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DISTRIBUTION AND PHYSIOLOGY OF
ZOOPLANKTON IN AN OXYGEN MINIMUM LAYER

by

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ABSTRACT

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Saanich Inlet, a British Columbia fjord, is deep, stratified, and has a permanent oxygen minimum layer below the sill depth of 80 meters. Zooplankton are exceptionally plentiful down to and below sill depth and several species inhabit the oxygen deficient zone.

The relationship between the vertical distribution of zooplankton and dissolved oxygen concentrations in Saanich Inlet was examined and related to results of experiments of their low oxygen tolerance levels, respiration rates, and respiratory blood pigment concentrations. Similar analyses were conducted in Bute Inlet, a control environment without an oxygen deficient zone.

All zooplankton was collected and quantified from predetermined depths utilizing the Brown-McGowan opening and closing net (Brown & McGowan, 1966) with a depth-time recorder. The survival of the species was measured at an oxygen concentration of 0.40 ml/l, the concentration at which the zooplankton aggregation occurred in Saanich Inlet. Laboratory experiments were run in oxygen tolerance equipment developed at the University of Victoria. Survival levels were determined in the field by lowering specimens in cylinders which were in communication with the environment. The Winkler method was used to determine respiration rates, while starch gel electrophoresis and spectrophotometric analyses were utilized for respiratory blood pigment assays.

The vertical distributions of the Saanich Inlet zooplankton reflect the trends observed in the oxygen tolerance tests. In general, the longer the organisms survived the tests, the deeper they occur in

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Saanich Inlet, and the more time they spend in the minimum layer.

Orchomenella obtusa and *Calanus plumchrus* could survive at oxygen levels of 0.4 ml/l for at least 24 hours. Their main populations inhabited the oxygen minimum continually.

Euphausia pacifica survived for the shortest period of time (1-2 hrs) of the species tested. Furthermore, this species was always situated above the oxygen deficient layer of Saanich Inlet. The Bute Inlet *E. pacifica* survived for similar short periods of time, suggesting that the oxygen minimum in Saanich Inlet was not influencing survival time. No significant respiration rate difference was found between the Bute and Saanich Inlet euphausiids, further supporting the hypothesis that *E. pacifica* has not adapted to the low oxygen environment.

Metridia lucens from both inlets survived for identical periods of time, again suggesting that no adaptation has occurred in this species.

Euchaeta japonica and *Cyphocaris challengeri* had similar vertical distributions and oxygen tolerance levels in Saanich Inlet. The Bute Inlet organisms survived for much shorter periods of time, indicating that a physiological adaptation has possibly taken place, however, the results of the respiration experiments for these animals proved to be contradictory. *E. japonica* had a considerably higher rate in Bute than in Saanich, but the reverse was observed for *C. challengeri*.

Parathemisto pacifica had a significantly higher respiration rate in Bute Inlet than in Saanich Inlet, but these results could not be related to oxygen tolerance values as Bute Inlet data was lacking.




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INTRODUCTION

In recent years, an increasing number of workers have been directing their studies towards the field of zooplankton physiology.

Marshall and Orr (1955, 1958) were among the first to investigate the physiological reactions of zooplankton. Working with copepods, they observed the varying influences of temperature, food, and season on respiration rates of these animals. Comparative data for the respiration rates of Calanoids has been studied by several workers including Conover (1956, 1959, 1960, 1968), Raymond and Gauld (1951), Anraku (1964), Haq (1967), Schindler (1968), and Comita (1968). The respiration rates of euphausiids and the factors affecting them have been reported by Lasker (1966), Paranjape (1967a), Pearcy and Small (1968), and Mauchline (1969). In addition, Conover (1959) and Armitage (1962) have determined the respiration rates of a few amphipods. Little work, however, has been done on the distributional relationship of zooplankton species to the oxygen minimum layer, and their physiological responses to low levels of oxygen. Vinogradov and Voronina (1961), working in the Arabian Sea, demonstrated the existence of a sparse zooplankton population down to tensions of 0.15 ml/l of oxygen; and suggested that the role of traces of sulphide, in situations where very low oxygen concentrations and high nitrite values occurred together, might be at least as important in limiting zooplankton abundance as the low oxygen values themselves. Longhurst (1966a) demonstrated the presence of abundant zooplankton in oxygen concentrations as low as 0.2 ml/l in the Eastern Pacific Minimum. This zooplankton was found to be dominated by resting copepodites of *Calanus helgolandicus*. Waldichuck and Bousfield (1962) and Bary (personal communication) have reported amphipods surviving in minimum concentrations of oxygen.

Few references exist which deal with laboratory or *in situ* experimentation on zooplankton from low oxygen environments. Sprague (1962) investigated the resistance of four freshwater crustaceans to lethal high temperatures and low oxygen. Teal and Carey (1967) found that *Euphausia mucronata* survived for short periods at unmeasurably low oxygen tensions in a closed vessel. Similar results were obtained by Childress (1968) studying the large mysid *Gnathophausia ingens*.

Fish (1968) working with *Euphausia pacifica*, *Orchomenella pinguis* (probably *O. obtusa*), and *Cyphocaris challengeri* from Saanich Inlet, attempted to relate their vertical distributions to decreasing oxygen, and increasing carbon dioxide concentrations. He found all three species to be stratified during the day, with *O. pinguis* occupying the deepest and *E. pacifica* the shallowest position. Furthermore, *O. pinguis* survived longest at low oxygen concentrations, while *E. pacifica* and *C. challengeri* had similar but considerably shorter survival times. Finally, Chaston (1969) determined that the freshwater copepod *Cyclops varicans* could tolerate 36 hours of anaerobic conditions.

Little research has been done on the analysis of blood pigments in the small arthropods, due to the technical difficulties involved in quantification of results. Simpler semi-quantitative techniques, have been used since 1948 (Fox), and were utilized until fairly recently (Green, 1956). In 1965 and 1966, Hoshi and Sugano, isolated, and quantified the blood hemoglobin of two Cladocera using a complex series of techniques. Wieser (1965) examined the haemocyanin and other blood components of 15 species of marine and terrestrial amphipods and isopods. In the most recent available paper, by Manwell (1966), the multiple hemoglobins of small and large larval *Chironomus* were analyzed.

Few geographic areas exist where a group of organisms and their physiological responses to a marine, oxygen deficient environment can be investigated as readily as is possible in Saanich Inlet, Vancouver Island. Furthermore, the principal constituent species of the oxygen minimum layer are relatively few and the inlet is readily accessible. Therefore, a program was developed to (1) determine the zooplankton species prevalent in the oxygen minimum; (2) examine quantitatively the vertical distribution of the larger dominant zooplankton present; (3) investigate the low oxygen tolerance levels of these zooplankton species; and (4) try to relate the previous observations to two possible influencing factors, respiration and quantity of blood pigment.

The unusual geological and hydrological features of Saanich Inlet have produced a pronounced oxygen minimum layer in this fjord (Herlinveaux, 1962).

As the present biological program was concerned with this oxygen deficient layer, it was necessary to study the seasonal changes in the physical properties of the water column.

Bute Inlet was selected as an oxygen rich control environment for the biological experiments conducted in Saanich Inlet. Tabata and Pickard (1957) have reviewed the physical oceanographic properties of Bute Inlet, and have indicated that Bute, a "large run-off inlet" (Pickard, 1961), has no oxygen minimum layer.

DESCRIPTION OF AREAS

Saanich Inlet

Saanich Inlet, a fjord on the southeast coast of Vancouver Island, is situated at $48^{\circ}35'N$ lat. and $123^{\circ}30'W$ long. (Fig. 1). It is classified by Pickard (1961) as a low run-off inlet. No large rivers enter the inlet. The nearest rivers are the Cowichan River, just North of the mouth of the inlet (Fig. 2) and the Fraser River, discharging into the Strait of Georgia, approximately 50 km Northeast of the Inlet. The width of the fjord varies from 0.4 to 7.6 km over its 25.7 km length (Gucluer and Gross, 1964). A sill at the mouth rises to within approximately 70 meters of the surface. This sill restricts the circulation of water between the inlet and Satellite Channel (Herlinveaux, 1962, 1968). Above sill depth, within the fjord, the water properties are similar to those of the approaches connecting it with the Strait of Georgia. The water below sill depth is almost totally isolated, oxygen deficient, and relatively stable throughout the year.

Bute Inlet

Bute Inlet, bounded by rugged mountains, is situated approximately 160 km Northwest of Vancouver, B. C. (Fig. 1), at $50^{\circ}35' N$ lat. and $125^{\circ}0' E$ long. Pickard (1961) refers to it as a high run-off inlet, resulting in circulation throughout the water column. The Homanthko and Southgate Rivers feed the head of the inlet (Fig. 3). The Orford, a smaller river, enters midway between the head and the mouth. As well, many seasonal streams discharge into Bute throughout its length. The waters of Bute Inlet are in contact at its mouth with the well mixed waters of Nodales and Cordero Channels through Yucalta and Arran rapids,

and also with the waters of the Strait of Georgia through Calm, Pryce, and Homfray Channels (Tabata and Pickard, 1957). The inlet's width varies from 2 to 4 kilometers over its 64 kilometer length.

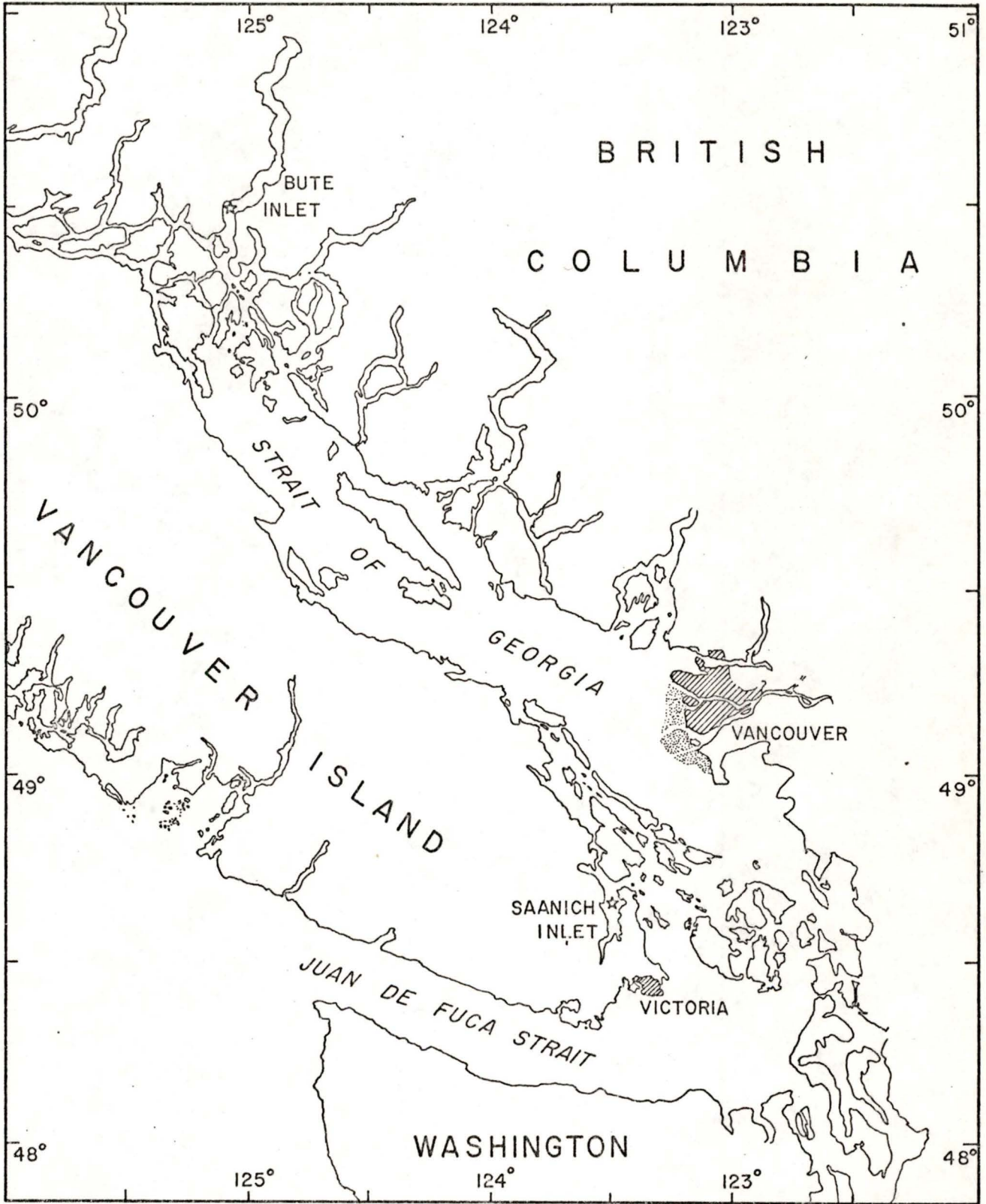


Fig. 1. Sampling Areas.

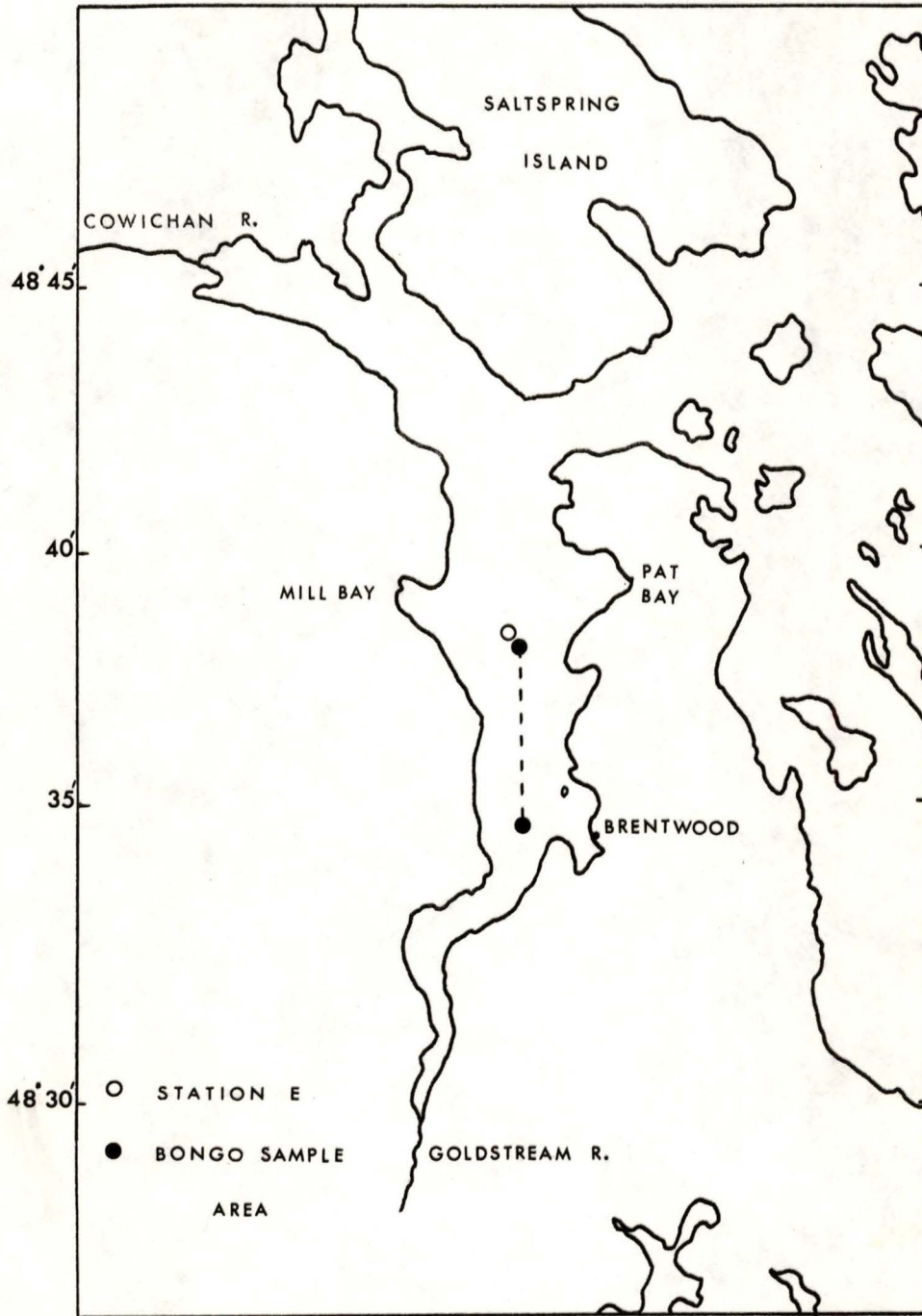


Fig. 2. Saanich Inlet.

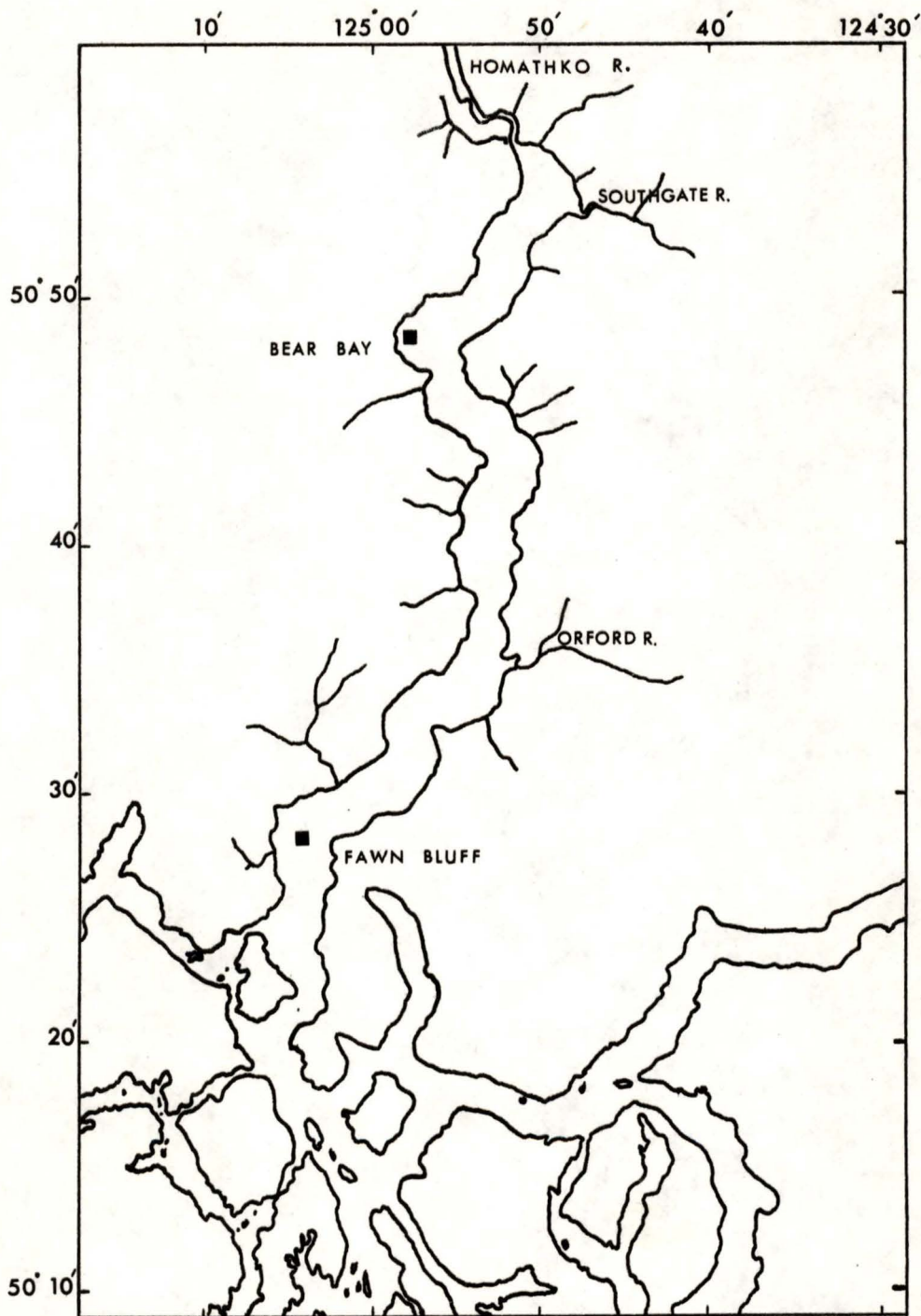


Fig. 3. Bute Inlet.

PART ONE: PHYSICAL OCEANOGRAPHY

METHODS AND MATERIALS

I. Field Methods

Station "E" (Dagg, 1970) was utilized for the collection of the physical oceanographic data in Saanich Inlet (Fig. 2). Its central location and sufficient depth (198 meters) favored this area over others. Sampling commenced on May 6, 1969, and was terminated on February 16, 1970.

Bute Inlet was sampled at the Fawn Bluff station on October 28, 1969, and was randomly selected (Fig. 3).

Research Vessels.

The facilities of the Vancouver I, on loan to the University of Victoria by the Department of Transport, were used for the majority of the Saanich Inlet sampling. On November 24, 1969, the CNAV Endeavor was used to sample Saanich Inlet. This ship was also used to sample Bute Inlet, between October 27 and 31, 1969.

Water Samples.

Water samples were obtained with Nansen bottles at standard oceanographic depths down to 175 meters in Saanich Inlet and 400 meters in Bute Inlet. Samples for oxygen determination were removed first and were collected in 300 ml B.O.D. bottles and immediately fixed for later titration in the lab. Samples for sulphide were drawn immediately after the oxygen samples into 60 ml ground-glass-stoppered reagent bottles modified to hold only 56 ml. These were also fixed for later determination in the lab. Finally, salinity samples were drawn and also returned to the lab for determinations.

Temperature

Bathythermographs were used on all occasions for temperature profiles and were calibrated with surface bucket temperature readings.

II. Laboratory Methods

Dissolved Oxygen.

Field fixed samples were returned to the lab and dissolved oxygen was determined by the Winkler method (U.S. Navy Hydrographic Office, 1968), with a few modifications. Manganous Sulphate was substituted for Manganous Chloride, and one ml of Sulphuric Acid was used instead of two ml of Hydrochloric acid, in the fixation procedure.

