse reaction of specimens towards the "unique properties" of deep water.

In the laboratory specimens of *E. pacifica* were, in general, more tolerant towards "home" water than towards "foreign" waters. Specimens migrated more readily and survived in larger numbers and for longer periods in "home" waters than in "foreign" waters or in mixtures of the two. Again, this was not attributable to temperature or salinity but rather to some other property or properties, and the reactions of specimens towards such, in waters from different but (geographically) continuous locations.

The nature of the "unique properties" is unknown. It is suggested that the small numbers, and often complete absence of expatriate species in Indian Arm, during periods when intruded water from outside was decreasing in influence through mixing and dilution with resident water, may be comparable to the relatively poor survival in the laboratory of populations of *E. pacifica* collected from outside (Strait of Georgia, Juan de Fuca Strait) of Indian Arm and placed in Indian Arm water. This would infer, for specimens associated with outside water, a deficiency of some essential property or properties or (and perhaps as well as) the presence of some deleterious property or properties in Indian Arm water. Similarly, the decrease in abundance and/or shift in distribution of a resident population of *E. pacifica* in Indian Arm, during periodic intrusions of outside water, may be comparable to the lessened capabilities for migration and survival in the
laboratory of *E. pacifica* collected in Indian Arm and placed in "foreign" waters (Strait of Georgia, Juan de Fuca Strait and Malaspina Strait). This would infer, for a population resident to Indian Arm, a deficiency of essential properties and/or the presence of deleterious properties in waters from outside of the inlet.


Institute of Oceanography, University of British Columbia, Data Report No.18, Indian Arm Cruises, 1960.


Regan, L. 1963. Field trials with the Clarke-Bumpus plankton sampler. Effects of coarse- and fine-meshed nets over a range of speeds on euphausiid collections. *University of British Columbia, Institute of Oceanography, Manuscript Rept.*, No. 16. 28 pp., 7 fig.


TABLE 1.
The maximum and minimum temperature, salinity and oxygen values recorded in Indian Arm from January, 1960, through August, 1961.

<table>
<thead>
<tr>
<th></th>
<th>Temperature (°C)</th>
<th>Salinity (°/oo)</th>
<th>Oxygen (ml/l)</th>
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<tbody>
<tr>
<td><strong>Maximum</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>2</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>0m</td>
<td>200m</td>
<td>0m</td>
</tr>
<tr>
<td><strong>Minimum</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
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<td>Apr. 20, 1960</td>
<td>Jan. 4, 1960</td>
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<tr>
<td>Depth</td>
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<td>6</td>
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TABLE 2.

_Euphausia pacifica_

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<th>NO. / m.³</th>
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<tbody>
<tr>
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<tr>
<td>1.0 - 4.9</td>
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</tr>
<tr>
<td>5.0 - 9.9</td>
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</tr>
<tr>
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<td>25.0 - 49.9</td>
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<tr>
<td>50.0 - 74.9</td>
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<tr>
<td>75.0 - 86.0</td>
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TABLE 3.

<table>
<thead>
<tr>
<th></th>
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<tr>
<td><em>Thysanoëssa spinifera</em></td>
<td>1.0 - 1.9</td>
</tr>
<tr>
<td><em>Thysanoëssa longipes</em></td>
<td>2.0 - 2.9</td>
</tr>
<tr>
<td><em>Thysanoëssa raschii</em></td>
<td>3.0 - 5.0</td>
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<tr>
<td></td>
<td>5.1 - 9.9</td>
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<tr>
<td></td>
<td>10.0 - 19.9</td>
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<tr>
<td></td>
<td>20.0 - 30.3</td>
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</tbody>
</table>
The maximum and minimum values of temperature and salinity in which the developmental stages of *Euphausia pacifica* were collected in Indian Arm, from September, 1960 to July-August, 1961.

<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>Temperature (°C)</th>
<th>Salinity (°/oo)</th>
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<tbody>
<tr>
<td></td>
<td>min.</td>
<td>max.</td>
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<tr>
<td>Adults</td>
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<td>Eggs</td>
<td>7.7</td>
<td>16.8</td>
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<tr>
<td>Nauplius I</td>
<td>8.0</td>
<td>11.0</td>
</tr>
<tr>
<td>Nauplius II</td>
<td>7.85</td>
<td>10.3</td>
</tr>
<tr>
<td>Metanauplius</td>
<td>7.85</td>
<td>9.4</td>
</tr>
<tr>
<td>First Calyptopis</td>
<td>8.0</td>
<td>12.4</td>
</tr>
<tr>
<td>Second Calyptopis</td>
<td>8.0</td>
<td>12.4</td>
</tr>
<tr>
<td>Third Calyptopis</td>
<td>7.1</td>
<td>12.5</td>
</tr>
<tr>
<td>First Furcilia</td>
<td>8.1</td>
<td>13.2</td>
</tr>
<tr>
<td>Third Furcilia</td>
<td>8.0</td>
<td>13.2(18.5)</td>
</tr>
<tr>
<td>Sixth Furcilia</td>
<td>8.0</td>
<td>13.8(18.5)</td>
</tr>
</tbody>
</table>
TABLE 5

The maximum and minimum values of temperature and salinity in which adult specimens of *Euphausia pacifica*, *Thysanoessa spinifera*, *Thysanoessa longipes* and *Thysanoessa raschii* were collected in Indian Arm, January, 1960 to July-August, 1961.