Dissolved Hydrogen Sulphide.

On return to the lab, sulphide values were determined spectrophotometrically using the method of Strickland and Parsons (1968). Surface water was used as a blank. Sulphide values were read on a Hitachi Perkin-Elmer Spectrophotometer at 600 nm in one centimeter cuvettes.

Salinity

Salinities were determined with a Hytech laboratory salinometer, model 6220.

RESULTS

I. Saanich Inlet

Temperature

All temperatures recorded during the study period, as determined from bathythermograph tracings, are listed in Table I. Vertical temperature profiles are given in Figure 4. This graph illustrates a marked annual cycle of temperature down to approximately 100 meters. Although quantitative data are not available, Herlinveaux (1962) indicated that surface warming commences in March, reaching a maximum in July. The cycle was most evident in the top 50 meters, where the surface thermocline occurs. Below 100 meters, water temperatures were more consistent throughout the year, and at 175 meters, the temperature was almost constantly 9.1 C°. Surface cooling had begun by August 26, and by November 24, a reverse thermocline existed.

Salinity

Salinity values of the study period are presented in Table II and graphed as vertical profiles in Figure 4. Densities were not calculated but Herlinveaux (1962) has shown that in Saanich Inlet the density values are determined almost completely by the salinities. The consistent positive salinity gradient is indicative of a fjord environment, and it, combined with weak surface circulation, are the major stabilizing factors present in Saanich Inlet. Precipitation and run-off appeared to affect only the top 50 meters of the water column. Below this depth, salinities, and thus densities, were influenced by exchanges of deep water from Satellite Channel. Table II illustrates this factor most clearly. From sill depth (75 m) to 100 m, salinities steadily increased from May 8 to

TABLE I. Physical Oceanography - Temperature in °C

Depth	May 8	June 10	July 17	August 26	September 25
0	13.9	17.4	17.1	14.0	11.6
10	8.6	12.3	15.0	13.3	11.2
20	8.2	11.2	14.5	12.5	11.0
30	8.1	10.6	13.9	12.0	10.8
50	7.7	8.0	9.0	9.0	9.6
75	7.6	8.1	8.9	9.1	9.4
100	7.8	8.2	8.9	9.2	9.2
125	9.2	9.2	9.0	9.1	9.2
175	9.5	9.1	9.0	9.1	9.1
Depth	Oct. 8	Nov. 24	Dec. 8	Jan. 23	Feb. 16
0	11.2	8.5	7.1	7.0	6.8
10	10.6	9.4	8.1	7.0	6.9
20	10.5	9.5	8.5	7.6	6.9
30	10.2	9.5	8.8	8.2	6.9
50	9.4	9.0	9.5	7.5	7.2
75	8.6	8.6	9.0	7.6	7.0
100	8.6	9.0	9.0	9.0	8.8
125	8.6	9.0	9.0	9.0	9.1
150	8.6	9.0	9.0	9.1	9.1
175	8.6	9.0	9.0	9.1	9.1

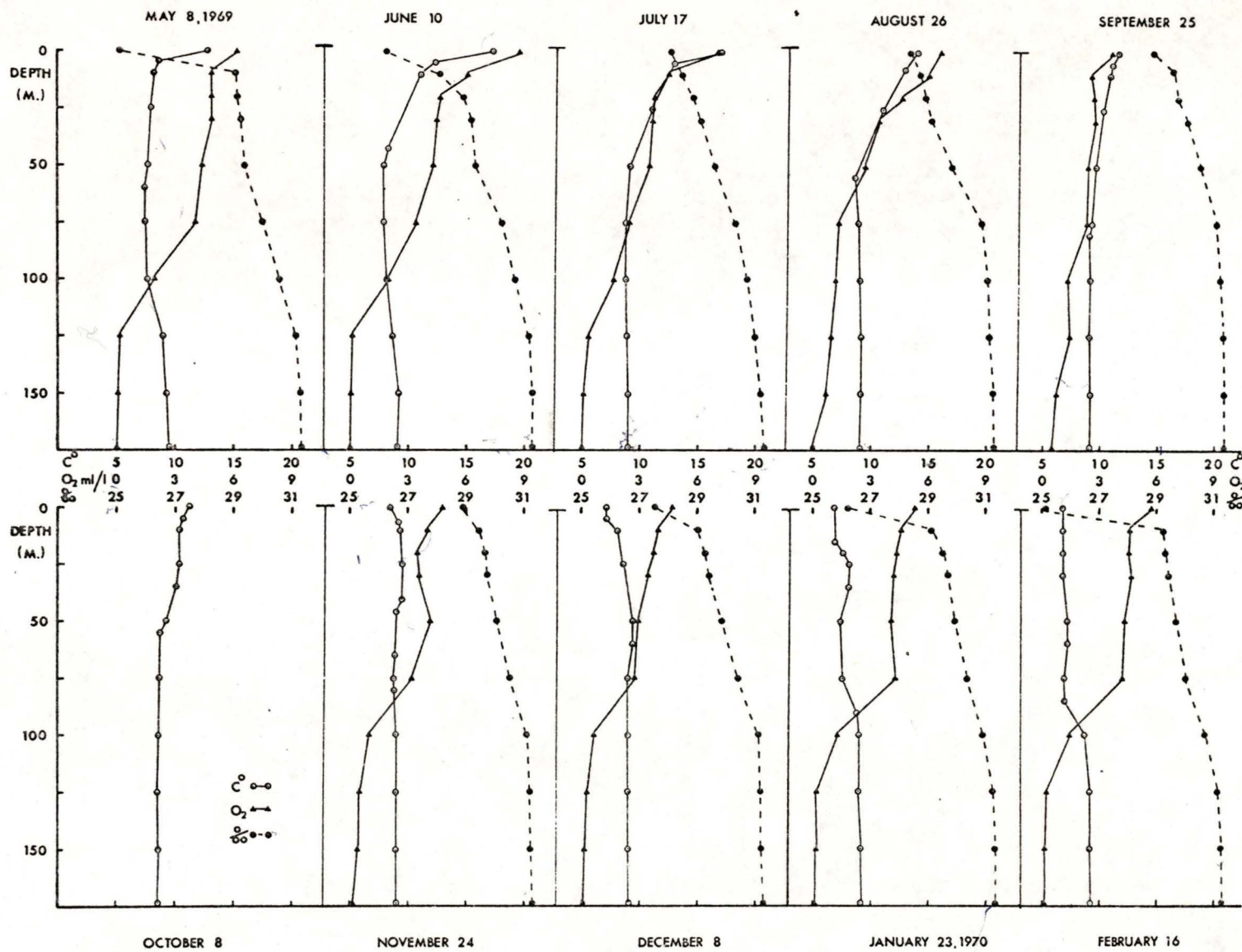


Fig. 4. Seasonal Vertical Profiles of Temperature, Salinity, and Oxygen.

TABLE II. Physical Oceanography - Salinity in 0/00

Depth	May 1	May 21	May 28	June 10	July 17	July 31
0	25.15	26.57	27.94	26.32	28.10	27.70
10	29.08	28.80	29.11	28.14	28.48	28.28
20	29.16	28.98	29.20	28.88	28.91	28.76
30	29.24	29.20	29.37	29.19	29.18	29.20
50	29.40	29.62	29.98	29.35	29.63	30.03
75	30.04	30.35	30.45	30.25	30.37	30.63
100	30.58	30.65	30.69	30.74	30.73	30.92
125	31.15	31.15	31.14	31.17	31.02	31.15
150	31.31	31.27	31.27	31.28	31.24	31.32
175	31.32	31.29	31.32	31.31	31.30	31.35
	Aug.26	Sept.25	Nov.24	Dec.8	Jan.12/70	Feb.16
0	28.73	28.96	28.88	27.58	26.24	25.18
10	28.76	29.59	29.49	29.05	29.18	29.35
20	28.94	29.80	29.67	29.28	29.54	29.40
30	29.15	30.09	29.75	29.45	29.68	29.47
50	29.84	30.56	30.04	29.85	29.88	29.76
75	30.91	31.14	30.50	30.43	30.27	30.02
100	31.08	31.24	31.11	31.10	30.90	30.76
125	31.17	31.30	31.22	31.17	31.22	31.19
150	31.24	31.34	31.26	31.20	31.29	31.23
175	31.26	31.36	31.28	31.22	31.32	31.25

September 25. The inflowing water did not affect the salinity at 125 meters until July 31, and at 175 meters the effect was negligible. Herlinveaux (1968) states "the extent of the penetration of exchange water depends on the density difference between the bottom waters of Satellite Channel and Saanich Inlet." From the data presented, it appears that the exchange water barely reached 175 meters.

Dissolved Oxygen.

Table III lists all the dissolved oxygen values determined during the sampling term. Figure 4 shows the monthly vertical profiles and illustrates the double oxycline pattern observed by Herlinveaux (1962), Fish (1968) and others. Surface and near surface oxygen values fluctuated considerably with time, from maxima on June 10 to minima by September 25 (Fig. 5). Phytoplankton concentrations, winds, and temperatures would have important roles in these variations. From 125 meters to the bottom, all fluctuations were directly due to intrusions of outside water into this region. Figure 5 clearly illustrates the influence of the intruding water mass. It began mixing at 125 meters midway through July, and by September 25, had reached 175 meters. When inflow ceased, the oxygen values began to decline, as oxygen was consumed by heterotrophs. Throughout most of the year however, the oxygen concentration below 100 meters was less than one milliliter per liter, and at 175 meters, was near 0.0 ml/l.

Hydrogen Sulphide

Hydrogen sulphide was found only in the bottom water, therefore, vertical profiles were not made, but Table IV summarizes the data collected. Figure 6 illustrates the seasonal variations found in

TABLE III. Physical Oceanography - Oxygen in ml/l

Depth	May 8	May 21	May 28	June 10	July 17
0	6.29	5.95	6.87	8.90	7.15
10	4.87	4.95	5.21	6.07	4.57
20	4.90	4.61	4.77	4.72	3.89
30	4.90	4.51	4.76	4.44	3.69
50	4.75	4.31	4.26	4.29	3.53
75	4.11	3.74	3.86	3.30	2.53
100	2.02	1.95	2.90	1.98	1.83
125	0.10	0.10	0.20	0.10	0.36
150	0.06	0.06	0.05	0.03	0.08
175	0.00	0.00	0.00	0.00	0.00
	July 31	Aug. 26	Sept. 25	Nov. 24	Dec. 8
0	5.65	6.74	3.76	4.81	4.81
10	4.20	6.02	2.74	3.86	4.01
20	3.29	4.62	2.76	3.52	3.78
30	3.18	3.46	2.86	3.67	3.50
50	3.02	2.87	2.67	3.92	2.99
75	2.02	1.28	2.53	3.17	2.88
100	1.47	1.22	1.27	1.01	0.60
125	0.92	0.98	1.38	0.53	0.36
150	0.05	0.68	0.75	0.36	0.16
175	0.00	0.00	0.59	0.24	0.12
	Jan. 12/70		Feb. 16		
0		5.44		5.83	
10		4.69		4.84	
20		4.31		4.79	
30		4.17		4.86	
50		4.14		4.30	
75		4.19		4.23	
100		1.21		1.50	
125		0.28		0.19	
150		0.15		0.14	
175		0.08		0.10	

Saanich Inlet at 150 and 175 meters as related to the oxygen concentration. The results suggest a gradual buildup of sulphide in the deeper water as spring and summer crops of plankton die off, but there appears to be considerable patchiness at these depths, where slight increases of oxygen can quickly oxidize any hydrogen sulphide present.

II. Bute Inlet

Temperature.

Tabata and Pickard (1957) indicated that high surface temperatures prevail in Bute Inlet in the summer. The present data indicated that by October 28, 1969, the temperature in the top 100 meters had begun to decrease from the summer values. A low of 8.5 C° was recorded at 100 meters (Fig. 7). Between 100 and 150 meters, the temperature increased to approximately 9.3 C°, and remained at this level down to the deepest record, 250 meters.

Salinity.

Salinity increased steadily with depth, from 23.43 at the surface, to 30.58 at 400 meters (Fig. 7).

Dissolved Oxygen.

Figure 7 presents the vertical oxygen profile. An oxycline was present, ranging from a maximum surface value of 4.61 ml/l to the minimum of 1.69 ml/l at 400 meters.

Hydrogen Sulphide.

The water column was tested for the presence of hydrogen sulphide, but it was not recorded at any depth.

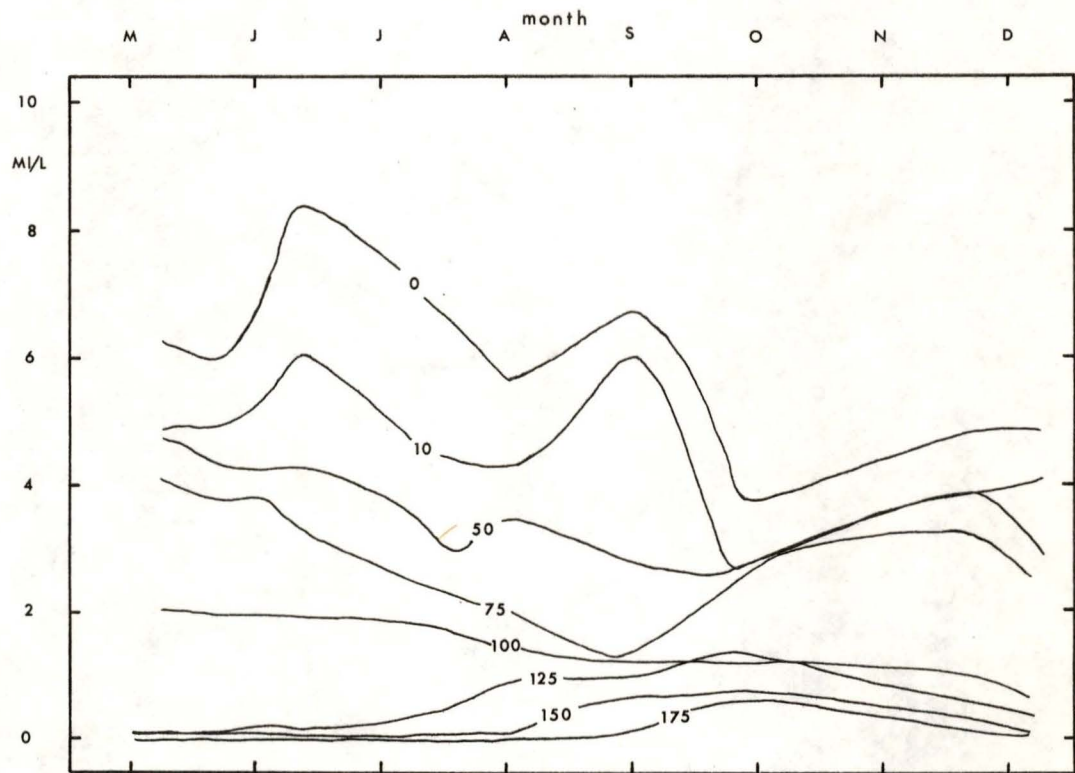


Fig. 5. Seasonal Cycle of Dissolved Oxygen at Eight Depths.

TABLE IV. Physical Oceanography - Sulphide in $\mu\text{gm-atoms/l.}$

Depth	May 8	May 21	May 28	June 10	July 17
0	0.000	0.000	0.000	0.000	0.000
75	0.000	0.000	0.000	0.000	0.000
100	0.000	0.000	0.000	0.000	0.000
125	0.000	0.000	0.000	0.000	0.000
150	0.037	0.550	0.444	0.814	0.000
175	2.627	5.550	6.179	7.585	0.106
	July 31	Aug.26	Sept.25	Nov.24	Dec.8
0	0.000	0.000	0.000	0.000	0.000
75	0.000	0.000	0.000	0.000	0.000
100	0.000	0.000	0.000	0.000	0.000
125	0.000	0.000	0.000	0.000	0.000
150	1.332	0.000	0.000	0.000	0.000
175	5.550	15.599	0.000	0.000	0.740
	Jan.12/70		Feb.16		
0		0.000		0.000	
75		0.000		0.000	
100		0.000		0.000	
125		0.000		0.000	
150		0.000		0.000	
175		0.000		0.000	

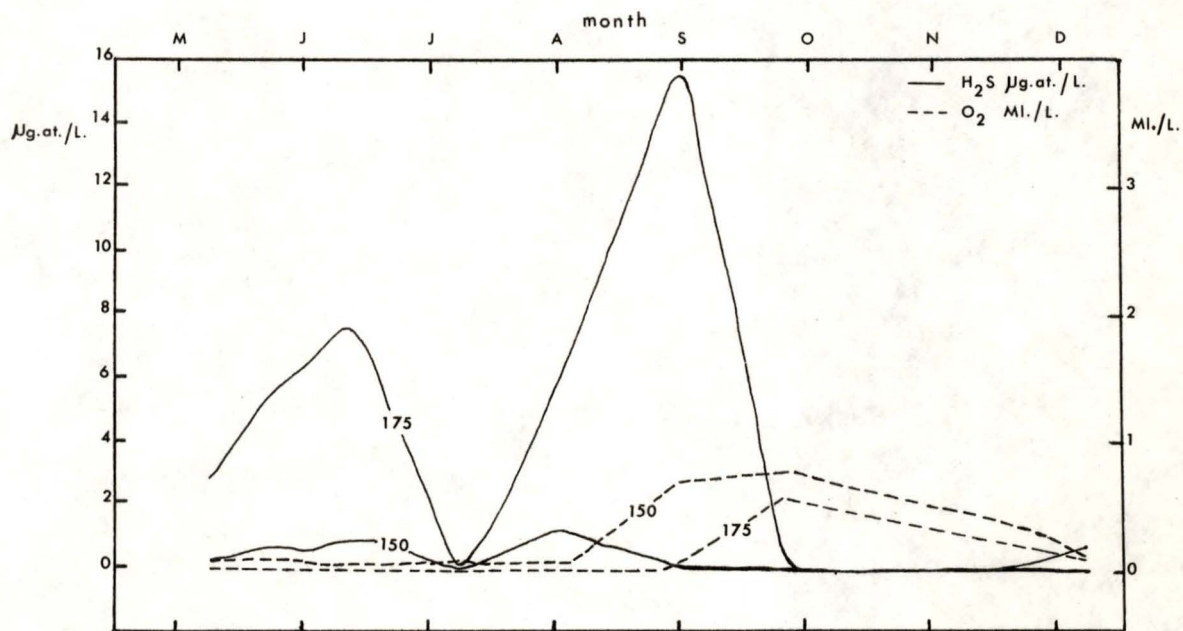


Fig. 6. Relationship Between Hydrogen Sulphide and Oxygen at 150 and 175 Meters.

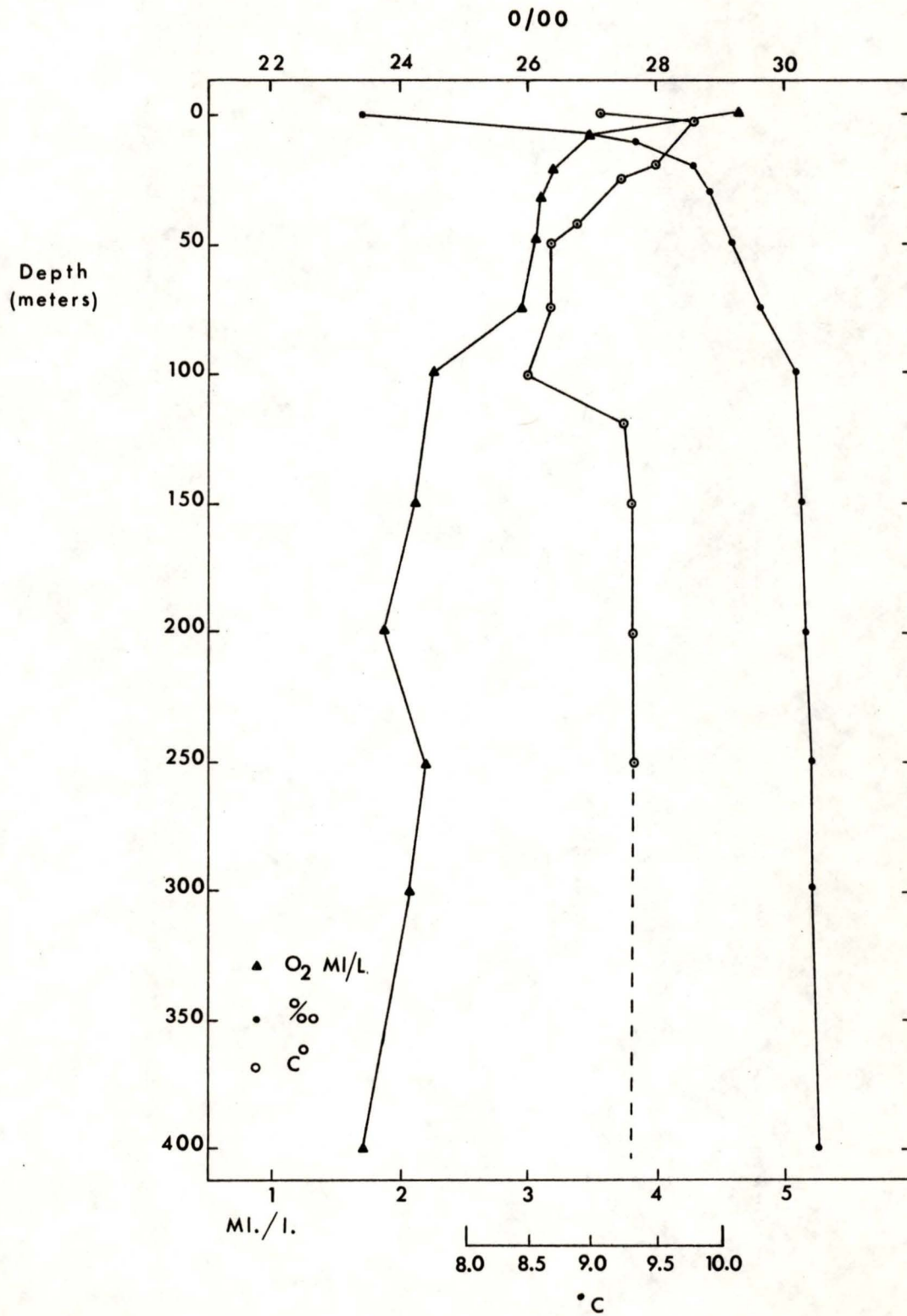


Fig. 7. Bute Inlet, October 28, 1969.

DISCUSSION

Bute Inlet was selected as a control for the biological program carried out in Saanich Inlet. The physical dimensions of the two are vastly different. Bute Inlet, with a length of 64 kilometers and a mean center depth of 600-650 meters (Tabata and Pickard, 1957), is considerably larger than Saanich Inlet, which is 25.7 kilometers long and averages 198 meters deep in the center (Herlinveaux, 1962).

The most apparent difference between the two inlets is the presence of an oxygen minimum layer in Saanich, which is absent in Bute. The latter is classified as a large run-off inlet (Pickard, 1961). This results in a large inflow of water at all levels of the water column, thus maintaining a relatively high oxygen concentration down to the bottom. Saanich Inlet, on the other hand, has only the small Goldstream River flowing into it. Circulation within the water column is minimal, being almost exclusively relegated to the top 75-100 meters, that is, sill depth.

Both inlets have similar salinity and temperature distributions with depth. Tabata and Pickard (1957) state that below 100 meters in Bute Inlet, the temperature remains constant at 8.0 to 8.2 C° throughout the year. However, the present study found the temperature at these depths to be approximately 9.3 C°. In Saanich Inlet the temperature below 100 meters was consistently 9.1 C°, in accordance with the data of Herlinveaux (1962).

The surface salinities of both inlets fluctuate seasonally. Below 100 meters, the salinities become relatively stable. The Bute

Inlet 150 meter value of 30.24 was only slightly lower than the 31.26 recorded in Saanich at the same time of year.

Hydrogen Sulphide has not, as far as is known, been recorded from Bute Inlet, but does occur in Saanich Inlet, usually deeper than 150 meters. Shallower than this, it was never found in a measurable concentration.

PART TWO: BIOLOGICAL OCEANOGRAPHY

METHODS AND MATERIALS

I. Sampling Areas

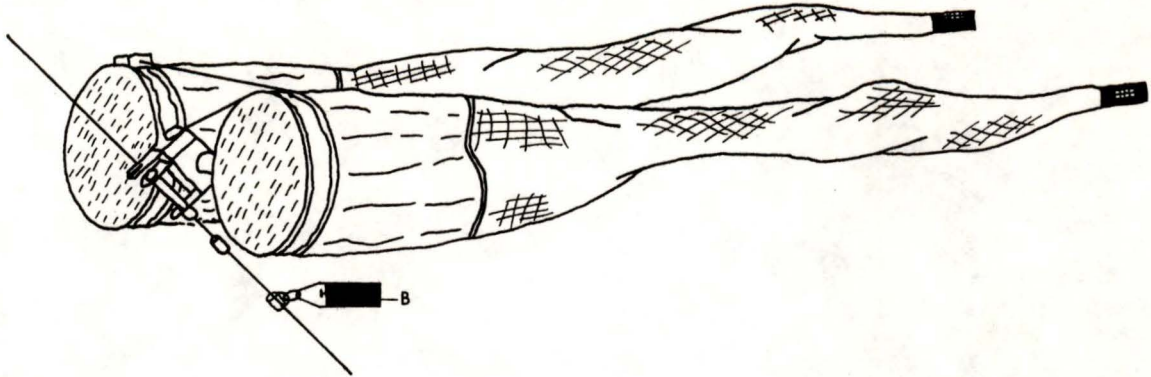
All of the Saanich Inlet zooplankton samples were collected from a two to three mile strip of deep water stretching south from Station "E" to a point opposite Brentwood (Fig. 2). The sampling commenced on May 13, 1969 and continued through the remainder of the year, terminating on February 10, 1970.

Zooplankton from Bute Inlet was collected from random points between Fawn Bluff and Bear Bay, during the period of October 27 to 31, 1969 (Fig. 3).

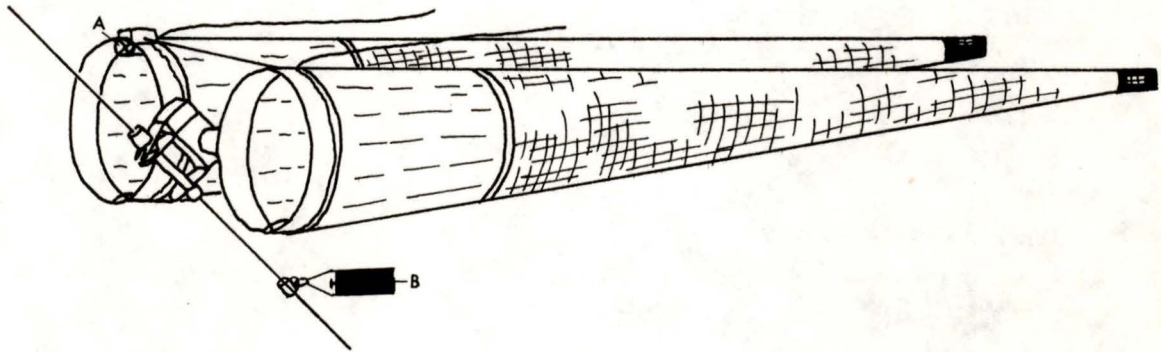
II. Sampling Methods

To determine the vertical distribution and migration patterns of the zooplankton in Saanich Inlet, a quantitative, discrete-depth sampler was required. There are several plankton samplers of this type in existence (Clarke and Bumpus, 1950; Aron, et al, 1964; Longhurst, et al, 1966b; Owre and Low, 1969). In this program, the paired opening and closing "Bongo Nets" by Brown and McGowan, 1966, with a mesh size of 333 microns, were utilized. Figure 8 illustrates the phases of operation of these nets. The nets are opened by a messenger and close when a set volume of water has been filtered. The unit was calibrated (Fig. 9) and the meter was set to sample for eight minutes (500 cubic meters of filtered water) at a ship speed of approximately three knots. A Bathykymograph, Marine Advisors Model T.1, was attached below the Bongo frame (Fig. 8) to record the depth sampled. This instrument also required calibration. Vertical lowering to known depths and pauses at these depths gave the results indicated in

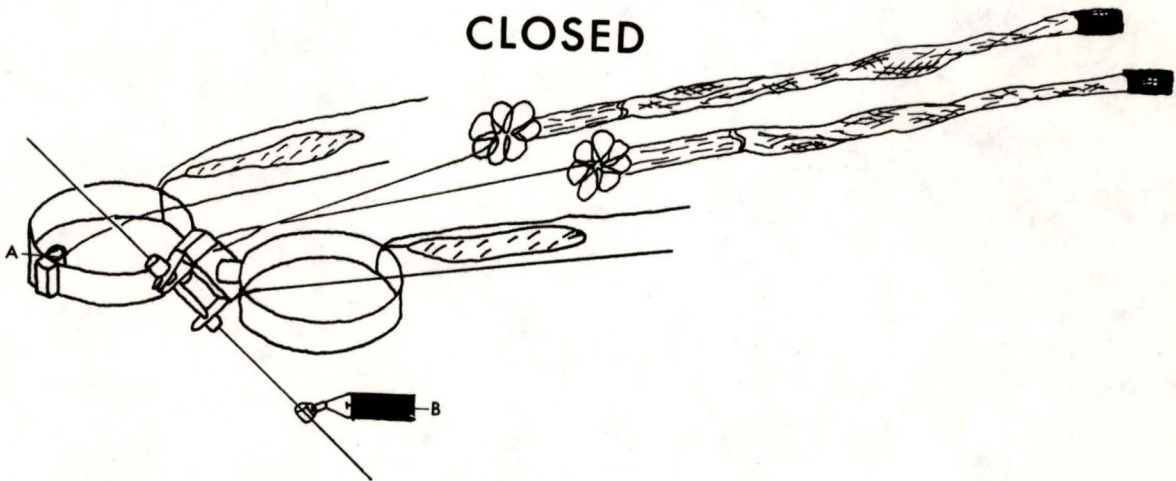
CLOSED



OPEN



CLOSED



A FLOWMETER

B BATHYKYOGRAPH

Fig.8. Diagrammatic Presentation of the Bongo Nets in Operation.

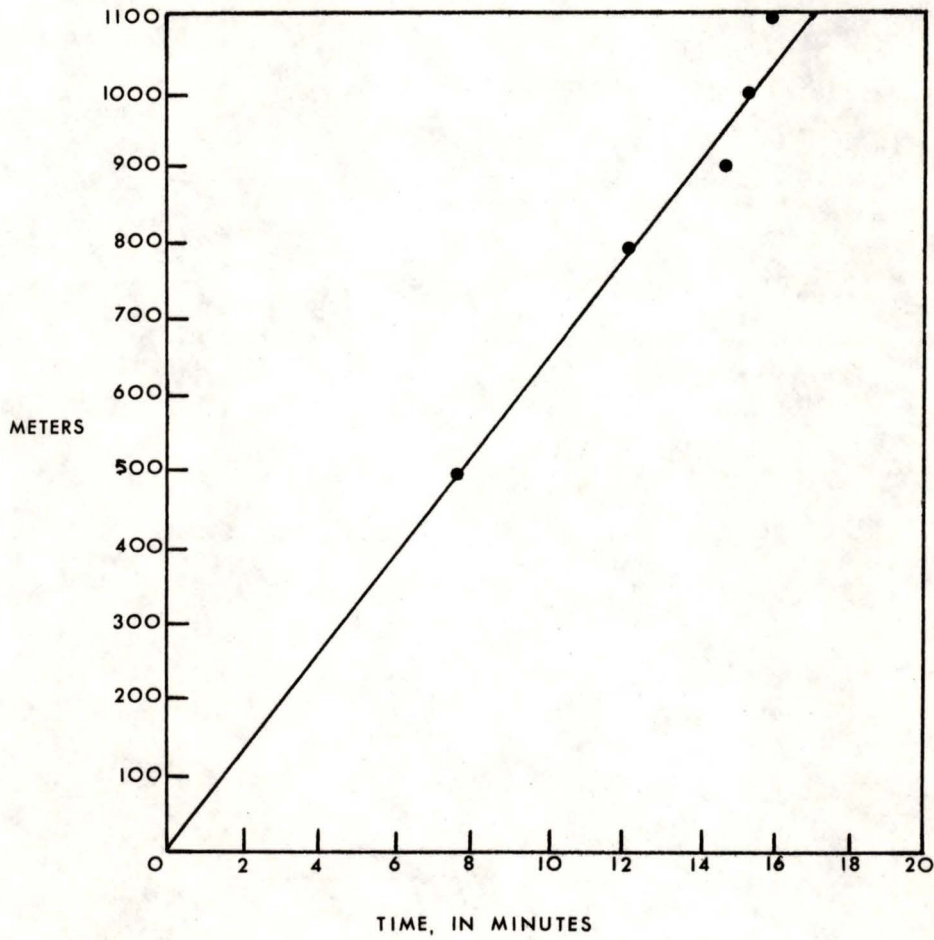
Bongo Calibration

Fig. 9. Distance Travelled by Bongo Nets Before Closing
as Related to Time Setting.

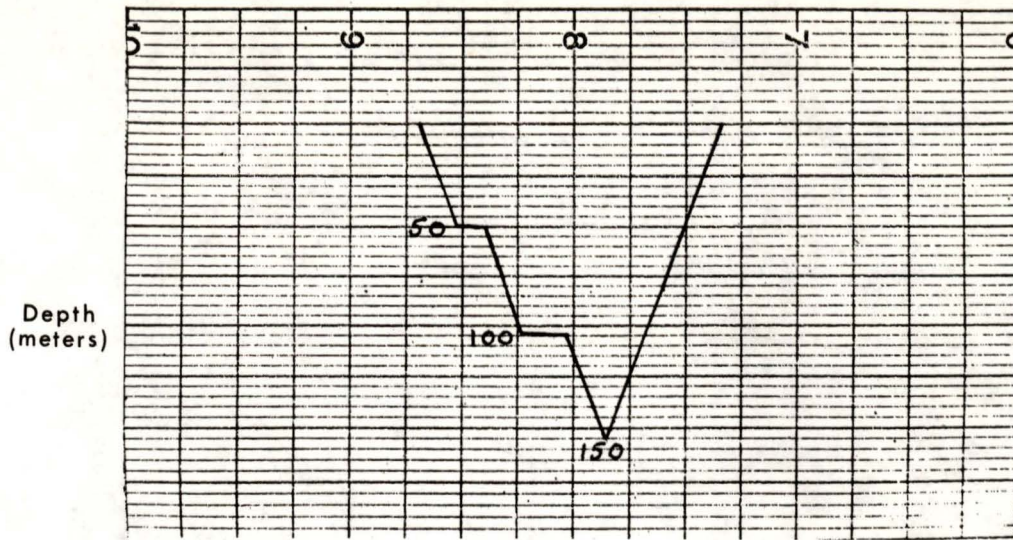


Fig.10. Bathymograph Calibration.

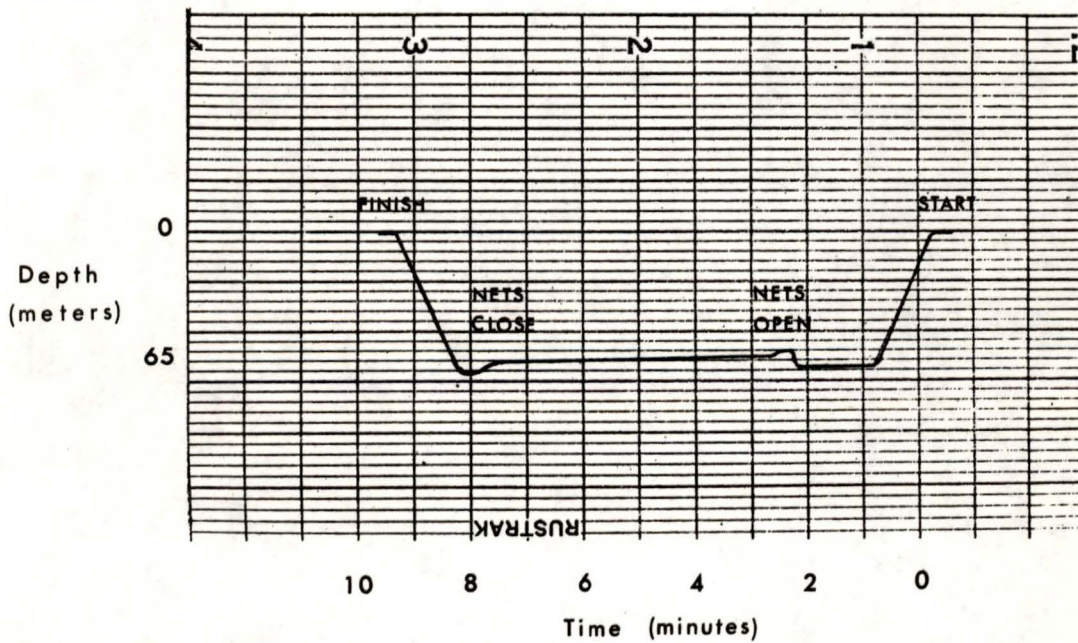


Fig.11. Example of a Bathymograph Tracing with Bongo Net in Operation.

Figure 10. Figure 11 exemplifies a Bathykymograph tracing with the Bongo nets in operation. Experience with the equipment showed that it was necessary to increase the speed of the launch just prior to messenger tripping of the Bongos in order to insure that both doors opened. Immediately after "tripping", the launch slowed to three knots and cruised at this speed. The time required for the nets to close was usually recorded, and the equipment was then brought to the surface. The water mass was sampled at 25 meter intervals from 25 to 150 meters. On deck, both nets were washed thoroughly into individual buckets. The samples were concentrated and preserved in 5% aqueous formaldehyde for later analysis in the laboratory.

All research animals used in the experiments were collected with standard one meter nets with a 330 micron mesh aperture. Eighteen inch long plastic codend buckets were used to prevent damage to the zooplankton.

The zooplankton in Saanich Inlet was collected with short (15-20 minutes) oblique tows extending down to 150 meters. In Bute Inlet, the day depth of the zooplankton was considerably deeper than this, therefore to reduce injury to the zooplankton, short oblique tows were made at night.

On board ship, the entire plankton catch was emptied into a polyethylene container filled with surface sea water. The plankton was then sorted with a 50 ml beaker into 1000 ml erlenmeyer flasks also containing surface water. These were then placed in coolers and transported to the laboratory. Immediately upon arrival, the zooplankton was selectively sorted with polyethylene spoons and placed in 1000 ml erlenmeyer flasks containing 75 meter sea water. The flasks were placed in a refrigerator set at $8^{\circ}\text{C}^{\pm} 0.5$.

III. Laboratory Work.

Zooplankton samples were split into aliquots using a Folsom plankton splitter, identified, and counted. Replicate samples were counted for each of the two samples collected at each of the sampling depths. The mean value at each depth was then determined from the four aliquots counted at each depth. These values were expressed as numbers per cubic meter and percent of species per depth (Appendices I & II). Occasionally one of the two sides of the sampler failed to open, in which case only two aliquots were counted. To illustrate the replicability of the samples taken from the left and right sides of the frame, total samples of *Orchomenella obtusa* were counted from 16 tows collected from the oxygen minimum layer of Saanich Inlet throughout the summer. A Student's T Test comparing the means (Table V) indicated no significant difference between the left and right nets when they function properly. Splitting of the samples into convenient fractions would tend to increase the error between aliquots. However, as four were usually counted, these errors were never significant.

IV. Experimental Sea Water

The chemical characteristics of the surface sea water fluctuated greatly with season. To keep the water quality as constant as possible, 75 meter water was utilized for all of the lab experiments. This water, in Saanich Inlet, had a mean salinity of 30.47, ranging between 31.14 on September 25, 1969 and 30.02 on February 16, 1970 (Table II). To obtain water of similar salinity in Bute Inlet, the samples had to be collected from 200 meters, where the salinity was 30.48.

A large volume, epoxy coated metallic sampler, was used to collect

TABLE V. The Number of *Orchomenella obtusa* per 500m³ of Water Filtered, in the Left and Right Sides of the Bongo Nets, over a Series of Sixteen Tows.

Tow Number	Date	Left	Right
1	May 23	32	29
2	June 9	12	18
3	June 9	23	27
4	June 9	32	26
5	June 13	21	26
6	July 8	63	44
7	July 8	31	37
8	July 9	25	19
9	July 9	34	28
10	July 29	23	21
11	July 29	15	23
12	July 29	29	22
13	Aug. 26	41	37
14	Aug. 26	75	87
15	Aug. 26	62	45
16	Aug. 26	45	51
		Total	568
		Mean	35.5

the sea water, It was then transported to the lab in 20 liter carboys where it was filtered with 0.45 micron membrane filters and stored, sealed, and in the dark, at 8°C until required. Antibiotics were not used as it was felt unnecessary considering the short periods of testing (Hargrave and Geen, 1968).

V. Oxygen Tolerance Tests

Criterion of Death

The field and laboratory experiments were based on the numbers of specimens surviving the conditions imposed. Fish, (1968) working on Saanich Inlet *Euphausia pacifica*, *Cyphocaris challengeri*, and *Orchomenella pinguis* (probably *O. obtusa*), used weak, sporadic movement of isolated appendages, particularly the pleopods, as his criterion of death. Sprague (1962) had to use the definition "inability to locomote in a normal coordinated fashion after a waiting period of 24 hours". This was a considerably better technique. In the present experiments, persistence of a heartbeat was used as the criterion of death. The heart was clearly visible under a dissecting microscope in all animals except *O. obtusa*. Fortunately, no *O. obtusa* died in the laboratory experiments, and thus, this problem did not arise. For this animal, the criterion of Sprague would have been used, as, in his animals, the heart was not visible externally. Animals without heartbeats were often left in sea water in the refrigerator for 12 to 24 hours. In no cases did they recover. Therefore, the criterion was considered accurate.

Field Experiments.

A series of experiments, in Saanich Inlet, was undertaken to determine the survival of *Calanus plumchrus*, *Euchaeta japonica*, *Metridia lucens*,

Euphausia pacifica, *Cyphocaris challengeri*, *Parathemisto pacifica*, and *Orchomenella obtusa* at oxygen concentrations ranging between 0.39 and 0.53 ml/l. Test animals were selected from a plankton tow made prior to each experiment. The tests were conducted on July 7 and November 24, 1969.

An experimental chamber, the "Euchaeta Cage" (Fig. 12), was used for the *in situ* experiments. The twelve cages built consisted of plexiglass and plastic mesh lids fitted onto plexiglass cylinders with mesh bottoms. This permitted contact with the environment through both ends. The cages were placed in a polyethylene bucket filled with surface sea water, and the experimental animals were introduced. When all of the chambers were filled, the lids were replaced, fastened with elastic bands, and the bucket containing these cages was lowered to the water surface. Here, they were removed from the bucket and placed in a large plastic basket held below the surface. This was attached to a line and float. When all of the "Euchaeta Cages" were in place, the basket was closed and lowered slowly, by hand, to 125 meters. In order to determine the treatment effect imposed by the handling and by the cages, a control set was lowered to 125 meters in Bute Inlet on October 29, 1969, where high oxygen concentrations prevail.