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature (°C)</th>
<th>Salinity(‰/oo)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>min.</td>
<td>max.</td>
</tr>
<tr>
<td><em>Euphausia pacifica</em></td>
<td>5.3</td>
<td>13.8</td>
</tr>
<tr>
<td><em>Thysanoessa spinifera</em></td>
<td>6.6</td>
<td>13.7</td>
</tr>
<tr>
<td><em>Thysanoessa longipes</em></td>
<td>7.6</td>
<td>10.3</td>
</tr>
<tr>
<td><em>Thysanoessa raschii</em></td>
<td>8.8</td>
<td>11.7</td>
</tr>
</tbody>
</table>
TABLE 6

The vertical migration of *Euphausia pacifica* in relation to salinity when varying temperature structures are superimposed upon similar salinity structures (Figs. 133, 134 and 135).

<table>
<thead>
<tr>
<th>Figure</th>
<th>Mean Salinity Gradient ($^\circ$/oo/cm)</th>
<th>Mean Temperature Gradient ($^\circ$/cm)</th>
<th>Salinity Range of Unrestricted Migration (100%)</th>
<th>Salinity Range of Decreasing Migration</th>
<th>Limiting Salinity With no Further Migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>133</td>
<td>0.38</td>
<td>0.08</td>
<td>$26.5-21.3^\circ$/oo</td>
<td>$19.7-8.5^\circ$/oo</td>
<td>$8.5^\circ$/oo</td>
</tr>
<tr>
<td>134</td>
<td>0.39</td>
<td>0.40</td>
<td>$26.9-22.2^\circ$/oo</td>
<td>$20.8-10.0^\circ$/oo</td>
<td>$10.0^\circ$/oo</td>
</tr>
<tr>
<td>135</td>
<td>0.42</td>
<td>0.58</td>
<td>$26.9-24.0^\circ$/oo</td>
<td>$22.9-14.8^\circ$/oo</td>
<td>$14.8^\circ$/oo</td>
</tr>
</tbody>
</table>
TABLE 7

The vertical migration of *Euphausia pacifica* in relation to temperature, when salinity structures are superimposed upon temperature structures (Fig. 136).

<table>
<thead>
<tr>
<th>Mean Temperature Gradient (°C/cm)</th>
<th>Mean Salinity Gradient (°/oo/cm)</th>
<th>Temperature Range of Unrestricted Migration (100%)</th>
<th>Temperature Range of Decreasing Migration</th>
<th>Limiting Temperature With No Further Migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) 0.41</td>
<td>0.00</td>
<td>9.0-14.7 °C</td>
<td>16.2-25.5 °C</td>
<td>25.5 °C</td>
</tr>
<tr>
<td>(b) 0.40</td>
<td>0.39</td>
<td>9.0-13.6 °C</td>
<td>14.7-23.0 °C</td>
<td>23.0 °C</td>
</tr>
<tr>
<td>(c) 0.58</td>
<td>0.42</td>
<td>9.0-13.0 °C</td>
<td>14.0-22.3 °C</td>
<td>22.3 °C</td>
</tr>
</tbody>
</table>
Survival in the laboratory of *Euphausia pacifica* in "home" water (Indian Arm) and in "foreign" waters (Strait of Georgia, Juan de Fuca Strait and Malaspina Strait). Euphausiids collected in Indian Arm. Temperature constant at 10 °C. Waters adjusted to similar salinities.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Date</th>
<th>Water</th>
<th>Salinity</th>
<th>Survival Percentage</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>143a</td>
<td>June 16 - Aug. 6, 1965</td>
<td>- I.A. (control)</td>
<td>26.9</td>
<td>80%</td>
<td>(52)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Geo.</td>
<td>26.3</td>
<td>nil</td>
<td>(9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>26.5</td>
<td>50%</td>
<td>(42)</td>
</tr>
<tr>
<td>143b</td>
<td>Dec. 9, 1965 - Jan. 20, 1966</td>
<td>- I.A. (control)</td>
<td>26.6</td>
<td>100%</td>
<td>(43)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Geo.</td>
<td>26.8</td>
<td>50%</td>
<td>(43)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>26.5</td>
<td>nil</td>
<td>(9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Geo.</td>
<td>26.8</td>
<td>30%</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>26.8</td>
<td>nil</td>
<td>(47)</td>
</tr>
<tr>
<td>144b</td>
<td>Feb. 25 - Mar. 30, 1966</td>
<td>- I.A. (control)</td>
<td>26.9</td>
<td>60%</td>
<td>(33)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>26.5</td>
<td>10%</td>
<td>(33)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Mal.</td>
<td>26.7</td>
<td>nil</td>
<td>(6)</td>
</tr>
<tr>
<td>145a</td>
<td>April 15 - June 1, 1966</td>
<td>- I.A. (control)</td>
<td>26.9</td>
<td>57%</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I.A.-J. de F. (1:1)</td>
<td>26.85</td>
<td>nil</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>26.8</td>
<td>13%</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- J. de F.</td>
<td>33.12</td>
<td>nil</td>
<td>(47)</td>
</tr>
<tr>
<td>145b</td>
<td>April 15 - June 1, 1966</td>
<td>- I.A. (control)</td>
<td>26.9</td>
<td>57%</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I.A.-Mal. (3:1)</td>
<td>26.88</td>
<td>10%</td>
<td>(39)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I.A.-Mal. (2:1)</td>
<td>26.87</td>
<td>nil</td>
<td>(34)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I.A.-Mal. (1:1)</td>
<td>26.85</td>
<td>nil</td>
<td>(6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Mal.</td>
<td>26.8</td>
<td>nil</td>
<td>(3)</td>
</tr>
</tbody>
</table>

I.A. - Indian Arm; Geo. - Strait of Georgia; J. de F. - Juan de Fuca Strait; Mal. - Malaspina Strait.