Laboratory Experiments

The majority of the oxygen tolerance tests were conducted in the laboratory, using the apparatus diagrammed in Figure 13. Sprague, 1962, working with freshwater isopods, used the equipment described by Shepard, 1955, to vary the oxygen concentration of water. Water of reduced oxygen content was obtained by a continuous-flow exchange column using nitrogen. However, this unit was considered too cumbersome to be placed in a constant

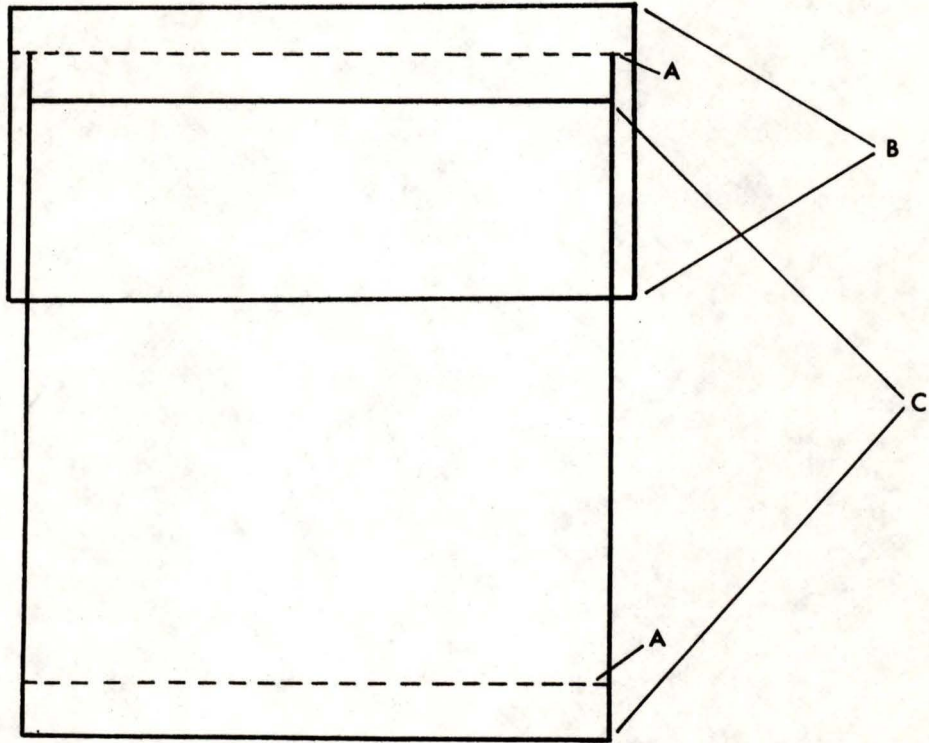


Fig. 12. Diagram of "Euchaeta Cage"

A = mesh
B = lid
C = body

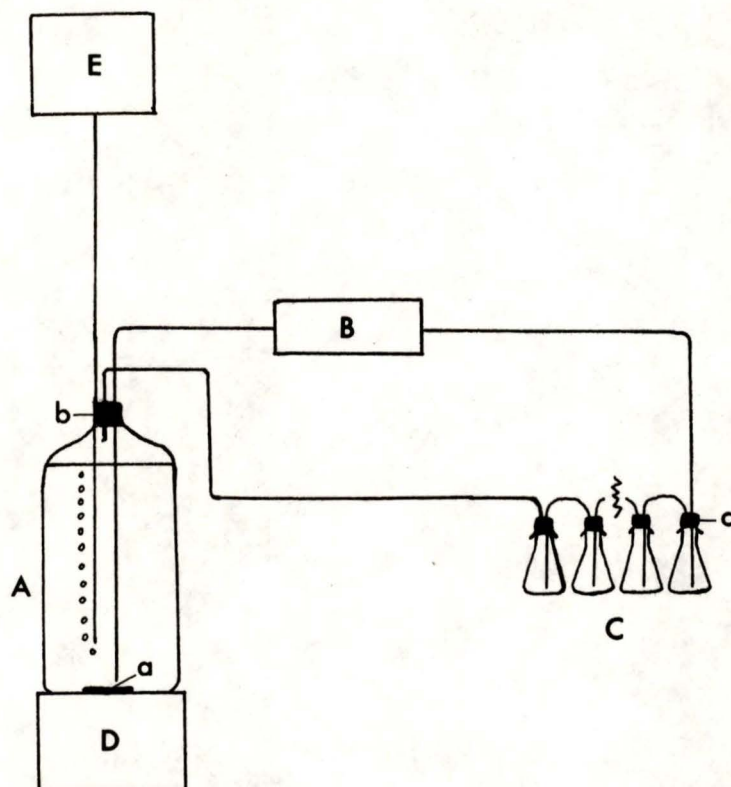


Fig. 13. Oxygen Tolerance Apparatus

- A = Water Bath
 - B = Water Pump (Cole-Parmer)
 - C = Animal Chambers
 - D = Magnetic Stirrer
 - E = Nitrogen Cylinder with Flowmeter Regulator
- a = Magnetic Stirring Bar
 - b = Rubber Stopper with Nitrogen and Water Incurrent and Excurrent Valves.
 - c = Rubber Stoppers with Nylon Mesh Attached to Prevent Flushing of Animals.

temperature refrigerator. The present design provided a continuous flow of sea water of specific, constant salinity, temperature, and oxygen to the experimental organisms. The entire system was housed in a temperature regulated refrigerator (Ambilo Labline Refrigerator) set at $8^{\circ}\text{C} \pm 0.5$. A L.A. Regulator Flowmeter, preset at 50 PSI to insure accurate flow readings, was attached to the nitrogen cylinders used in the experiments. The nitrogen was bled off at 2 liters per minute into the bottom of a 6.6 liter polyethylene water bath fitted onto a magnetic stirrer. The nitrogen, after mixing with the water, escaped through a valve in the top of the bath. Deoxygenated water was pumped, with a Cole-Parmer Masterflex Pump (Model 7015), into the bottom of 25 ml experimental flasks. These sealed flasks (erlenmeyers), fitted with two-hole stoppers, provided a continually changing supply of deoxygenated water to the experimental animals. Nylon mesh covered the out-flow tube of each flask to prevent transferral of animals between bottles. Any number or size of flasks could be attached at any one time, but usually only ten 250 ml containers were used. The last flask in the set was always used for oxygen determinations. The pump was stopped, the flask replaced with a new empty one, and the pump restarted. Oxygen analysis was by the modified Winkler Method described on page 10. The water, after circulating through all the chambers, re-entered the water bath. The water was replaced after each experiment to ensure that bacteria did not become a problem.

Initial tests using carmine dye indicated that all the water in the test bottles was being replaced continually. Furthermore, after observing the reactions of animals to various rates of water exchange, it was decided to use a flow rate of 40-50 ml/minute. This was sufficient to replace all

of the water in a chamber within five minutes without disturbing the zooplankton. Although it was not required, the water bath was also equipped with an oxygen valve to allow mixing of oxygen with nitrogen, producing almost any oxygen concentration desired. The preliminary testing resulted in a range of oxygen values from 5.5 ml/l to 0.16 ml/l. Furthermore, all oxygen values tested deviated no more than ± 0.2 ml/l over a twenty-four hour period. This was satisfactory for testing purposes. In the present study, the oxygen concentration averaged 0.39 ml/l.

Further experimentation indicated that it took approximately 25-30 minutes for the desired oxygen concentration to become equilibrated throughout the water. Therefore, the water was circulated through the experimental chambers for thirty minutes prior to the actual testing of the animals. After this time, the water flow was stopped, the animals were placed in the chambers, and the chambers were resealed and reconnected to the test apparatus. With experience, this procedure took approximately five minutes for ten flasks. The test began when the flasks, containing the zooplankton, were resealed. All experiments were run in the dark. Light was only allowed to enter when samples for Winkler determination were removed. Oxygen determinations were made regularly throughout the experimental run. The mean oxygen concentration was calculated from the mean value of determinations, each of which was weighted in relation to the time elapsed since the previous calculation. However, ten minutes after the experiments had begun, the oxygen concentration usually remained stable for the duration of the test. Upon completion of the experiment, the flasks were disconnected from the apparatus and opened individually for inspection. They were analyzed in the same order as that in which they

had been placed in the flasks at the beginning of the experiment, in order to ensure equal time subjection. A dissecting microscope was used to determine survival in all of the animals except those which were obviously healthy.

The measure of resistance used in this work was the time required for half of the animals to die at 8°C and a mean oxygen concentration of 0.39 ml/l. The parameters of weight, developmental stage, and sex were not considered. Therefore, only adults of all of the species were analyzed. The graphic procedure of Litchfield and Wilcoxon (1949) was followed to obtain the 50% survival time. Percentage survival was plotted against the length of exposure on logarithmic-probability (probit) paper.

The Saanich Inlet laboratory experiments commenced on May 21 and were completed on August 20, 1969. Bute Inlet animals were tested between October 27 and 31, 1969. In one other test of the equipment, experimental animals were subjected to twenty-four hours of high oxygenation, 4.5 ml/l, to determine the effect of the artificial conditions on their survival.

VI. Respiration Determinations

A great variety of equipment is available for the determination of respiration rates of zooplankton (Kanwisher, 1959; Raymond, 1959; Lasker, 1966; and Topping, 1966). In the present experiments, oxygen consumption of the zooplankton was determined by the modified Winkler Method (page 10). Paranjape, 1967a; Conover, 1968; and Schindler, 1968, using this technique, found minimal standard errors of titration (0.02 ml oxygen/liter) which are in agreement with the results of the present study.

The method had two disadvantages. First, oxygen consumption could only be determined over a single time period in any one experiment.

However, as all experiments were run for twenty-four hours, this fault was not of importance. Second, and more important, attempts to determine respiration rates of the zooplankton at low oxygen concentrations failed. In almost all cases, the animals were dead before the twenty-four hour time period had elapsed. Shortening of this time to six hours resulted in relatively higher survival rates, but the shortened time period produced erratic results. Also, it was difficult to maintain similar oxygen concentrations in both the experimental and control bottles. Oxygen electrodes, such as those described by Kanwisher, 1959; Teal and Carey, 1967; Childress, 1968; and Fish, 1968, might have produced better results at low concentrations of oxygen. The electrodes produce a continuous recording of the oxygen concentration within the test chamber, therefore indicating the respiration rate of the organisms within. Several oxygen analyzers were tested (Beckman Model 777; Precision Scientific Cat. No. 68850; and YSI Model 59), but none proved to be sufficiently accurate. Fish, 1968, also had considerable difficulty obtaining accurate measurements, but still used this technique. Other disadvantages of the oxygen electrodes are that it takes considerably more time to test a certain number of animals (as compared to the Winkler technique), and the water within the chamber has to be stirred fairly rapidly to obtain readings.

Due to the inability to obtain accurate values at low oxygen concentrations, oxygen saturated water had to be used in all of the experiments. Respiration was measured using 60 ml glass stoppered bottles. Anraku, 1964, and Paranjape, 1967 a, b, indicated that this size was sufficient providing crowding was not a problem. Three experimental animals of a particular species were placed in a small quantity of water

in a bottle. Three such bottles, plus two controls (empty) were then flushed simultaneously with oxygen saturated water for 7 minutes at a rate of 50mls per minute. Nylon mesh at the outlet of each bottle prevented loss of experimental animals. All of the bottles were filled completely, sealed bubble-free, and placed in compartments of a "black box". This unit was then placed in the constant temperature refrigerator at 8°C. After twenty-four hours, the condition of the animals was checked, and the bottle contents were fixed and analyzed for oxygen (Conover, 1956, 1959).

The experimental animals were rinsed in distilled water to remove any excess salt, dried in a Virtis Freeze Drier, and weighed with a Cahn electrobalance ($\pm 0.002\text{mg}$). All of the results were expressed as $\mu\text{l O}_2$ consumed / milligram dry weight and $\mu\text{l O}_2$ consumed / animal (Appendix III).

The experimental animals used from Saanich Inlet were *Euchaeta japonica*, *Euphausia pacifica*, *Cyphocaris challengerii*, *Parathemisto pacifica*, and *Orchomenella obtusa*. These same animals, with the exception of *Orchomenella obtusa*, were tested from Bute Inlet. The zooplankton were allowed to acclimatize for twenty-four hours in their new environment before tests were conducted. As the experiments usually followed the acclimatization period, the zooplankton were never fed.

The experiments for Bute Inlet were conducted from October 28 to November 1, 1969. Respiration analysis for Saanich Inlet was commenced on July 24, 1969, and completed on February 17, 1970. Respiration rates of the experimental animals in $\mu\text{l O}_2/\text{mg dry wt / hr}$ were related to season of the year; and Bute and Saanich values were compared statistically using the methods of Sokal and Rohlf, 1969. Regressions, plotting $\mu\text{l O}_2/\text{animal}$

versus dry weight, were calculated by season and locality, and their significances were determined.

VII. Respiratory Pigment Analysis

An attempt was made to extract, identify, and quantify the respiratory blood pigments of the experimental zooplankton species. A variety of techniques have been developed, but primarily for the larger terrestrial and aquatic arthropods (Redfield, 1929, 1930; Manwell and Baker, 1963; Wieser, 1965). Only recently has research been directed towards the smaller organisms such as zooplankton and insects. Hoshi and Sugano (1965, 1966), using ultracentrifugation, Sephadex-G 200 gel filtration, and DEAE-Cellulose column chromatography, isolated, purified, and determined some properties of the blood hemoglobin of the freshwater cladocera *Moina macropoda* and *Moina rectirostris*. Manwell, 1966, employing starch gel electrophoresis on hemoglobin samples of small and large larval *Chironomus*, spectrophotometrically quantified the results. The present study was patterned after the latter technique.

The experimental animals were collected from Bute Inlet on October 29, 1969, and from Saanich Inlet on November 10, 1969. To prevent interspecific mixing of pigments due to leakage within samples, the live animals to be analyzed were sorted, separated into vials by species, frozen, and stored.

Prior to electrophoresis, 50-100 milligrams of a single zooplankton species was homogenized in 3 mls of distilled water using a Cole-Parmer homogenizer, Centrifuged for one hour at 16,000 rpm and 0°C. To concentrate this material, the supernatant was freeze dried and reconstituted in 0.1 ml of distilled water.

The horizontal method of starch gel electrophoresis was used throughout these experiments. The technique used in making and handling the starch gels was similar to that of Smithies (1959). The actual electrophoresis was performed in Poulik's buffer at 0°C and 200-250 volts. The dianisidine stain described by Owen and Smith, 1961, was employed for detection of both hemoglobin and hemocyanin (Manwell and Baker, 1963). The dye, when used with hydrogen peroxide, is specific for both pigments.

In order to determine the pigments present in the study animals, three controls were used: Standard Hemocyanin from *Megathura crenulata* (Mann Research Laboratories), fresh, oxygenated *Cancer magister* hemocyanin (Hoar and Hickman, 1967), and human hemoglobin. The position of the bands formed by the controls were compared with those of the zooplankton species.

Samples were inserted and run for four to six hours. Staining followed immediately and bands which developed were mapped. Portions of the gel containing the blood pigments, were then removed, frozen, homogenized, and centrifuged at 16,000 rpm for three hours. The supernatant was analyzed spectrophotometrically with a Unicam Sp 800 B ultraviolet spectrophotometer in one centimeter Spectrosil Precision Cuvettes.

RESULTS

I. Vertical Distribution and Migration

Bongo tows were begun on May 23, continued throughout the summer, and were completed on October 8, 1969. During this period, the oxygen minimum layer was sampled 50 times. Between May 23 and June 13, the minimum was sampled at all depths between 190 meters and 120 meters in order to determine where the zooplankton, if present, occurred. One large aggregation was found. It was invariably situated between 120 and 130 meters. This extreme stratification remained throughout the summer. The aggregation moved slightly in the fall presumably due to the increase in oxygen concentration between 125 and 150 meters. Below 130 meters the only zooplankton found consistently was *Orchomenella obtusa*. It was present in small numbers at every depth sampled, including one tow at 190 meters.

Six species of zooplankton were analyzed in detail, the results of which are presented later in this section as the vertical migration and distribution profiles. Other species, when found, were simply recorded as being present. No attempt was made to quantify these results.

On May 23 and June 13, all species present in the oxygen minimum layer at 125 meters were counted. The data, presented as numbers per cubic meter, are illustrated in Table VI. *Calanus plumchrus*, *Pseudocalanus minutus*, and *Metridia lucens* were the most abundant species. They continued to be the most abundant forms at this depth throughout the study. The other species were present in much lower concentrations on these and all succeeding occasions.

TABLE VI. Species Found in the Oxygen Minimum, in Number/m³, on May 23 and June 13.

Species	May 23	June 13
<i>Calanus plumchrus</i>	159.22	113.52
<i>Eucalanus bungii bungii</i>	0.76	0.24
<i>Euchaeta japonica</i>	2.11	0.77
<i>Metridia lucens</i>	34.20	32.00
<i>Pseudocalanus minutus</i>	94.10	249.00
<i>Cyphocaris challengerii</i>	0.03	0.08
<i>Orchomenella obtusa</i>	2.46	1.50
<i>Parathemisto pacifica</i>	0.16	0.22
<i>Euphausia pacifica</i>	0.00	0.03
<i>Neomysis rayii</i>	0.05	0.06

Table VII lists all of the species found in the oxygen minimum layer during the study period. (The descriptive terms used in the table are defined by Fulton, 1968.) However, it must be kept in mind that, with the exception of *Orchomenella obtusa*, *Calanus plumchrus*, and *Pseudocalanus minutus*, none of the zooplankton forms migrated deeper than 130 meters; that is, approximately 10-15 meters into water of less than 1 ml/l oxygen. Thus the oxygen minimum layer appears to be a barrier preventing deeper migration of the organisms. Six invertebrate phyla, encompassing twenty-seven genera, were present at some time within the oxygen minimum layer. The Cnidarians and Ctenophores were abundant in late June and July, decreasing in numbers thereafter. *Sagitta elegans*, *Tomopteris renata*, and *Clione limacina* were found on occasion at 125 meters, but their main populations stayed well above this level. The remaining genera tended to center their populations at the edge of the minimum layer, or only a few meters inside, and were, therefore, present in most samples.

To determine the length of time that the oxygen minimum layer was inhabited by the zooplankton six species were analyzed in detail. The species selected were *Calanus plumchrus*, *Euchaeta japonica*, *Euphausia pacifica*, *Cyphocaris challengerii*, *Orchomenella obtusa*, and *Parathemisto pacifica*. The results are illustrated in Figs. 14 to 19. In each graph percent of the species is plotted against time of day and depth. Also shown are the total numbers taken from the water column, and the depth of the oxygen minimum layer.

TABLE VII. Species Occurring in the Oxygen Minimum Layer of Saanich Inlet

Phylum	Species	Abundance*
Cnidaria	<i>Aglantha digitale</i>	seasonally abundant
	· <i>Aequorea aequorea</i>	rare
	· <i>Phialidium gregarium</i>	common
	· <i>Aegina rosea</i>	rare
Ctenophora	· <i>Pleurobrachia pileus</i>	seasonally abundant
	· <i>Beroë cucumis</i>	rare
Annelida	· <i>Tomopteris renata</i>	rare
Chaetognatha	<i>Sagitta elegans</i>	rare
Mollusca Pteropoda	· <i>Clione limacina</i>	rare
	· <i>Limacina helicina</i>	common
Arthropoda Copepoda	<i>Calanus plumchrus</i>	very abundant
	<i>Calanus cristatus</i>	rare
	<i>Pseudocalanus minutus</i>	abundant
	<i>Eucalanus bungii bungii</i>	common
	<i>Euchaeta japonica</i>	abundant
	<i>Metridia lucens</i>	abundant
Mysidacea	<i>Neomysis rayii</i>	rare
Amphipoda	<i>Parathemisto pacifica</i>	abundant
	<i>Euprimno abyssalis</i>	rare
	<i>Cyphocaris challengerii</i>	abundant
	<i>Orchomenella obtusa</i>	abundant
Euphausiacea	<i>Euphausia pacifica</i>	abundant
	<i>Thysanessa longipes</i>	common
	<i>Thysanessa raschii</i>	common
	<i>Thysanessa spinifer</i>	rare
Decapoda	<i>Spirontocaris sica</i>	rare
	<i>Munida quadrispina</i>	common

*Terms described by Fulton, 1968.

Calanus plumchrus did not migrate up on any of the three sampling days (Fig. 14). The aggregation remained at 125 meters continually except at midnight on August 26, when approximately 60% of the population descended to 150 meters.

Euchaeta japonica, on the other hand, vertically migrated daily (Fig. 15). The day depth of the population appeared to be governed by the depth of the oxygen minimum layer. Thus, on August 26, when the minimum was situated at 120 meters, the majority of the species was located at 125 meters. This compares to a maximum day depth of 100 meters on July 9 when the oxygen minimum was at 110 meters. Furthermore, the figure suggests that *E. japonica* is perhaps responding to more than a lack of oxygen. On July 9, the main population was located ten meters above the 1 ml/l oxycline; whereas on July 29 and August 26, it was situated five to ten meters within the minimum. Other possible influencing factors will be considered in the discussion section of this thesis.

The majority of *Euphausia pacifica* remained above the level of the oxygen minimum layer on all three sampling days (Fig. 16). On July 9 none entered this layer. Six percent descended into the minimum at noon on July 29, and 18% on August 26. Although the percent of the population entering the layer at these times is not as great as that of *E. japonica*, the pattern is similar. The daily vertical migrations of the euphausiids are also illustrated in the Figure and are similar to those observed by other workers (Lewis, 1954; Mauchline, 1960, 1966a; Brinton, 1967).