1 unfiltered seawater; 2 undiluted; 3 circles; 4 triangles
TABLE 9

Survival in the laboratory of *Euphausia pacifica* in "home" and "foreign" waters. *Euphausiids collected in Juan de Fuca Strait.* Temperature constant at 10°C. Waters adjusted to similar salinities.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Date</th>
<th>Water</th>
<th>Salinity</th>
<th>Survival Percentage</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>146a</td>
<td>Dec. 9, 1965-</td>
<td>- J.de F. (control)</td>
<td>32.8</td>
<td>80% (43)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Jan. 20, 1966</td>
<td>- J.de F.</td>
<td>26.5</td>
<td>100% (43)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>- Geo.</td>
<td>26.8</td>
<td>50% (43)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I. A.</td>
<td>26.6</td>
<td>80% (43)</td>
<td></td>
</tr>
<tr>
<td>146b</td>
<td>Jan. 26 -</td>
<td>- J. de F.</td>
<td>26.8</td>
<td>60% (31)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Feb. 25, 1966</td>
<td>- Geo.</td>
<td>26.8</td>
<td>20% (31)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>- I. A.</td>
<td>26.9</td>
<td>30% (31)</td>
<td></td>
</tr>
</tbody>
</table>

J. de F. - Juan de Fuca Strait; Geo. - Strait of Georgia; I. A. - Indian Arm.

1 undiluted seawater
TABLE 10

Survival in the laboratory of *Euphausia pacifica* in "home" and "foreign" waters. *Euphausiids collected in the Strait of Georgia.* Temperature constant at 10°C. Waters adjusted to similar salinities.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Date</th>
<th>Water</th>
<th>Salinity</th>
<th>Survival Percentage</th>
<th>Survival days</th>
</tr>
</thead>
<tbody>
<tr>
<td>147a</td>
<td>July 27 - Sept.3,1965</td>
<td>-Geo. 1</td>
<td>26.3</td>
<td>nil</td>
<td>(34)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-I.A. 1</td>
<td>26.4</td>
<td>nil</td>
<td>(37)</td>
</tr>
<tr>
<td>147b</td>
<td>Sept. 8 - Oct.16,1965</td>
<td>-Geo. 1</td>
<td>26.8</td>
<td>50%</td>
<td>(37)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-I.A. 1</td>
<td>26.6</td>
<td>40%</td>
<td>(37)</td>
</tr>
</tbody>
</table>

J. de F. - Juan de Fuca Strait; Geo.- Strait of Georgia; I. A. - Indian Arm.  

1 unfiltered seawater
Fig. 1 -- Indian Arm, British Columbia, and adjacent regions.

a -- Location of oceanographic and plankton stations in Indian Arm.

b -- Locations of collections of euphausiids and seawater for laboratory studies (A - Indian Arm, B - Malaspina Strait, C - Strait of Georgia and D - Juan de Fuca Strait).
Fig. 2 — Mean temperature-salinity (T-S) curves for the period from September, 1960 to July-August, 1961, for those standard depths applicable at Stations 2, 6, 9, 12 15 and 23 (see text). Fluctuations in temperature and salinity are shown for surface water (between 0 and about 5m), transition water at intermediate depths (approximately 5 to 75m) and for deep water (between about 75m and the bottom at 200m).
Fig. 3 -- Temperature-salinity diagram of Indian Arm for January, 1960. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 4 -- As above, for February, 1960.
Fig. 5 -- Temperature-salinity diagram of Indian Arm for March, 1960. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 6 -- As above, for April, 1960.
Fig. 7 -- Temperature-salinity diagram of Indian Arm for June, 1960. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 8 -- As above, for July, 1960.
Fig. 9 -- Temperature-salinity diagram of Indian Arm for September, 1960. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 10 -- As above, for October, 1960.
Fig. 11 -- Temperature-salinity diagram of Indian Arm for December, 1960. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 12 -- As above, for January, 1961.
Fig. 13 -- Temperature-salinity diagram of Indian Arm for February, 1961. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 14 -- As above, for March, 1961.
Fig. 15 -- Temperature-salinity diagram of Indian Arm for April, 1961. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.

Fig. 16 -- As above, for June, 1961.
Fig. 17 — Temperature-salinity diagram of Indian Arm for July-August, 1961. Inserts show isotherms (a) and isohalines (b) in longitudinal sections of the inlet.
Fig. 18 -- Fluctuations in the distribution of density in Indian Arm as shown by the three selected isopycnals of $\tau$ 19.5, 20.75 and 21.0, between January and June, 1960.
Fig. 19 -- Fluctuations in the distribution of density in Indian Arm as shown by the three selected isopycnals of $\sigma_t$ 19.5, 20.75 and 21.0, between July 1960, and January, 1961.
STATION NUMBERS

JUL. '60

SEP. '60

OCT. '60

DEC. '60

JAN. '61
Fig. 20 — Fluctuations in the distribution of density in Indian Arm as shown by the three selected isopycnals of $\sigma_t$ 19.5, 20.75 and 21.0, between February and July - August, 1961.
Fig. 21 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of adults of Euphausia pacifica are shown in relation to total ranges of temperature (°C) and salinity (o/oo) for the period from September, 1960, to July-August, 1961. In this and in Figs. 22-27 specimens are shown only as being present (points within a line or lines) or absent.
Fig. 22 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of eggs (points within solid lines) and first nauplius stage (within dotted lines) of Euphausia pacifica are shown in relation to total ranges of temperature (°C) and salinity (°/oo) for the period from September, 1960, to July-August, 1961. Eggs were collected only during March through July-August, 1961; first nauplius stage collected only during April through July-August, 1961.
Fig. 23 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of second nauplius stage (points within dotted lines) and metanauplius (within solid lines) of *Euphausia pacifica* are shown in relation to total ranges of temperature (°C) and salinity (‰) for the period from September, 1960, to July-August, 1961. Specimens were collected only during April through July-August, 1961.
Euphausia pacifica

Temperature vs. Salinity

June, July-August

September, October

March, April

December, January, February

Salinity (‰)

Temperature (°C)
Fig. 24 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of first, second and third calyptopis stages (points within solid line) as a group, are shown in relation to total ranges of temperature (°C) and salinity (°/oo) for the period from September, 1960, to July-August, 1961. Calyptopii were collected only during September and October, 1960, and April through July-August, 1961.
Euphausia pacifica

Calyptopis I, II, III

JUNE, JUL.-AUG.

SEPT., OCT.

MAR., APR.

DEC., JAN., FEB.
Fig. 25 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of first, third and sixth furcilia stages (points within solid lines), as a group, are shown in relation to total ranges of temperature (°C) and salinity (°/oo) for the period from September, 1960, to July-August, 1961. Furcilia were collected only during September and October, 1960, and during April through July-August, 1961.
Fig. 26 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences (points within solid line) of adults of Thysanoessa spinifera are shown in relation to total ranges of temperature (°C) and salinity (°/oo) for the period from September, 1960, to July-August, 1961.
Fig. 27 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm in which the occurrences of adult specimens of *Thysanoessa longipes* (points within solid line) and *Thysanoessa raschii* (within dotted line) are shown in relation to total ranges of temperature (°C) and salinity (°/oo) for the period from September, 1960, to July-August, 1961.
Thysanoessa longipes
ADULTS

Thysanoessa raschi
ADULTS

JUNE, JUL.-AUG.
MAR., APR.
DEC., JAN., FEB.
SEPT., OCT.
Fig. 28 — The geographical occurrences of adults of *Euphausia pacifica*; (a), *Thysanoessa spinifera* (b), *Thysanoessa longipes* (c) and *Thysanoessa raschii* (d) in longitudinal sections of Indian Arm for the period from September, 1960, through July-August, 1961. Specimens are shown only as being present (hatched areas) or absent.
STATION NUMBERS

**Euphausia pacifica ADULTS**

**Thysanoessa spinifera ADULTS**

**Thysanoessa longipes ADULTS**

**Thysanoessa raschii ADULTS**
Fig. 29 — The geographical occurrences of the developmental stages (eggs (a); first (b) and second (c) nauplius stages; metanauplius (d); first, second and third calyptopis stages (e); and first, third and sixth furcilia stages (f) ) of Euphausia pacifica in longitudinal sections of Indian Arm for the period from September, 1960, through July-August, 1961. Specimens are shown only as being present (hatched areas) or absent.
Fig. 30 — Temperature-salinity-plankton (T-S-P) diagram showing night (blocked-in circles) and day (open circles) occurrences of adults of Euphausia pacifica in relation to temperature and salinity for January, 1960. Insert shows the occurrences in subsurface waters on an expanded scale. Relative abundance (no./m³) is indicated by the diameter of circle (see Table 2). Depths, in metres, indicate vertical ranges of groups of temperature-salinity intercepts and euphausiids at six stations in Indian Arm.

Fig. 31 — As above, for February, 1960.
Fig. 32 — Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Euphausia pacifica* for March, 1960. For details, see caption of Fig. 30.

Fig. 33 — As above, for April, 1960.
Fig. 34 — Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Euphausia pacifica for June, 1960. For details, see caption of Fig. 30.

Fig. 35 — As above, for July, 1960. Insert not included.
Fig. 36 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Euphausia pacifica* for September, 1960. For details, see caption of Fig. 30.

Fig. 37 -- As above, for October, 1960.
Fig. 38 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Euphausia pacifica for December, 1960. For details, see caption of Fig. 30.

Fig. 39 -- As above, for January, 1961.
Fig. 40 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults *Euphausia pacifica* for February, 1961. For details, see caption of Fig. 30.

Fig. 41 -- As above, for March, 1961.
Fig. 42 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Euphausia pacifica for April, 1961. For details, see caption of Fig. 30.

Fig. 43 -- As above, for June, 1961. Insert not included.
Fig. 44 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Euphausia pacifica* for July-August, 1961. For details, see caption of Fig. 30.
Fig. 45 (a-o) — Longitudinal sections of Indian Arm showing occurrences during the night (blocked-in circles) and day (open circles) of adults of Euphausia pacifica, between January, 1960, and July-August, 1961. Relative abundance (no./m$^3$) is indicated by the diameter of the circle.
Fig. 46 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing occurrences of eggs of Euphausia pacifica for March, 1961. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and eggs were obtained at six stations. Insert: the occurrences in longitudinal section of Indian Arm. Relative abundance (no./m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 47 -- As above, for April, 1961.
Fig. 48 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing occurrences of eggs of Euphausia pacifica for June, 1961. For details, see caption of Fig. 46.