The distribution of *Cyphocaris challengeri* in relation to the oxygen minimum layer was very similar to that exhibited by *E. pacifica*. None entered the minimum layer on July 9. Twenty-seven percent descended

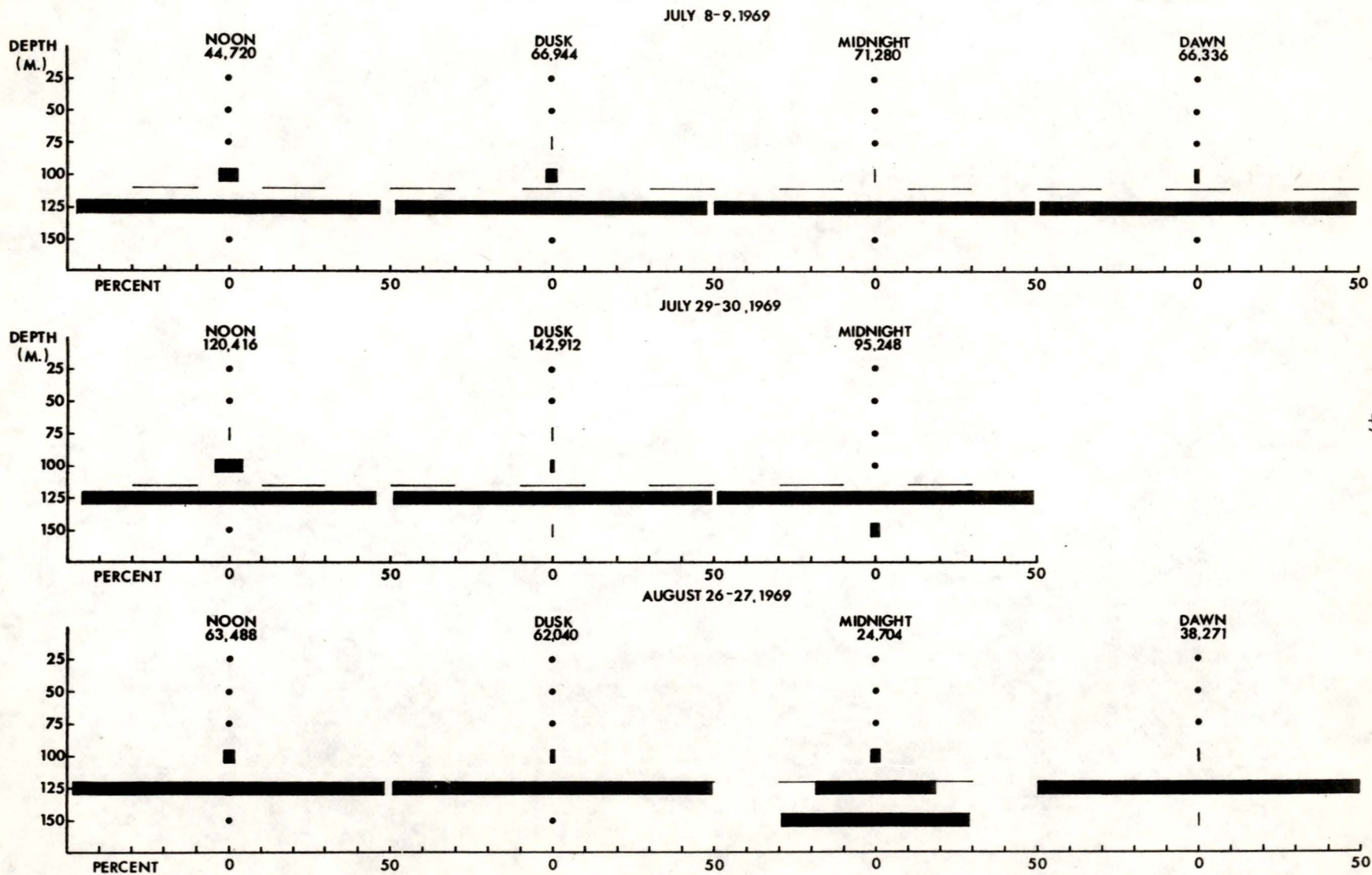


Fig. 14. Vertical Distribution of *Calanus plumchrus* in Saanich Inlet on Three Occasions.

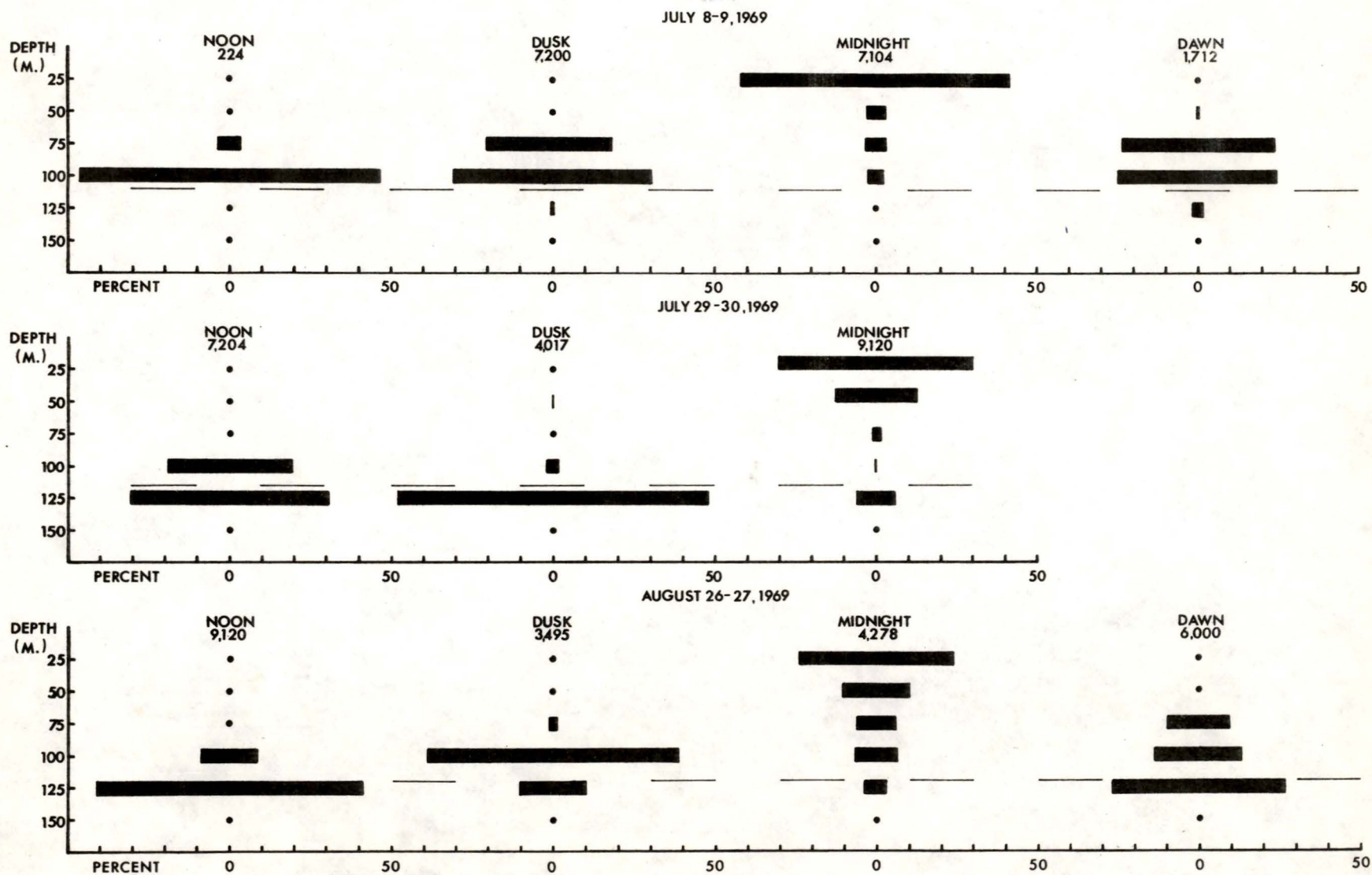


Fig. 15. Vertical Distribution of *Euchaeta japonica* in Saanich Inlet on Three Occasions.

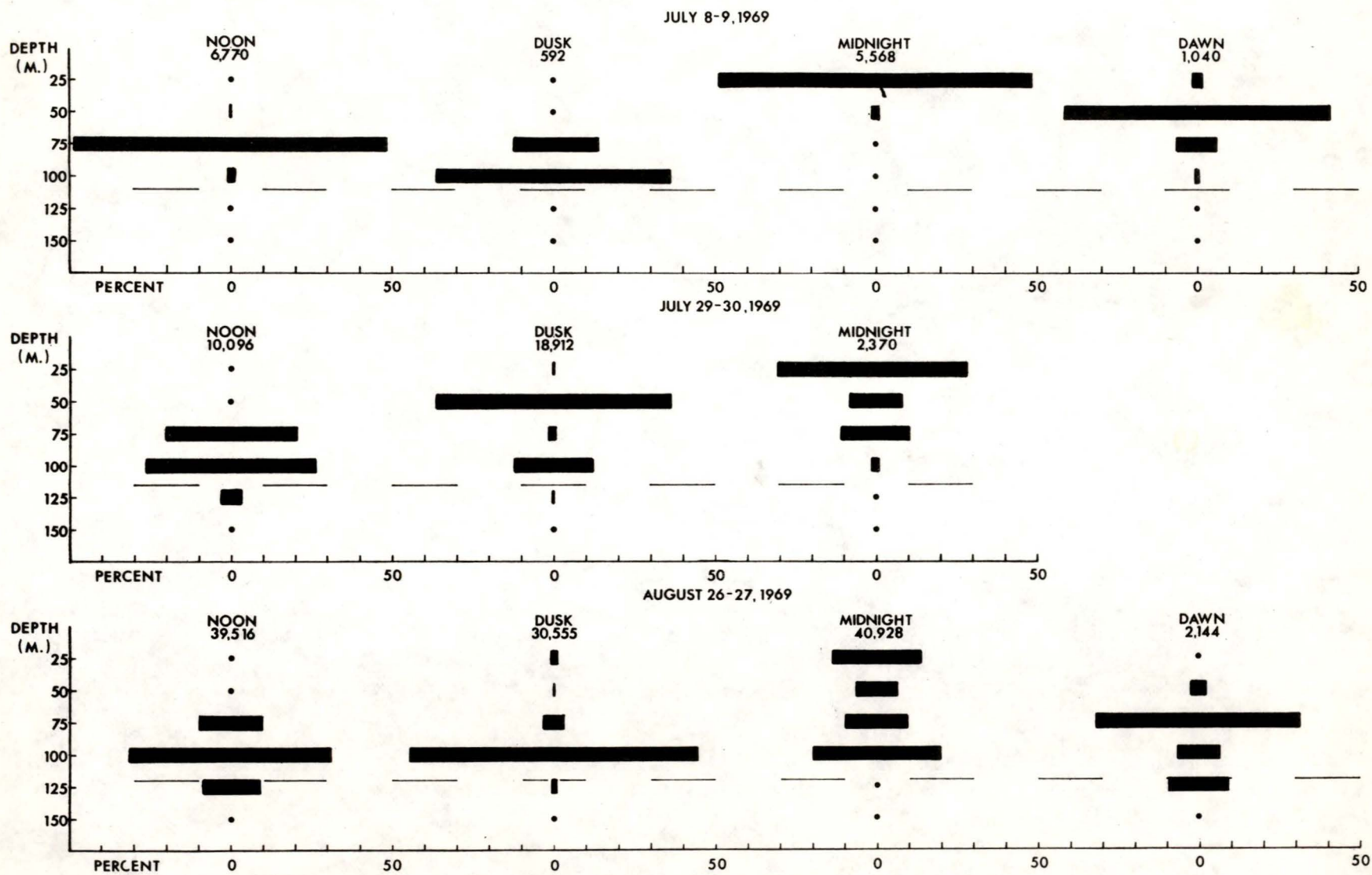


Fig. 16. Vertical Distribution of *Euphausia pacifica* in Saanich Inlet on Three Occasions.

into it on July 29, and 49% on August 26. *C. challengeri* also underwent diel vertical migrations (Fig. 17).

The relationship of *Parathemisto pacifica* to the oxygen minimum layer was not quite as clear as were the previous three organisms. *P. pacifica* occurred in the layer on all three sampling days (Fig. 18). Approximately 6% were found at 125 meters on July 9, as compared to 50% on July 29 and 17% on August 26. The daily vertical migrations were again present, but the population was more dispersed throughout the water column than were those of the three previous crustacea.

The aggregation of *Orchomenella obtusa* was centered within the oxygen minimum layer at 125 meters on all occasions except at dawn on July 9 (Fig. 19). Furthermore, this species was found at all sampled depths of the oxygen minimum layer, suggesting that it was least restricted by the lack of oxygen and other deterrent factors. *O. obtusa* was observed to vertically migrate, but the pattern was not as distinct nor as obvious as those discussed previously. The majority of the population remained at 125 meters, although small percentages migrated up to 50 meters at midnight on July 9 and August 26.

One final set of Bongo samples was taken from Saanich Inlet on October 8, 1969, when the oxygen concentration between 125 and 175 meters reached its highest level for the year. One hundred and twenty-five meter and 150 meter depths were sampled, and the results are listed in Table VIII, expressed as number per cubic meter. In comparing these values with those of July 8 - 9, it is seen that *Euphausia pacifica* and *Parathemisto pacifica* were present deeper and in greater numbers than at any previous sampling time. For *Euchaeta japonica*, *Calanus plumchrus*, *Cyphocaris challengeri*,

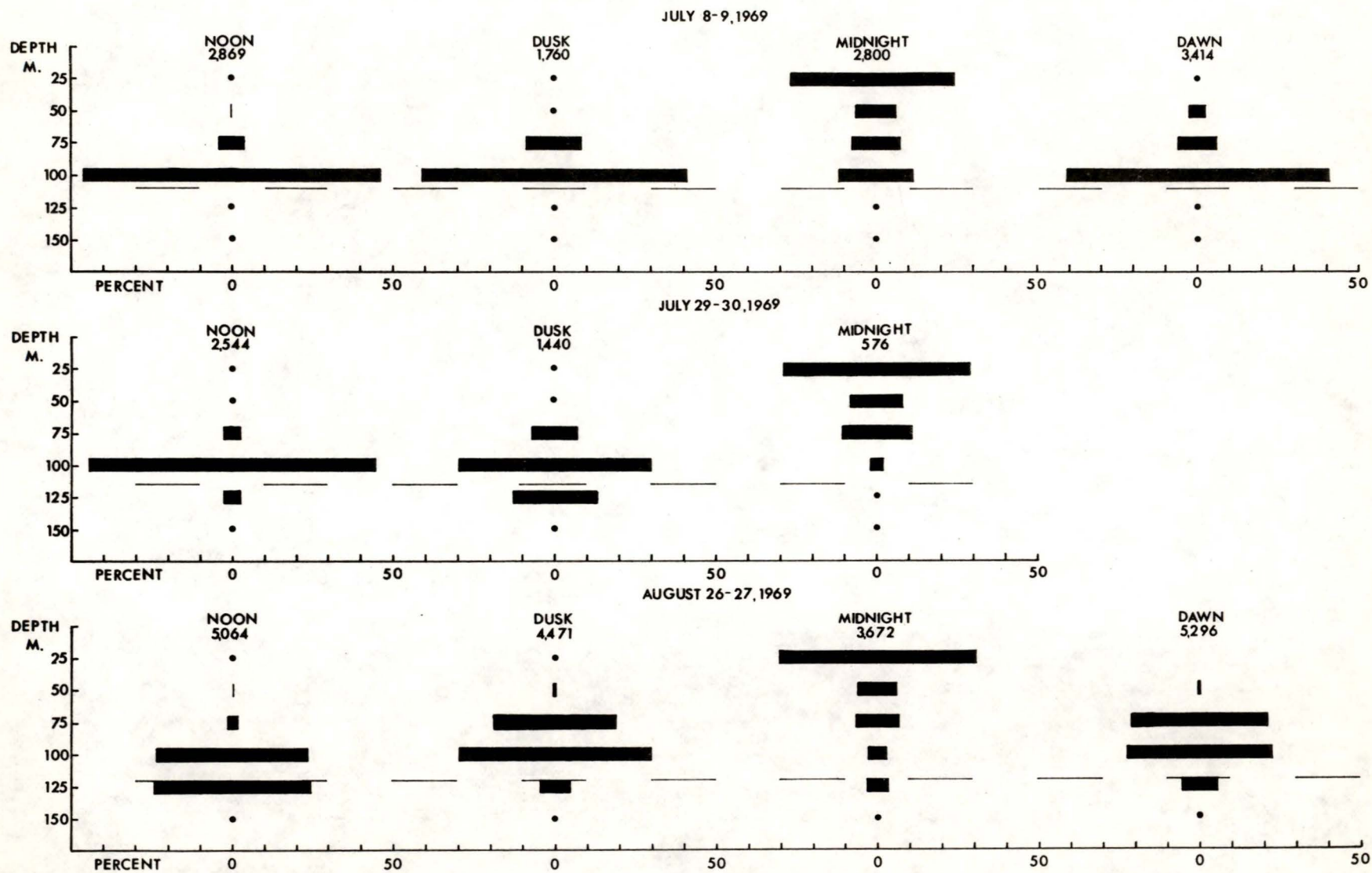


Fig. 17. Vertical Distribution of *Cyphocaris challengerii* in Saanich Inlet on Three Occasions.

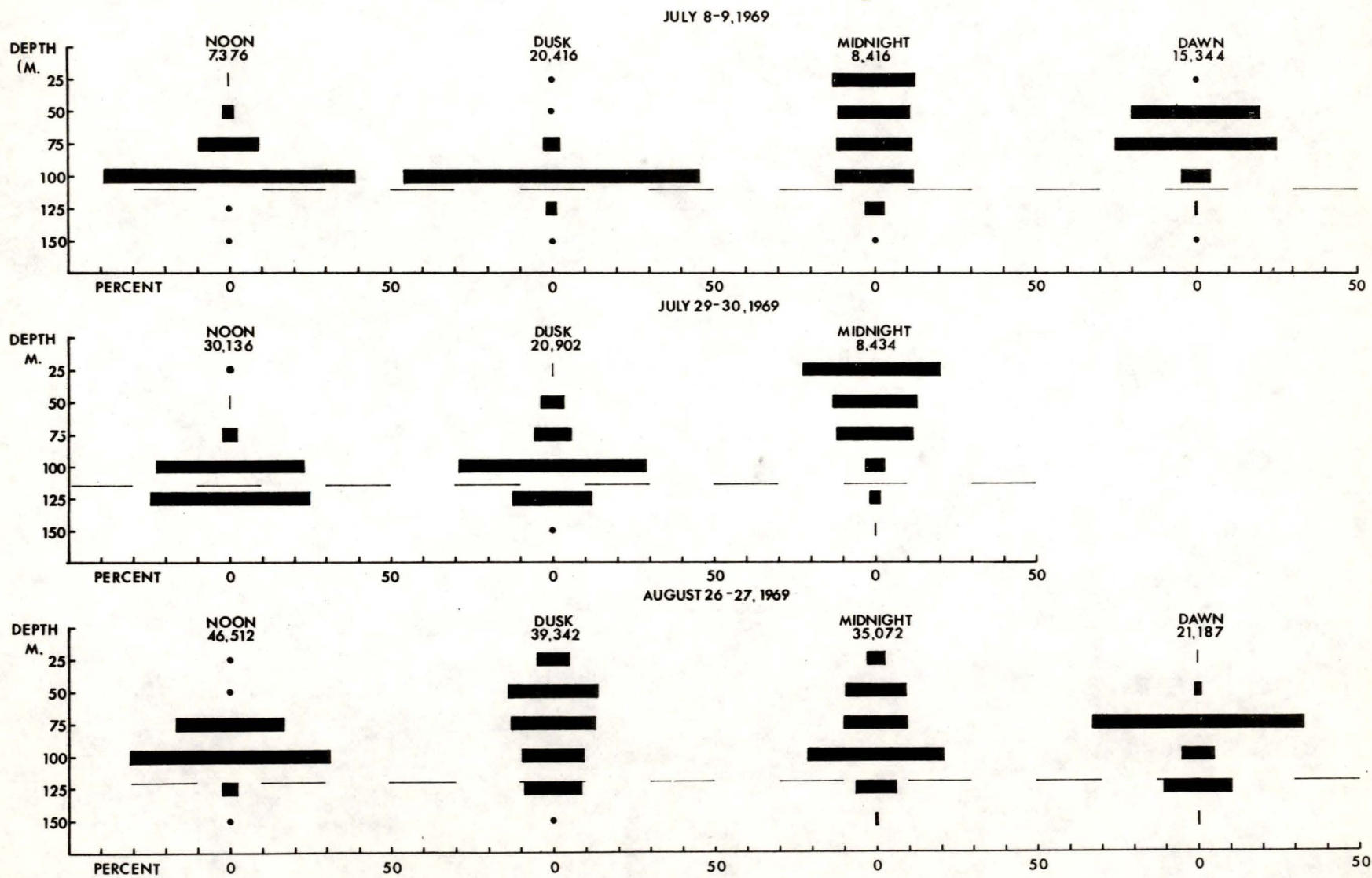


Fig. 18. Vertical Distribution of *Parathemisto pacifica* in Saanich Inlet on Three Occasions.