Fig. 49 — As above, for July-August, 1961.
JUNE, 1961

JULY - AUGUST, 1961
Fig. 50 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first nauplius stage of *Euphausia pacifica* for April, 1961. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and nauplii were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).
Fig. 51 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first nauplius stage of *Euphausia pacifica* for June, 1961. For details, see caption of Fig. 50.

Fig. 52 -- As above, for July- August, 1961.
Fig. 53 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the second nauplius stage of Euphausia pacifica for April, 1961. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and nauplii were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).
Fig. 54 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the second nauplius stage of Euphausia pacifica for June, 1961. For details, see caption of Fig. 53.

Fig. 55 -- As above, for July-August, 1961.
Fig. 56 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of metanauplius of Euphausia pacifica for April, 1961. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and metanauplii were obtained at six stations. Insert: occurrences in a longitudinal section of Indian Arm. Relative abundance (no./m$^3$) is indicated by the diameter of the circle (see Table 2).
Fig. 57 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of metanauplius of Euphausia pacifica for June, 1961. For details, see caption of Fig. 56.

Fig. 58 -- As above, for July-August, 1961.
Fig. 59 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first calyptopis stage of Euphausia pacifica for September, 1960. Depths, in metres, indicated the vertical range from which groups of temperature-salinity intercepts and calyptopii were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no./m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 60 -- As above, for April, 1961.
Fig. 61 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first calyptopis stage of *Euphausia pacifica* for June, 1961. For details, see caption of Fig. 59.

Fig. 62 -- As above, for July-August, 1961.
Fig. 63 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the second calyptopis stage of Euphausia pacifica for September, 1960. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and calyptopii were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 64 -- As above, for April, 1961.
Fig. 65 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the second calyptopis stage of Euphausia pacifica for June, 1961. For details, see caption of Fig. 63.

Fig. 66 — As above, for July-August, 1961.
Fig. 67 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the third calyptopis stage of *Euphausia pacifica* for October, 1960. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and calyptopii were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 68 — As above, for April, 1961.
Fig. 69 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the third calyptopis stage of *Euphausia pacifica* for June, 1961. For details, see caption of Fig. 67.

Fig. 70 -- As above, for July-August, 1961.
Fig. 71 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first furcilia stage of Euphausia pacifica for September, 1960. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and furcilia were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 72 -- As above, for April, 1961.
Fig. 73 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the first furcilia stage of Euphausia pacifica for June, 1961. For details, see caption of Fig. 71.

Fig. 74 -- As above, for July-August, 1961.
Fig. 75 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the third furcilia stage of *Euphausia pacifica* for September, 1960. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and furcilia were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no./m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 76 -- As above, for April, 1961.
Fig. 77 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the third furcilia stage of Euphausia pacifica for June, 1961. For details, see caption of Fig. 75.

Fig. 78 — As above, for July-August, 1961.
Fig. 79 -- Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the sixth furcilia stage of *Euphausia pacifica* for September, 1960. Depths, in metres, indicate the vertical range from which groups of temperature-salinity intercepts and furcilia were obtained at six stations. Insert: the occurrences in a longitudinal section of Indian Arm. Relative abundance (no. /m$^3$) is indicated by the diameter of the circle (see Table 2).

Fig. 80 -- As above, for October, 1960.
Fig. 81 — Temperature-salinity-plankton (T-S-P) diagram of Indian Arm showing the night (blocked-in circles) and day (open circles) occurrences of the sixth furcilia stage of Euphausia pacifica for June, 1961. For details, see caption of Fig. 79.

Fig. 82 — As above, for July-August, 1961
Fig. 83 -- Temperature-salinity-plankton (T-S-P) diagram showing night (blocked-in circles) and day (open circles) occurrences of adults of Thysanoessa spinifera in relation to temperature and salinity for January, 1960. Insert shows the occurrences in subsurface waters on an expanded scale. Relative abundance (no./10 m$^3$) is indicated by the diameter of the circle (see Table 3). Depths, in metres, indicate vertical ranges of groups of temperature-salinity intercepts and euphausiids at six stations in Indian Arm.

Fig. 84 -- As above, for February, 1960.
Fig. 85 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa spinifera for March, 1960. For details, see caption of Fig. 83.

Fig. 86 -- As above, for April, 1960.
Fig. 87 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa spinifera for June, 1960. For details, see caption of Fig. 83.

Fig. 88 -- As above, for July, 1960.
Fig. 89 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa spinifera* for September, 1960. For details, see caption of Fig. 83.

Fig. 90 -- As above, for October, 1960.
Fig. 91 — Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa spinifera for December, 1960. For details, see caption of Fig. 83.

Fig. 92 — As above, for January, 1961.
Fig. 93 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa spinifera* for February, 1961. For details, see caption of Fig. 83.

Fig. 94 -- As above, for March, 1961.
Fig. 95 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa spinifera for April, 1961. For details, see caption of Fig. 83.

Fig. 96 -- As above, for June, 1961.
Fig. 97 — Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa spinifera* for July-August, 1961. For details, see caption of Fig. 83.
Fig. 98 (a–o) -- Longitudinal sections of Indian Arm showing occurrences during the night (blocked-in circles) and day (open circles) of adults of Thysanoessa spinifera, between January, 1960, and July-August, 1961. Relative abundance (no. /10m³) is indicated by the diameter of the circle.
Fig 99 -- Temperature-salinity-plankton (T-S-P) diagram showing night (blocked-in circles) and day (open circles) occurrences of adults of *Thysanoessa longipes* in relation to temperature and salinity for January, 1960. Relative abundance (no. /10m³) is indicated by the diameter of the circle (see Table 3). Depths, in metres, indicate the vertical range of groups of temperature-salinity intercepts and euphausiids at six stations in Indian Arm.

Fig. 100 -- As above, for February, 1960.
Fig. 101 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa longipes* for March, 1960. For details, see caption of Fig. 99.

Fig. 102 -- As above, for April, 1960.
Fig. 103 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa longipes* for June, 1960. For details, see caption of Fig. 99.

Fig. 104 -- As above, for July, 1960.
JUNE, 1960

TEMPERATURE (°C) vs. SALINITY (%0)

JULY, 1960

TEMPERATURE (°C) vs. SALINITY (%0)
Fig. 105.— Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa longipes* for September, 1960. Insert shows the region which is presented on an expanded scale in subsequent months. For details, see caption of Fig. 99.

Fig. 106 — As above, for October, 1960. Insert shows the occurrences in subsurface waters on an expanded scale of temperature and salinity.
Fig. 107 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa longipes* for December, 1960. For details, see caption of Figs. 99 and 106.

Fig. 108 -- As above, for January, 1961.
Fig. 109 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa longipes* for April, 1961. For details, see captions of Figs. 99 and 106.

Fig. 110 -- As above, for June, 1961.
Fig. 111 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa longipes for July-August, 1961. For details, see captions of Fig. 99 and 106.
Fig. 112 (a-o) — Longitudinal sections of Indian Arm showing occurrences during the night (blocked-in circles) and day (open circles) of adults of *Thysanoessa longipes*, between January, 1960, and July-August, 1961. Relative abundance (no. /10m³) is indicated by the diameter of the circle.
Fig. 113 -- Temperature-salinity-plankton (T-S-P) diagram showing night (blocked-in circles) and day (open circles) occurrences of adults of Thysanoessa raschii in relation to temperature and salinity for July, 1960. Depths, in metres, indicate the vertical range of groups of temperature-salinity intercepts and specimens at six stations. Insert shows the occurrence in a longitudinal section of Indian Arm. Relative abundance (no. /10m$^3$) is indicated by the diameter of the circle (see Table 3).

Fig. 114 -- As above, for September, 1960.
Fig. 115 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of Thysanoessa raschii for October, 1960. For details, see caption of Fig. 113.

Fig. 116 -- As above, for December, 1960.
Fig. 117 -- Temperature-salinity-plankton (T-S-P) diagram of occurrences of adults of *Thysanoessa raschii* for July-August, 1961. For details, see caption of Fig. 113.
Fig. 118 -- Temperature and salinity structures in Indian Arm with respect to the vertical distribution and abundance of Euphausia pacifica at Station 9, night and day collections combined, February, 1961.
Fig. 119 -- Temperature and salinity structures in Indian Arm with respect to the vertical distribution and abundance of Euphausia pacifica at Station 9, night and day collections combined, March, 1961.
Fig. 120 -- Temperature and salinity structures in Indian Arm with respect to the vertical distribution and abundance of *Euphausia pacifica* at Station 9, night and day collections combined, June, 1961.
Fig. 121 -- Photograph of apparatus used in observing the migration of euphausiids in temperature and salinity structures in the laboratory. Front view.
Fig. 122 — Photograph of apparatus used in observing the migration of euphausiids in temperature and salinity structures in the laboratory. Back view.
Fig. 123 — Photographs of apparatus used in observing the migration of euphausiids in the laboratory. Layers of differing salinities are alternately stained in order to demonstrate the establishment and nature of the salinity structure (salinity variation of 1.3 °/oo between layers or a mean gradient of 0.4 °/oo/cm over the entire column).
Fig. 124 — Vertical migration in the laboratory (numbers reaching a particular level as percentage of total migrations) of Euphausia pacifica from Indian Arm, in salinity structures composed of "home" water (Indian Arm) and of "foreign" waters (Strait of Georgia, Juan de Fuca Strait). Mean salinity gradient of 0.4 °/oo/cm; temperature constant.

- - - - - : mean percentage migration for five tests in salinity structures composed of Indian Arm water. Twenty adults in each test. Individual tests on April 1 ( ■ ), April 2 ( ● ), April 30 ( ▼ ), June 26 ( ▲ ) and July 9 ( X ), 1964.