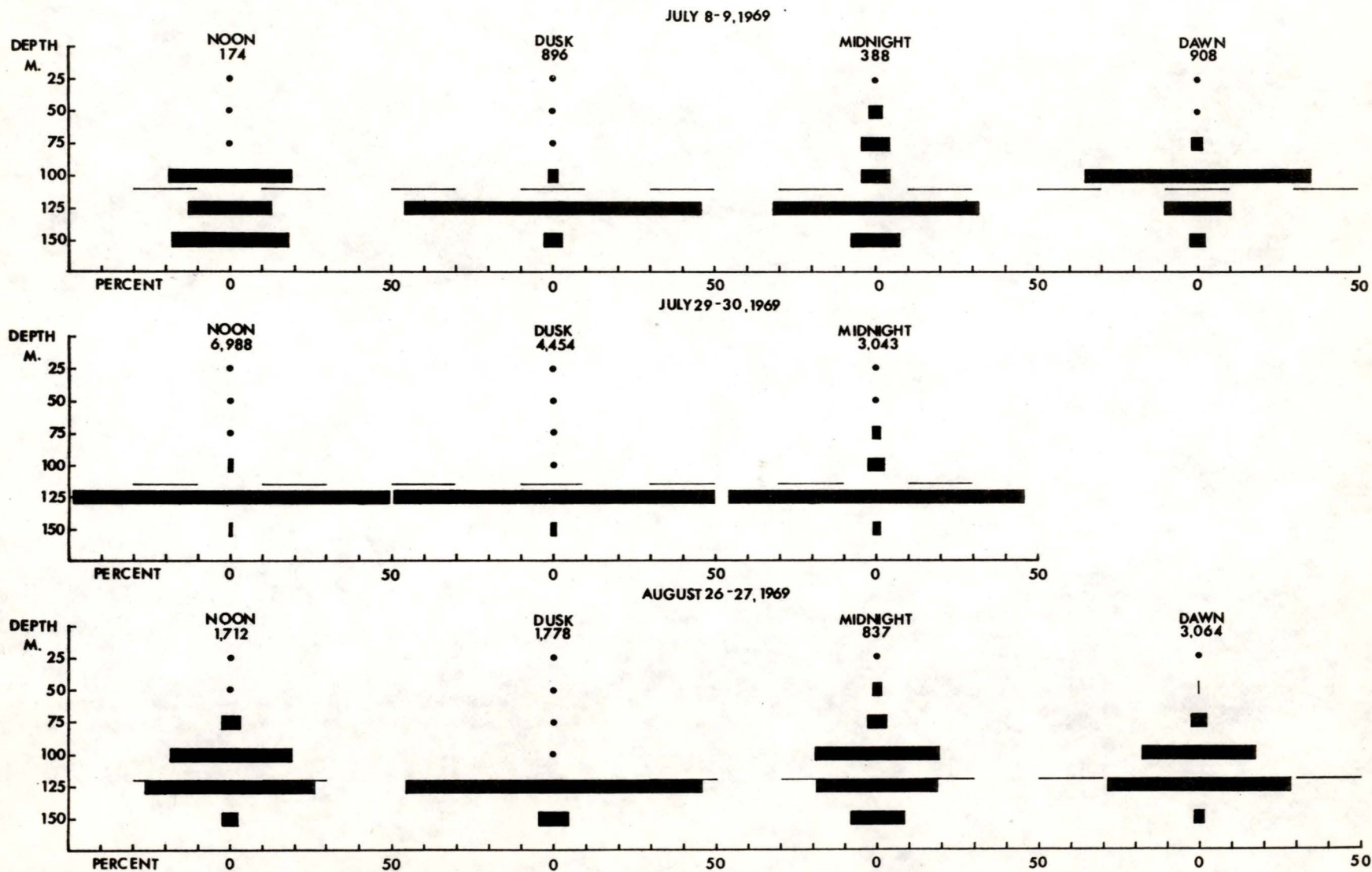


Fig. 19. Vertical Distribution of *Orchomenella obtusa* in Saanich Inlet on Three Occasions.

and *Orchomenella obtusa* this was not the case. The extreme stratification of all the zooplankton in Saanich Inlet probably resulted in these species being present at an intermediate depth and, therefore, they were missed by the sampling.

To demonstrate that the day depths of these crustacea from Saanich Inlet were not their preferred depths, two Bongo tows, at 200 and at 400 meters, from Bute Inlet were analyzed. This was sufficient to illustrate that the experimental species migrated considerably deeper when oxygen deficient water was not a barrier (Table IX). There are many references (Lewis, 1954; Marshall and Orr, 1955; Mauchline, 1960, 1966a; Banse, 1964) which suggest that these organisms migrate deeper than observed in Saanich Inlet, but this fact was best illustrated by utilizing a nearby area, Bute Inlet, with similar physical oceanographic conditions with the exception of the oxygen minimum layer.

II. Oxygen Tolerance Tests.

The low oxygen tolerance levels of seven zooplankton species from Saanich Inlet were investigated utilizing the oxygen tolerance equipment described in Methods and Materials (page 32). Samples collected from a control environment (Bute Inlet) were tested under similar conditions to determine whether the oxygen tolerance levels exhibited by the Saanich Inlet forms are common to all members of the same species. Due to a shortage of time it was not possible to run as many tests nor as many animals in Bute Inlet as was possible in Saanich, but the data were usually sufficient for comparisons. To attempt to validate the lab results which had simulated 125 meter oxygen minimum conditions, containers exposed to the environment ("Euchaeta cages") were lowered into the oxygen minimum

TABLE VIII. Experimental Species Found at 125 and 150 meters in Saanich Inlet on July 8 and October 8, 1969, at noon (in numbers per cubic meter).

Species	125 m		150 m	
	July	Oct.	July	Oct.
<i>Calanus plumchrus</i>	78.69	0.12	0.00	27.00
<i>Euchaeta japonica</i>	0.00	14.50	0.00	0.00
<i>Euphausia pacifica</i>	0.00	84.00	0.00	1.32
<i>Cyphocaris challengerii</i>	0.00	0.14	0.00	0.00
<i>Parathemisto pacifica</i>	0.00	15.90	0.00	17.20
<i>Orchomenella obtusa</i>	0.09	0.88	0.12	2.52

TABLE IX. Experimental Species Found at 200 and 400 meters in Bute Inlet on October 29, 1969. (in numbers per cubic meter).

Species	200 m	400 m
<i>Calanus plumchrus</i>	28.21	62.60
<i>Euchaeta japonica</i>	0.21	0.80
<i>Euphausia pacifica</i>	0.20	0.00
<i>Cyphocaris challengerii</i>	1.99	1.77
<i>Parathemisto pacifica</i>	0.56	0.50

layer in Saanich to a depth of 125 meters. This is the depth at which the majority of the organisms aggregated during daylight. These cages were also lowered to 125 meters in Bute Inlet to determine the treatment effect, if any.

The Saanich Inlet lab experiments commenced on May 21 and were completed on August 20. Bute Inlet animals were tested between October 27 and October 31. Initially animals were subjected to an oxygen concentration of 4.5 ml/l to determine the effect of the equipment on their survival. The data, summarized in Table X, indicates that the zooplankton could survive for at least 24 hours under laboratory conditions of high oxygenation. All succeeding experiments were run between 0.26 and 0.49 ml/l, with a mean concentration of 0.39 ml/l. Variability in percent survival was often great. Thus it was convenient to combine all of the data and express the results as mean survival values related to time. The data is summarized in Table XI.

Mean tolerance levels as determined from the Saanich Inlet "Euchaeta Cage" experiments (Table XII) were similar in most cases to those obtained in the laboratory. Furthermore the "Euchaeta Cage" control test in Bute Inlet indicated that the treatment the animals received was tolerable for at least 24 hours (Table XIII). Casualties were noted only in *Metridia lucens*. These animals appeared to have been killed on the ascent of the cages to the surface as oil droplets had just begun to ooze from their bodies. Therefore, the "Euchaeta Cage" data for *Metridia lucens* was not analyzed.

All data was plotted on probit graph paper. Mortality was expressed in terms of units of the standard deviation (probits) and cumulative

TABLE X. Oxygen Tolerance Test Controls¹

Species	No. tested	% Survival
<i>Calanus plumchrus</i>	10	100
<i>Euchaeta japonica</i>	10	100
<i>Metridia lucens</i>	20	100
<i>Cyphocaris challengeri</i>	10	100
<i>Orchomenella obtusa</i>	5	100
<i>Parathemisto pacifica</i>	5	100
<i>Euphausia pacifica</i>	5	100

¹The test ran for twenty-four hours at an oxygen concentration of approximately 4.5 ml/l.

TABLE XI. Laboratory Oxygen Tolerance Data for Saanich Inlet.

Length of Test (hrs)	Average O ₂ conc	<i>E. japonica</i>		<i>C. challengerii</i>		<i>P. pacifica</i>	
		No. Used	% Surv	No. Used	% Surv	No. Used	% Surv
1	0.4	40	95	10	100	10	100
2	0.4	36	83	10	100	10	100
3	0.45	14	71	7	100	15	100
4	0.49	78	49	16	50	12	92
5	0.38	25	40	18	33	14	71
6	0.39	15	0	10	20	8	63
10	0.43	10	0	10	0	20	30
12	0.42	10	0	10	0	-	-
13	0.40	6	0	10	0	7	10
15	0.36	-	-	-	-	-	-
20	0.26	-	-	-	-	7	0
25	0.26	-	-	-	-	-	-

	Average O ₂ conc	<i>O. obtusa</i>		<i>E. pacifica</i>		<i>C. plumchrus</i>	
		No. Used	% Surv	No. Used	% Surv	No. Used	% Surv
1	0.4	-	-	20	20	10	100
2	0.4	-	-	20	0	10	100
3	0.45	-	-	19	0	10	100
4	0.49	-	-	6	0	10	100
5	0.38	-	-	-	-	10	100
6	0.39	-	-	4	0	10	100
10	0.43	10	100	-	-	10	100
12	0.42	5	100	2	0	10	100
13	0.40	5	100	-	-	10	100
15	0.36	-	-	-	-	10	100
20	0.26	5	100	-	-	10	100
25	0.26	10	100	-	-	10	100

	Average O ₂ conc	<i>M. lucens</i>	
		No. Used	% Surv
1	0.4	20	100
2	0.4	74	95
3	0.45	10	100
4	0.49	90	86
5	0.38	40	80
6	0.39	10	50
10	0.43	10	0
12	0.42	10	0
13	0.40	-	-
15	0.36	-	-
20	0.26	-	-
25	0.26	-	-

TABLE XII. "Euchaeta Cage" Tolerance Data from Saanich Inlet. (Combined Data from July 8 and November 24.)

Length of Test (hrs)	Average O ₂ conc	<i>E. japonica</i>		<i>C. challengeri</i>		<i>P. pacifica</i>	
		No. Used	% Surv	No. Used	% Surv	No. Used	% Surv
2	0.36-0.53	20	85	20	95	10	100
4	0.36-0.53	25	35	10	40	15	100
6	0.53	10	10	10	30	10	80
12	0.36	15	0	5	10	5	0

	Average O ₂ conc	<i>O. obtusa</i>		<i>E. pacifica</i>		<i>C. plumchrus</i>	
		No. Used	% Surv	No. Used	% Surv	No. Used	% Surv
2	0.36-0.53	5	100	10	70	10	100
4	0.36-0.53	10	100	9	0	10	100
6	0.53	10	100	10	0	-	-
12	0.36	5	100	4	0	5	100

TABLE XIII. "Euchaeta Cage" Controls from Bute Inlet¹

Genus and Species	No. Tested	Live	Dead	% Survival
<i>Calanus plumchrus</i>	20	19	1	95
<i>Euchaeta japonica</i>	30	30	0	100
<i>Metridia lucens</i>	20	7	13*	35
<i>Cyphocaris challengeri</i>	20	20	0	100
<i>Parathemisto pacifica</i>	15	15	0	100
<i>Euphausia pacifica</i>	12	12	0	100

*These animals appeared to have been killed on the ascent of the cages to the surface, as they had freshly burst.

¹The experiment was conducted over a twenty-four hour period at a depth of 125 meters, a temperature of 9.25°C, and an oxygen concentration of 2.19 ml/l.

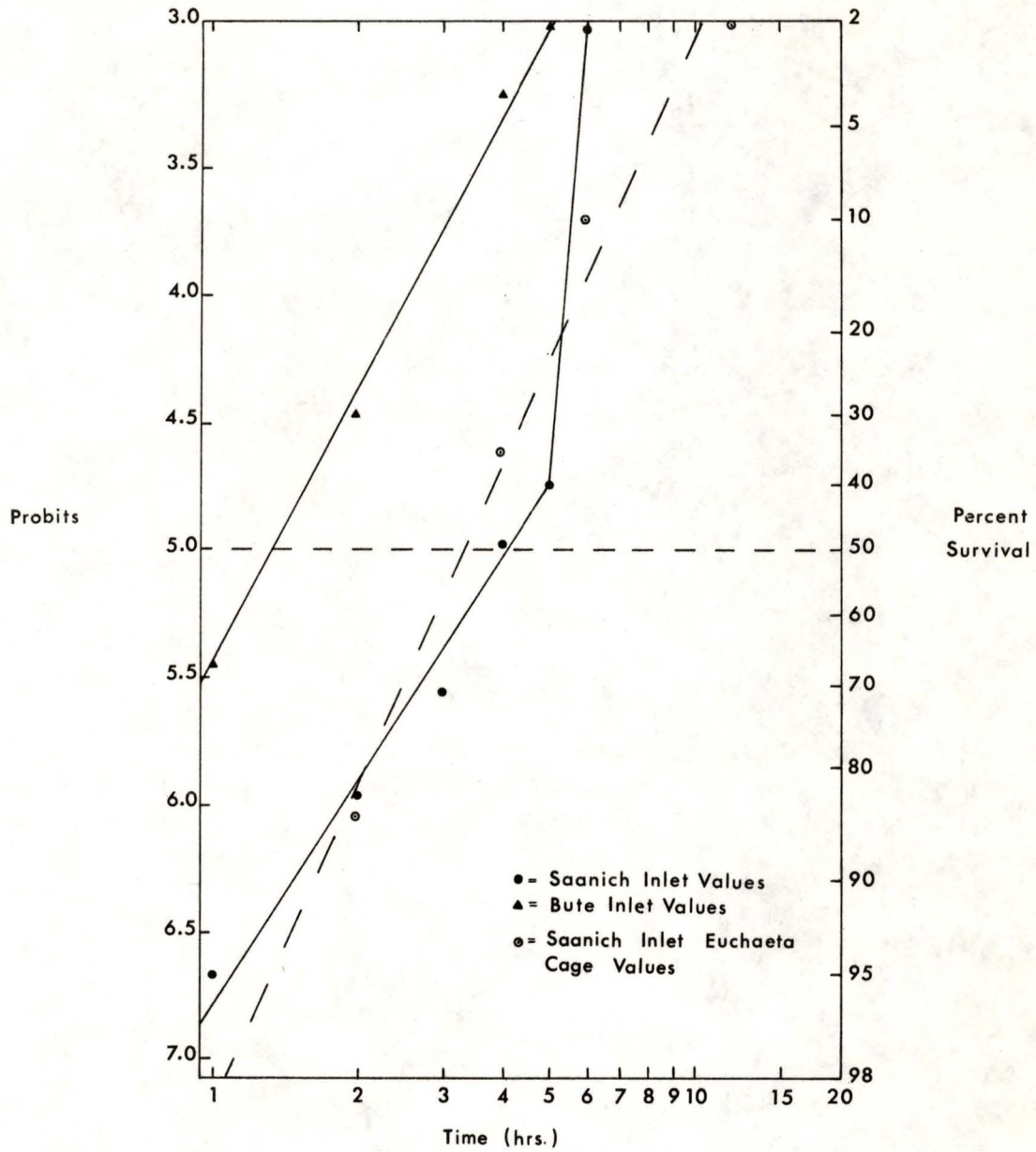


Fig.20. Percent Survival of *E. japonica* at 0.39 ml./l. Oxygen.

percent death versus time transposed into logarithms. The points were then eyefitted to straight lines. This made it possible to estimate the 50% survival time at the test oxygen concentration.

All *Calanus plumchrus* and *Orchomenella obtusa* survived after 25 hours (Table XI). Lack of funds prevented the bubbling of nitrogen into the water for longer periods than this and, thus, the tolerance experiments for these two animals were abandoned at this time.

Figure 20 interprets the percent survival of *Euchaeta japonica* at the mean oxygen concentration of 0.39 ml/l. The data for the Saanich Inlet lab experiments indicate a 50% survival time of 4 hours, and total death of all *E. japonica* between 5 and 6 hours. The Saanich Inlet "Euchaeta Cage" data produced a straight line graph with a 50% tolerance time of 3 hours, 15 minutes. Unfortunately, no tests were run at times between 6 and 12 hours. Therefore, it was not possible to determine whether *E. japonica* would survive much longer than 6 hours. Only 10% survived the 6 hour run suggesting that all would be dead after 7 hours. The 50% survival time for *E. japonica* in the Bute lab experiment was only 1 hour, 20 minutes, and the remaining *E. japonica* died between 4 and 5 hours.

The tolerance levels of *Metridia lucens* were also determined. As stated earlier, "Euchaeta Cage" data was not analyzed for this species as these animals were unable to tolerate the stress imposed by the cages. Figure 21 indicates that the copepod, in both locations, had a similar response, with a 50% mortality time of 6 hours. Furthermore, the remainder died between 6 and 10 hours in Saanich, and between 5 and 11 hours in Bute.

The 50% survival value of 4 hours in the laboratory for *Cyphocaris challengeri* was very close to the 3 hour, 40 minute estimate from the *in situ* "Euchaeta Cage" experiment in Saanich Inlet (Fig. 22). However, after 12 hours in the cage, 10% were still alive, as compared to total

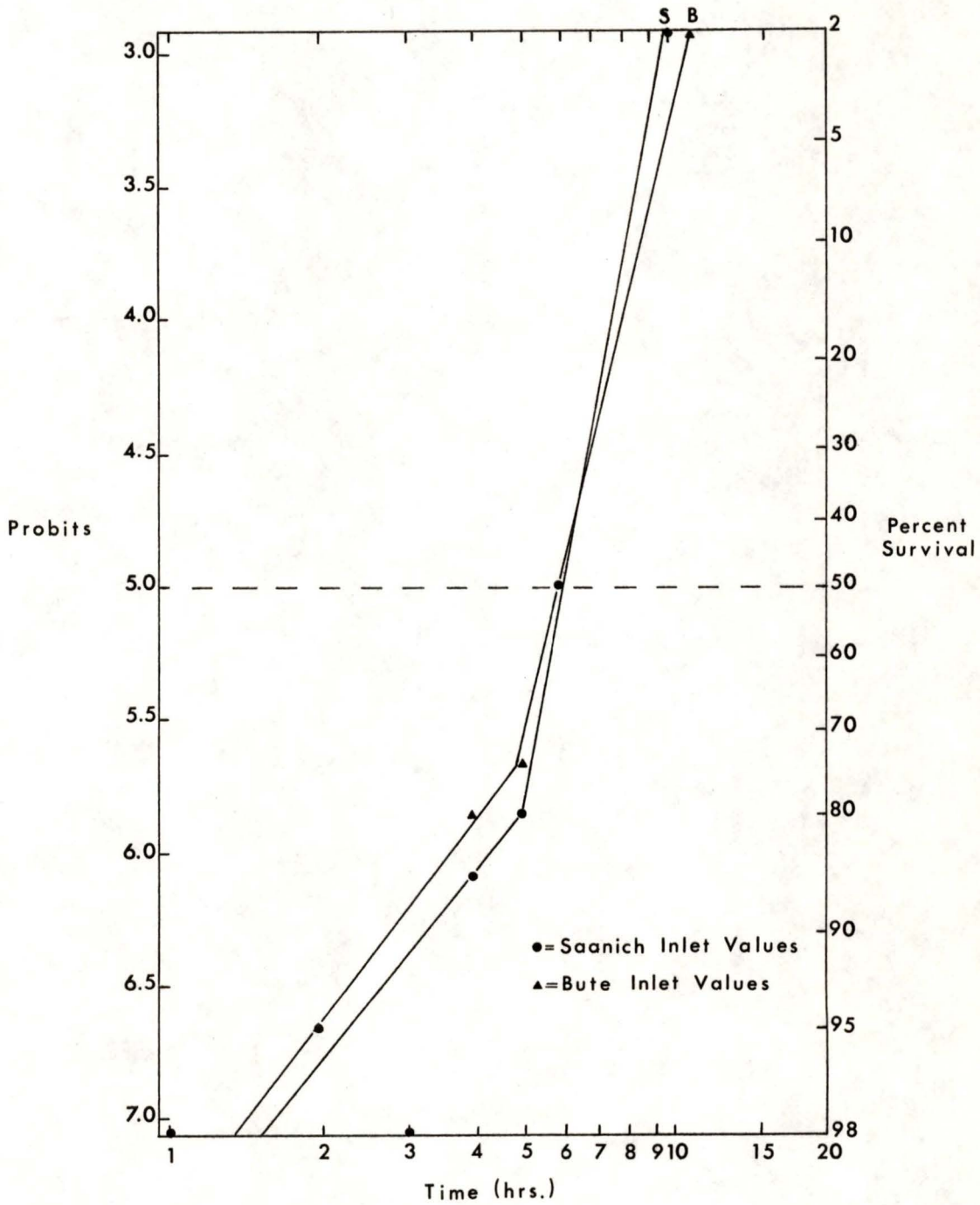


Fig. 21. Percent Survival of *M. lucens* at 0.39 ml. Oxygen.

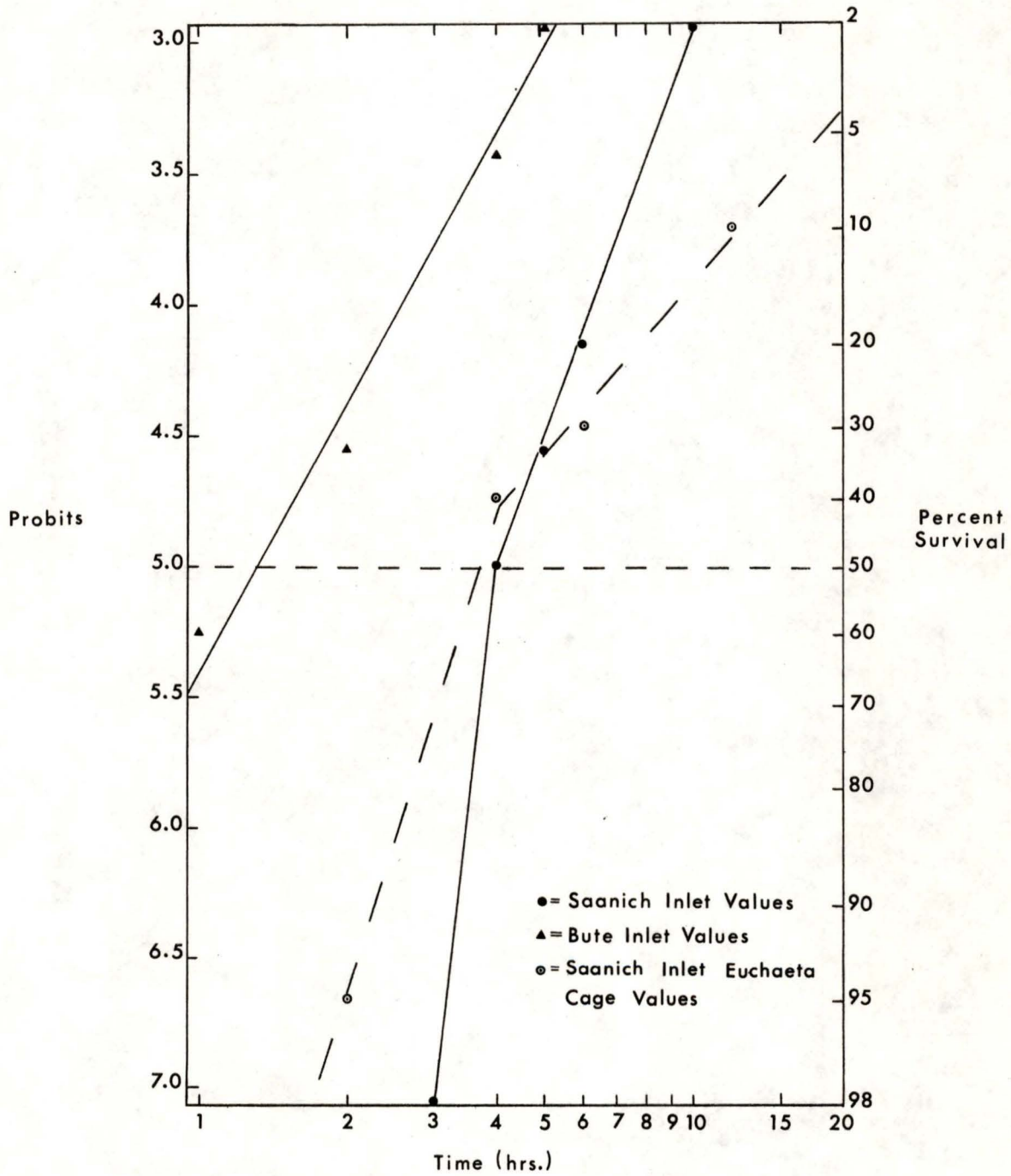


Fig. 22. Percent Survival of *C. challengeri* at 0.39 ml./l. Oxygen.

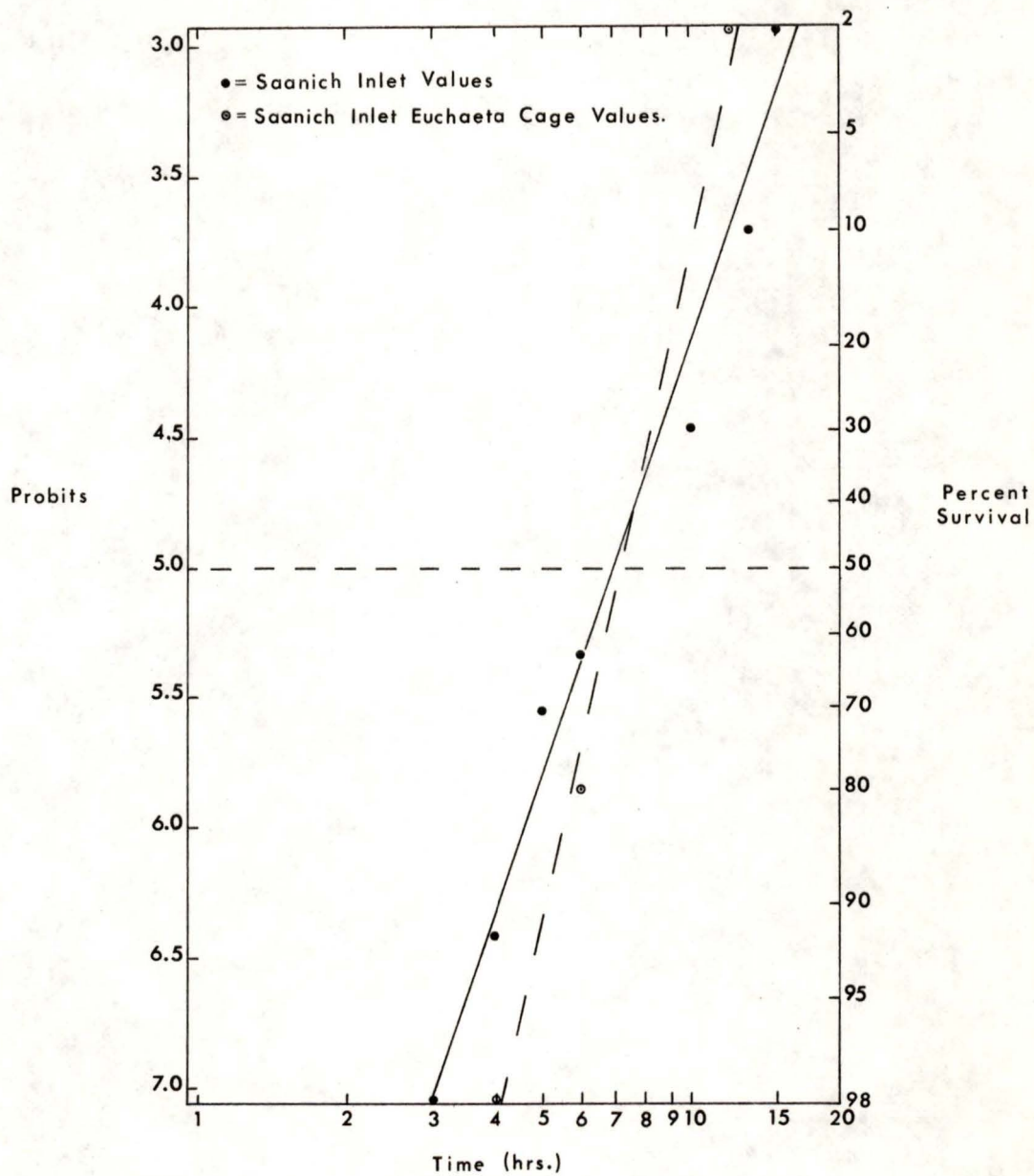


Fig. 23. Percent Survival of *P. pacifica* at 0.39 ml. Oxygen.

death in the lab after 10 hours. The 50% survival level of *C. challengeri* in Bute Inlet was only 1 hour, 20 minutes, the same time as that of *E. japonica* in Bute, and 4-1/2 hours exposure produced total mortality.

The scarcity of *Parathemisto pacifica* in Bute Inlet prevented them from being subjected to the low oxygen tests. Figure 23 illustrates the Saanich Inlet laboratory and *in situ* results. Seven hours at 0.39 ml/l were required to produce the 50% survival level for this species. Total mortality was achieved after approximately 17 hours in the laboratory, and after 12 hours in the "Euchaeta Cages".

The last animal analyzed was *Euphausia pacifica*. Tables XI and XII summarize the results of the laboratory work for this species in both Bute and Saanich Inlets, and the *in situ* work in Saanich Inlet. *E. pacifica* was capable of surviving, in all cases, for only short periods of time. In the Bute and Saanich laboratory experiments, 20% survived for a considerably longer period. Seventy percent were still alive after 2 hours, and total mortality occurred between 2 and 4 hours.

Summarizing the Saanich Inlet data all *Calanus plumchrus* and *Orchomenella obtusa* survived for 25 hours. Thus, no 50% survival level was discerned. *Parathemisto pacifica* had a 50% lethal time of 7 hours for both the laboratory and *in situ* experiments. *Metridia lucens* had to be subjected to the low oxygen for 6 hours to achieve 50% mortality in both experimental situations. *Euchaeta japonica* and *Cyphocaris challengeri* took 4 hours to reach the 50% level in the laboratory. In the field, this time was shortened to 3 hours, 40 minutes for *C. challengeri*, and 3 hours, 25 minutes for *E. japonica*. *Euphausia pacifica* was the least tolerant of the experimental crustacea to the low oxygen concentration. In the lab,

only 20% survived after 1 hour, and all were dead after 2 hours. In the field, 70% survived 2 hours and total mortality was achieved by 4 hours.

III. Respiration Determination.

The oxygen consumption rate of the zooplankton of Saanich Inlet was hypothesized to be a factor influencing their vertical distribution patterns and their low oxygen tolerance levels. Therefore, the respiration rates of five species of zooplankton from Saanich and four from Bute, the control environment, were measured and compared statistically in order to determine the validity of the hypothesis.

The experimental animals analyzed from Saanich Inlet were *Euchaeta japonica*, *Euphausia pacifica*, *Cyphocaris challengeri*, *Parathemisto pacifica*, and *Orchomenella obtusa*. These same species, with the exception of *O. obtusa*, were tested from Bute Inlet. All respiration data is in Appendix III.

For the most accurate statistical analysis, homogeneity of variances is a fundamental assumption, thus all data analyzed was transformed to logarithms, and all tests performed on the transformed data. An initial Bartlett's Test (Sokal and Rohlf, 1969) indicated that transformation produced homogeneity. To facilitate the interpretation of graphs, all figures were plotted using the untransformed data (Conover, 1959). These statistical variables (means, standard errors, regression equations, and correlation coefficients) are summarized in Table XIV. In this study, Anovas were performed and $P < .05$ was used as the level of significance unless otherwise stated.

The respiration rate of Saanich Inlet *Euphausia pacifica* varied

TABLE XIV. Statistical Data of Respiration

	Month	N	\bar{Y}	$S_{\bar{Y}}$	S	\hat{Y}	r
<u>Saanich Inlet</u>							
<i>Parathemisto pacifica</i>	July	4	1.555	0.22	0.440	0.77+.60987X	1.001
	August	23	1.214	0.11	0.504	0.95+.33076X	0.486
	November	15	1.038	0.03	0.130	0.13+.95203X	0.978
	February	6	0.993	0.03	0.084	-0.46+1.1670X	0.956
<i>Cyphocaris challengeri</i>	July	3	0.611	0.12	0.205		
	August	22	0.651	0.06	0.286	1.07+131477X	0.414
	November	15	0.849	0.09	0.343	1.90+.17200X	0.265
	February	3	1.004	0.19	0.336		
<i>Euphausia pacifica</i>	August	13	0.804	0.04	0.152	1.63+.35978X	0.719
	September	9	0.652	0.07	0.193	2.58+.29128X	0.791
	November	9	0.501	0.04	0.109	-0.07+.51247X	0.951
	February	6	0.642	0.04	0.101	0.38+.51800X	0.782
<i>Euchaeta japonica</i>	August	33	0.679	0.05	0.310	0.38+.24813X	0.329
	November	15	0.641	0.04	0.146	0.59+.18560X	0.178
	February	6	0.650	0.02	0.048	0.07+.58510X	0.834
<i>Orchomenella obtusa</i>	July	2	0.378	0.05	0.074		
	August	21	0.280	0.02	0.090	0.24+.24201X	0.512
	February	3	0.328	0.02	0.032		
<u>Bute Inlet</u>							
<i>P. pacifica</i>	November	12	1.585	0.21	0.736	0.24+1.1291X	0.838
<i>C. challengeri</i>	November	15	0.525	0.03	0.119	0.66+.36347X	0.571
<i>E. pacifica</i>	November	6	0.495	0.02	0.040	0.51+.42762X	0.984
<i>E. japonica</i>	November	15	0.738	0.05	0.192	0.59+.18560X	0.178

with season. However, none of the variations were significant at the .05 level. Oxygen consumption was highest in August, decreased steadily until November, and then began increasing again until February (Fig. 24). The Saanich and Bute values for November were found to be not significantly different. All of the regression equations, plotted in Figures 25 and 26, had significant regression slopes and correlation coefficients.

Figure 27 illustrates the seasonal fluctuations in respiration for *Euchaeta japonica*. The trend was very similar to that shown by *E. pacifica*, with higher values in August and February than in November; but again, none of these variations was significant. Furthermore, no significant difference at .05 was found between Bute and Saanich copepods in November. All of the regressions shown in Figures 28 and 29 had significant slopes, but, as the respiration measurements were quite variable, only the Bute Inlet and Saanich Inlet February regressions had significant correlation coefficients.

Parathemisto pacifica had a significantly higher respiration rate in July, than it did for the remainder of the year in Saanich Inlet (Fig. 30). Furthermore, it had a significantly higher oxygen consumption rate in Bute Inlet in November than it did in Saanich Inlet at the same time. Significant correlation coefficients were calculated for all of the regressions except the August values for Saanich Inlet (Figs. 31 and 32).

Cyphocaris challengerii also had significant seasonal differences in respiratory rates. However, the trend was the reverse of that shown by the previous three species. The respiration rate was lowest in

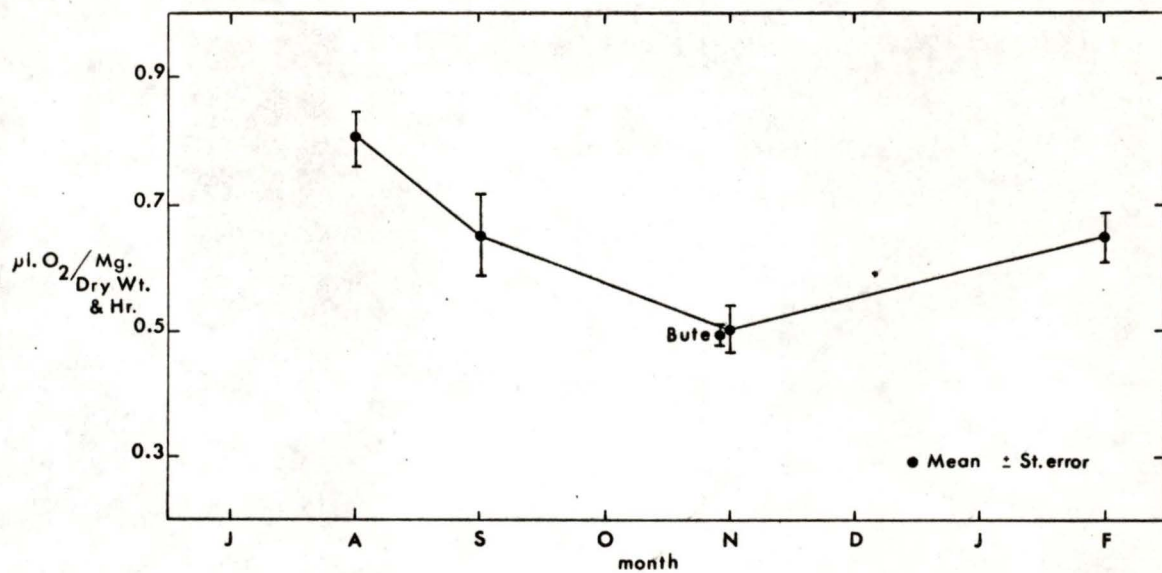


Fig. 24. Seasonal Respiration Rate of *Euphausia pacifica*.

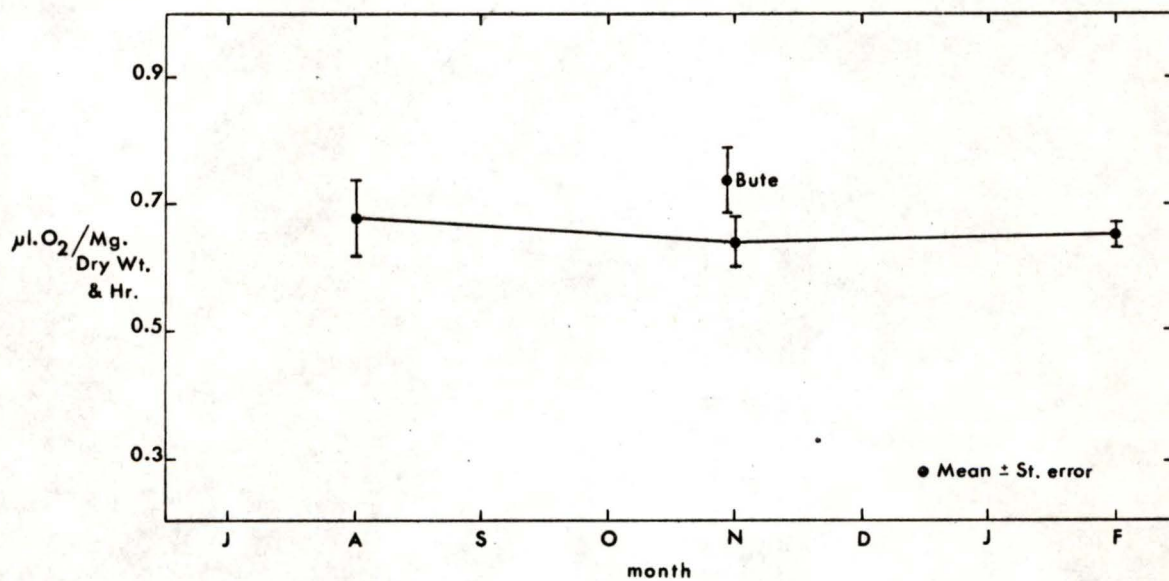


Fig. 27. Seasonal Respiration Rate of *Euchaeta japonica*.

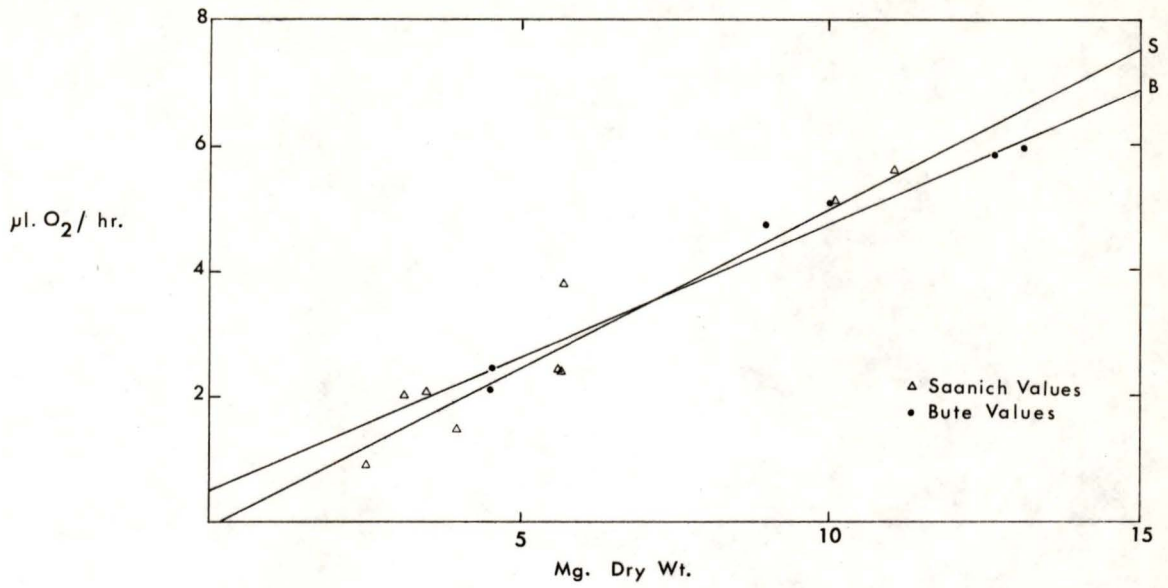


Fig.25. Regressions of Saanich and Bute November Values of Euphausia pacifica.

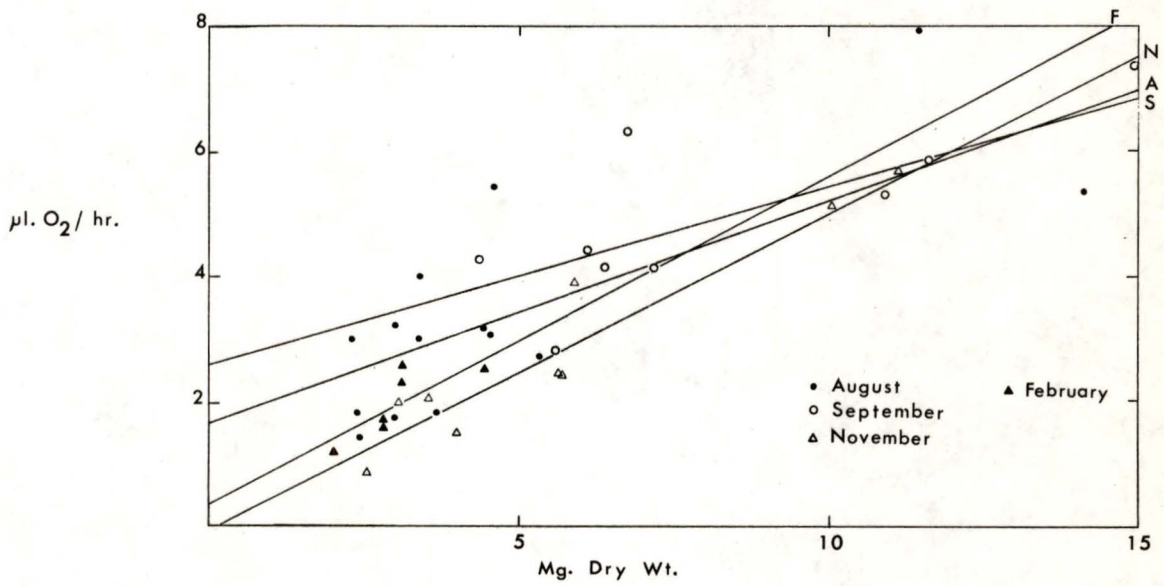


Fig.26. Regressions of Saanich Inlet Euphausia pacifica.

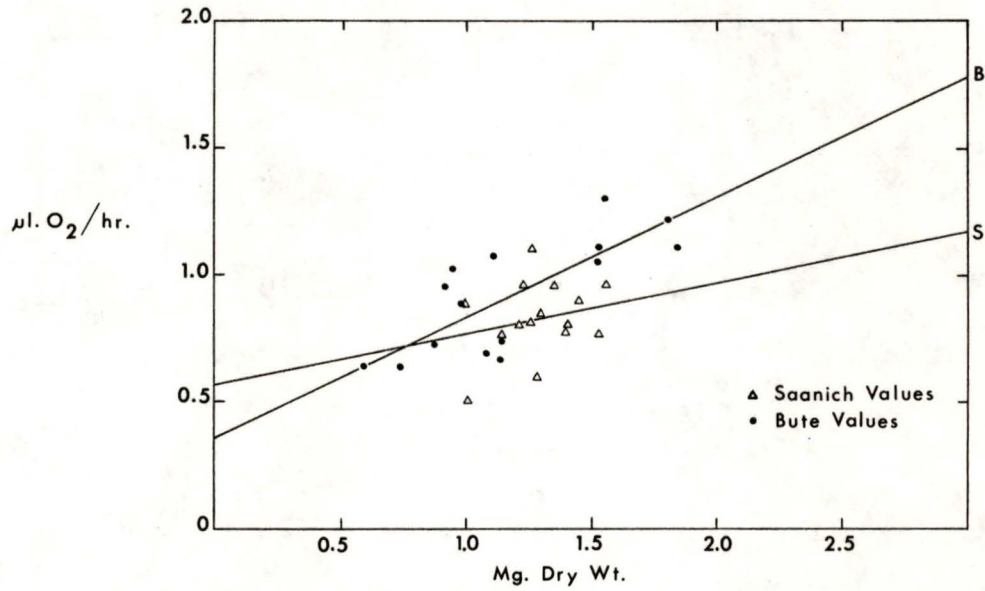


Fig. 28. Regressions of Saanich and Bute November Values of *Euchaeta japonica*.