- - - - - : mean percentage migration for three tests in salinity structures composed of "foreign" waters. Twenty adults in each test. Individual tests on May 23 ( □ ) and June 12 ( ○ ), 1964, in Juan de Fuca Strait water, and on September 29 ( △ ), 1964, in Strait of Georgia water.
Fig. 125 -- Vertical migration in the laboratory of Euphausia pacifica, adults and furcilia, from Indian Arm in a salinity structure composed of Indian Arm water. Mean salinity gradient of 0.4 °/oo/cm; temperature constant. Twenty adults and 20 furcilia in the test. June, 26, 1964.
Fig. 126 — Vertical migration in the laboratory of Euphausia pacifica from Indian Arm in relation to rate of change in salinity structures. Twenty adults in each of two tests in salinity structures with salinity decreasing in "steps" approximating 1.3 °/oo (A) and 3.0 °/oo (B) per layer. Temperature constant. July 9, 1964.
Fig. 127 — A composite diagram showing maximum and minimum salinities in relation to the vertical migration of adult Euphausia pacifica in the laboratory. ○ - mean percentage migration for five tests, April - July, 1964, in a mean salinity gradient of 0.4 °/oo/cm; ● - percentage migration for one test, May 23, 1964, in a mean salinity gradient of 0.3 °/oo/cm. Twenty specimens in each test. Temperature constant.
Fig. 128 — Comparison of the vertical migration in the laboratory of Euphausia pacifica and Thysanoessa spinifera from Indian Arm in a salinity structure composed of Indian Arm water. Twenty adults of each species in each of two tests, in a structure with salinity decreasing at approximately 3.0 °/oo per layer. Temperature constant. July 9, 1964.
I OH 20-
CL 30'
Q 40H 504

SALINITY (‰)

0 5 10 15 20 25 28

DEPTH (cm)

% MIGRATION

O Euphausia pacifica
■ Thysanoessa spinifera

100 94 20
100 67
100
100
Fig. 129 — Vertical migration in the laboratory of Thysanoessa longipes from the Strait of Georgia in a salinity structure composed of Strait of Georgia water. Fifteen adult euphausiids in a mean salinity gradient of 0.4 °/oo/cm. Temperature constant. September 30, 1964.
SALINITY (%)

SALINITY (‰)

DEPTH (cm)

% MIGRATION

Thysanoëssa longipes
Fig. 130 -- Vertical migration in the laboratory (numbers reaching a particular level as percentage of total migrations) of Euphausia pacifica from Indian Arm in temperature structures composed of Indian Arm water. Salinity constant. Individual tests on October 22 (△, ○), 1965, and on March 3 (□), 1966. Twenty adults in each test.
Fig. 131 — A summary diagram showing temperature structures in the laboratory in relation to the migration of Euphausia pacifica from Indian Arm. Salinity constant. Migration tests on October 15 - 22, 1965 and on March 3, 1966. Twenty adults in each test.
Fig. 132 -- Vertical migration in the laboratory of Thysanoessa spinifera from Indian Arm in a temperature structure composed of Indian Arm water. Salinity constant. Twenty adults in a temperature structure of 0.68 °C/cm. March 3, 1966.
Thysanoëssa spinifera

% MIGRATION

TEMPERATURE (°C)
Fig. 133 — Vertical migration in the laboratory of *Euphausia pacifica* from Indian Arm in combined temperature and salinity structures composed of Indian Arm water. Mean percentage migration of five tests, April - July, 1964. Twenty adults in each test.
Fig. 134 — Vertical migration in the laboratory of Euphausia pacifica from Indian Arm in combined temperature and salinity structures composed of Indian Arm Water. Twenty adults in the test. October 12, 1965.
Fig. 135 — Vertical migration in the laboratory of *Euphausia pacifica* from Indian Arm in combined temperature and salinity structures composed of Indian Arm water. Twenty adults in the test. March 4, 1966.
Fig. 136 — A summary diagram showing the effect on the vertical migration of *Euphausia pacifica*, with respect to temperature, when salinity structures are imposed upon temperature structures. Solid line represents the mean percentage migration for three tests, October 15 - 22, 1965. Dashed line represents a migration test on October 12, 1965. Dotted line represents a migration test on March 4, 1966. Twenty adults in each test.
The image contains a graph with the x-axis labeled 'Temperature (°C)' and the y-axis labeled 'Migration (%)'. The graph shows three curves labeled 'a', 'b', and 'c', each with different markers and line styles. The table below the graph lists the mean gradient data for each curve:

<table>
<thead>
<tr>
<th></th>
<th>T C/cm</th>
<th>S%°/cm</th>
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</thead>
<tbody>
<tr>
<td>a</td>
<td>0.41</td>
<td>0.00</td>
</tr>
<tr>
<td>b</td>
<td>0.40</td>
<td>0.39</td>
</tr>
<tr>
<td>c</td>
<td>0.58</td>
<td>0.42</td>
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</tbody>
</table>
Fig. 137 — A summary diagram comparing the distribution and migration of *Euphausia pacifica* with respect to temperature and salinity, in Indian Arm and in the laboratory.

Laboratory results are presented as contours at 0, 25, 50, 75, 100% migrations in conditions of:

- o - salinity structures with constant temperature (mean of five tests, April – July, 1964)
- • - temperature structures with constant salinity (mean of three tests, October 15 – 22, 1965)
- combined temperature and salinity structures; △ - one test, October 12, 1965 and □ - one test, March 4, 1966.

Presence in the field (Indian Arm) relative to temperature and salinity: \ ////////// between December and March, 1960 - 1961; ////////// between April and October, 1961.)
Fig. 138 — Summary diagrams comparing the general occurrences and the migrations of Euphausia pacifica, with respect to temperature and salinity in Indian Arm and in the laboratory.

**top** — Distributional limits of *E. pacifica* in Indian Arm for one year (1960 - 1961).
- Zone 1 — maximum abundance of specimens
- Zone 2 — specimens few or rare
- Zone 3 — specimens not collected

**bottom** — Migration of *E. pacifica* in the laboratory.
- Zone A — unrestricted migration
- Zone B — decreasing migration
- Zone C — no migration
Fig. 139 -- Vertical migration in the laboratory of Euphausia pacifica in "home" water (Indian Arm) and in "foreign" water (Juan de Fuca Strait), when neither temperature nor salinity are limiting. Salinities are indicated; temperature, 10°C. Migrations in three variations of light intensity indicated by ↓; 15 adults in each test. June 18, 1965.

a. Migration in a column of Indian Arm water with no salinity decrease (control).
b. Migration in a column of Indian Arm water with a small salinity decrease (1.32 °/oo) separating lower and upper waters.
c. Migration in a column containing two waters (Indian Arm and Juan de Puca Strait) separated by a small salinity decrease (1.07 °/oo).
Fig. 140 — Vertical migration in the laboratory of Euphausia pacifica in "home" water (Juan de Fuca Strait) and in "foreign" water (Indian Arm), when neither temperature nor salinity are limiting. Salinities are indicated; temperature, 10°C. Migrations in three variations of light intensity indicated by; ↓; 15 adults in each test. December 10, 1965.

a. Migration in a column of Juan de Fuca Strait water with no salinity decrease (control).

b. Migration in a column of Juan de Fuca Strait water with a small salinity decrease (0.94 °/oo) separating lower and upper waters.

c. Migration in a column containing two waters (Juan de Fuca Strait and Indian Arm) separated by a small salinity decrease (0.26 °/oo).
Fig. 141 — Survival in the laboratory of Euphausia pacifica from Indian Arm in dilutions of Indian Arm water. Ten adults transferred to progressively diluted waters at two day intervals until none survived; 10 adults in control at 26.9 °/oo during the ten days of March 12 - 21, 1966.
Fig. 142 -- Survival in the laboratory of Euphausia pacifica from Indian Arm in dilutions of Indian Arm water. Seventeen adults transferred to progressively diluted waters at two-day intervals until none survived; 17 adults in control at 26.9 °/oo during the twelve days of April 18 – 29, 1966.
Fig. 143 — Survival in the laboratory of Euphausia pacifica in "home" water (Indian Arm) and in "foreign" waters (Strait of Georgia, Juan de Fuca Strait). Indian Arm specimens in "home" water acts as a control.

a.-- 10 adults/4 litres in each of the three waters. Salinity range, 26.3 - 26.9 °/oo; temperature, 10°C. June 16 - August 6, 1965.

b.-- 10 adults/4 litres in each of the three waters. Salinity range, 26.5 - 26.8 °/oo; temperature, 10°C. December 9, 1965 - January 20, 1966.
Fig. 144 — Survival in the laboratory of Euphausia pacifica in "home" (Indian Arm) and in "foreign" waters (Strait of Georgia, Juan de Fuca Strait and Malaspina Strait). Specimens in Indian Arm water act as a control.

a — 10 adults/4 litres of each of the three waters. Salinity range, 26.8 - 26.9 °/oo; temperature, 10°C. January 26 - March 14, 1966.

b — 20 adults/4 litres in Indian Arm (control) and Juan de Fuca Strait waters; 10 adults/4 litres of Malaspina Strait water. Salinity range, 26.5 - 26.9 °/oo; temperature, 10°C. February 25 - March 30, 1966.
Survival in the laboratory of *Euphausia pacifica* in "home" water (Indian Arm), in "foreign" water (Juan de Fuca Strait) and in a mixture of equal parts of the two. Specimens in Indian Arm water act as a control. Ten adults/4 litres (total of 40 animals) in each (circles) of Indian Arm, diluted Juan de Fuca Strait and mixture waters, with a salinity range of 26.8 - 26.9 °/oo. Ten adults/4 litres in undiluted (33.1 °/oo - triangles) water from Juan de Fuca Strait. Temperature, 10°C. April 15 - June 1, 1966.

Survival in the laboratory of *Euphausia pacifica* in "home" water (Indian Arm), in "foreign" water (Malaspina Strait) and in three mixtures of these. Ten adults/4 litres (total 40 animals) in Indian Arm water (control); 10 adults/4 litres in Malaspina water and in each of the mixtures. Salinity, 26.8 - 26.9 °/oo; temperature, 10°C. April 15 - June 1, 1966.
Fig. 146 — Survival in the laboratory of Euphausia pacifica in "home" water (Juan de Fuca Strait) and in "foreign" waters (Strait of Georgia, Indian Arm). Specimens in Juan de Fuca water (diluted and undiluted) act as controls. Temperature, 10°C.

a -- 10 adults/ 4 litres in each of diluted Juan de Fuca Strait, Strait of Georgia and Indian Arm waters, with a salinity range of 26.5 - 26.8 °/oo; 10 adults/ 4 litres in undiluted (32.8 °/oo) water from Juan de Fuca Strait. December 9, 1965 - January 20, 1966.

b -- 10 adults/ 4 litres in each of diluted Juan de Fuca Strait, Strait of Georgia and Indian Arm waters, with a salinity range of 26.8 - 26.9 °/oo. January 26 - February 25, 1966.
Fig. 147 — Survival in the laboratory of *Euphausia pacifica* in "home" water (Strait of Georgia) and in "foreign" water (Indian Arm). Specimens in Strait of Georgia water act as a control.


b — 10 adults / 4 litres in the two waters. Salinity range, 26.6 - 26.8 ‰; temperature, 10°C. September 8 - October 16, 1965.