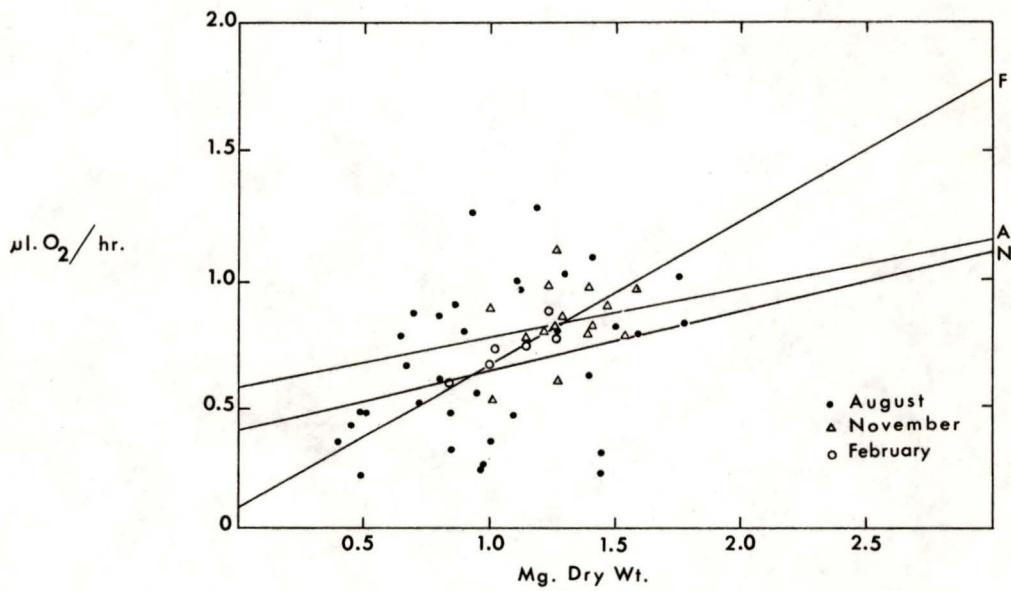


Fig. 29. Regressions of Saanich Inlet *Euchaeta japonica*.

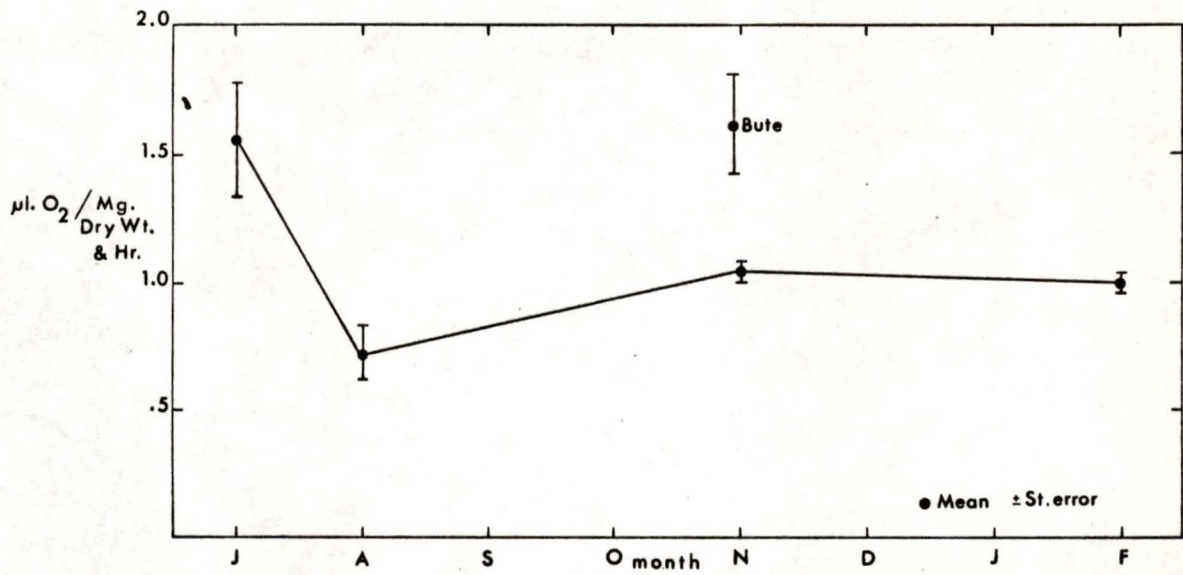


Fig. 30. Seasonal Respiration Rate of *Parathemisto pacifica*.

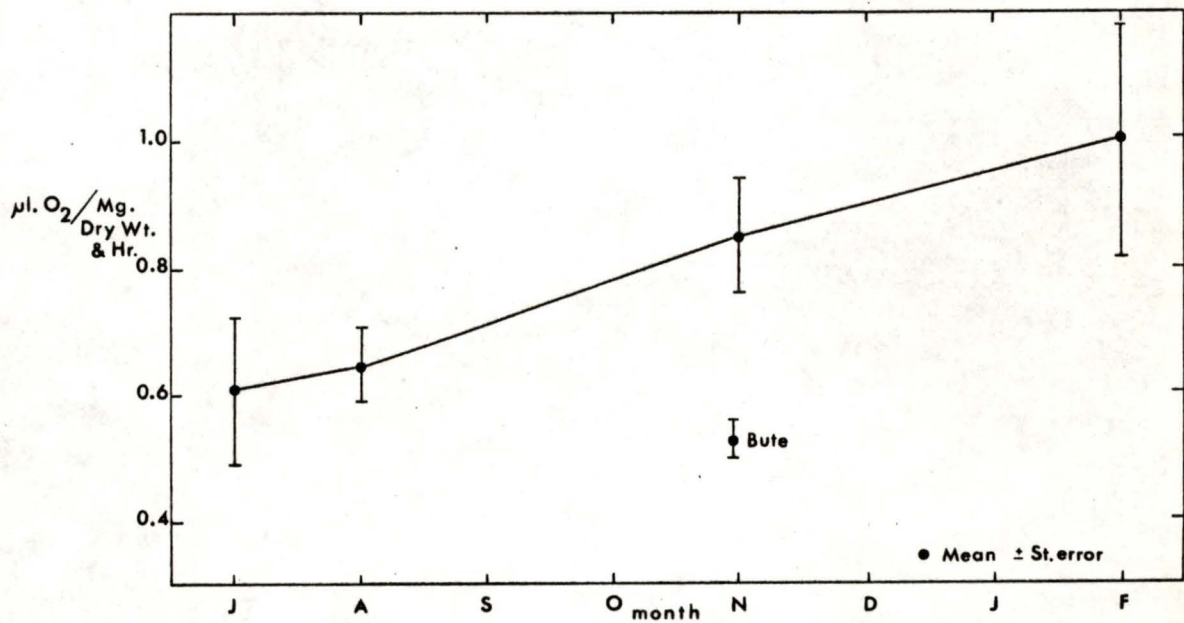


Fig. 33. Seasonal Respiration Rate of *Cyphocaris challengeri*.

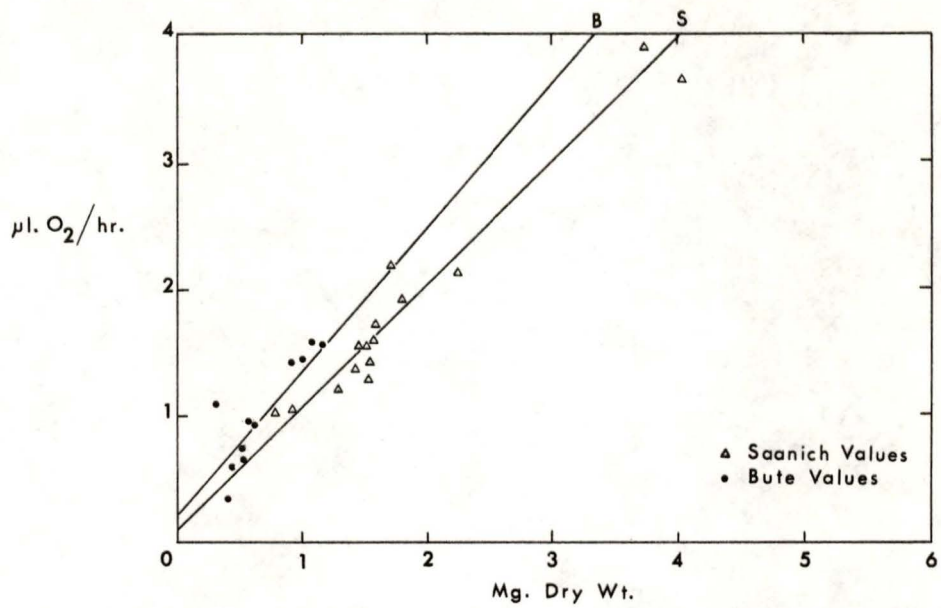


Fig. 31. Regressions of Saanich and Bute November Values of Parathemisto pacifica.

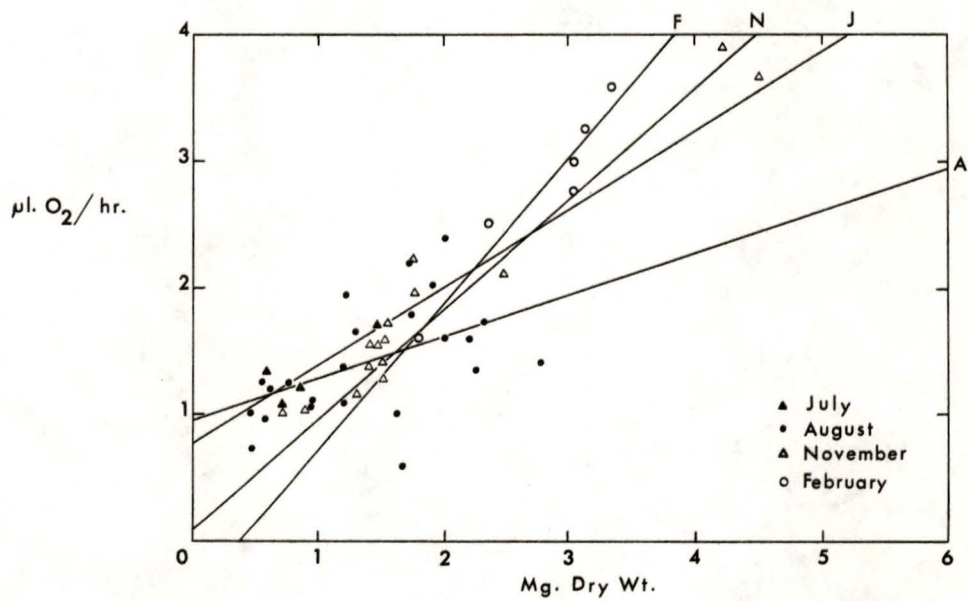


Fig. 32. Regressions of Saanich Inlet Parathemisto pacifica.



July 1969, increasing steadily to its maximum in February 1970 (Fig. 33). In comparing the Bute and Saanich Inlet respiration data, *C. challengerii* from Bute had a significantly lower rate than did the Saanich Inlet animals, this also being opposite to anything observed previously. The regressions for *C. challengerii*, Figures 34 and 35, indicate the great variability found in the respiration rate of this species.

Orchomenella obtusa was not tested from Bute Inlet, and thus no comparisons can be made between the areas. Figure 36 shows that seasonal variations in respiration rate were minimal and therefore, not significant for this species. The regression for the respiration measurements for August is presented in Figure 37.

As the variances between species were heterogeneous, even after transformation, no statistical comparison was attempted. The data (Table XIV) indicates that *Orchomenella obtusa* consistently had a considerably lower respiration rate, expressed in μl of oxygen per milligram of dry weight per hour, than did the remaining species.

Parathemisto pacifica had by far the highest respiration rate throughout the year, followed by *Cyphocaris challengerii*, *Euchaeta japonica*, and *Euphausia pacifica*, in that order. Except in the case of *Cyphocaris challengerii*, which had a lower respiration rate than did *Euchaeta japonica*, the Bute Inlet observations correspond to those observed in Saanich Inlet animals.

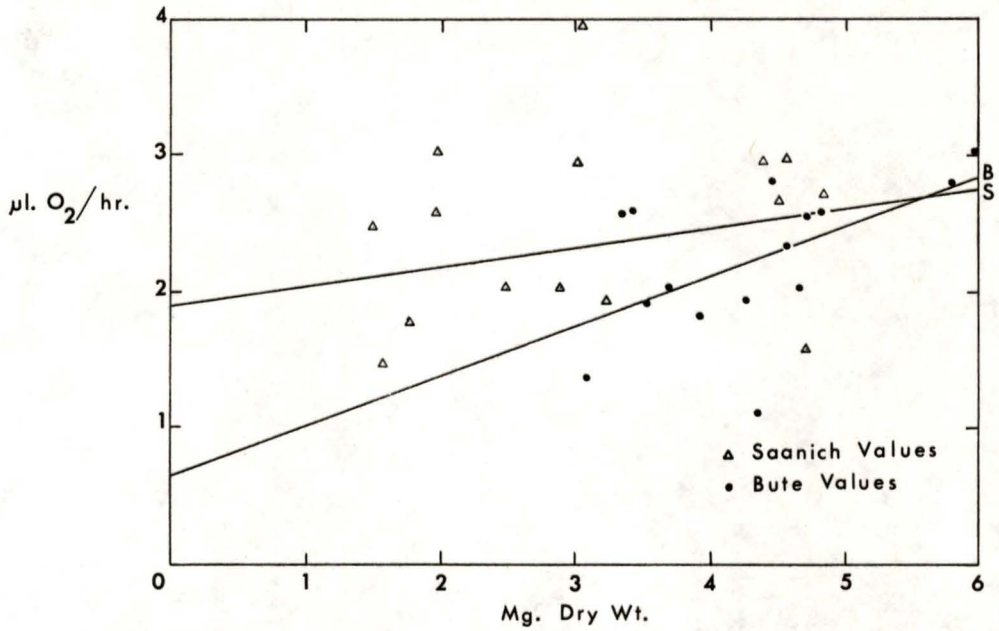


Fig. 34. Regression of Saanich and Bute November Values of Cyphocaris challengeri.

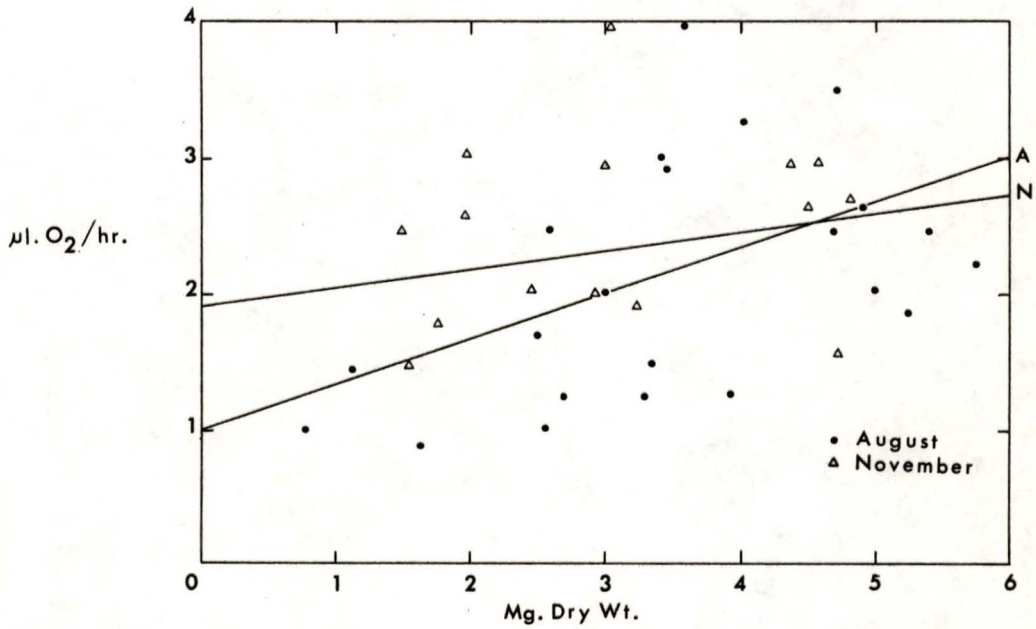


Fig. 35. Regressions of Saanich Inlet Cyphocaris challengeri.

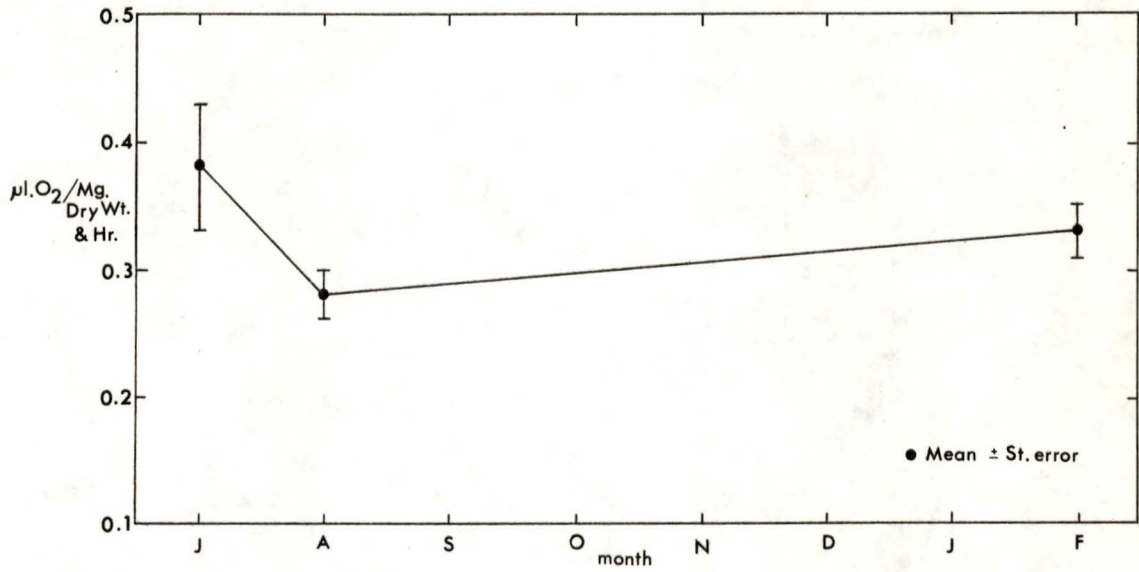


Fig. 36. Seasonal Respiration Rate of *Orchomenella obtusa*.

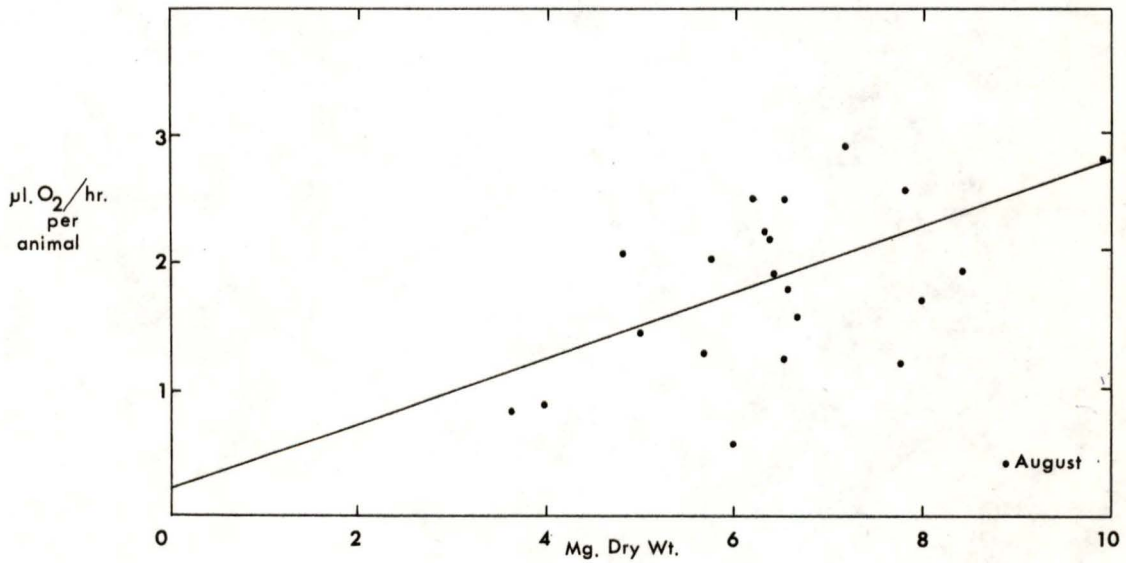


Fig. 37. Regression of Saanich Inlet *Orchomenella obtusa*.

IV. Respiratory Blood Pigment Analysis.

The respiratory pigments of four species of zooplankton - *Euchaeta japonica*, *Euphausia pacifica*, *Cyphocaris challengeri*, and *Orchomenella obtusa*, were analyzed with starch gel electrophoresis. Several spectrophotometric techniques were also attempted in order to quantify these pigments. Analyses began February 6, and terminated March 28, 1970.

Figure 38 illustrates the bands of respiratory pigment formed by the four species analyzed, plus those of crab and human blood. *Cancer magister*, both amphipods, and the euphausiid, had distinct, similar bands located 4.5 to 4.7 cm above the level of the inserts. *Orchomenella obtusa* had one other, wider band between 5.5 and 6.5 cm. *Euchaeta japonica*, the only copepod analyzed, had a distinct band situated from 6.0 to 6.2 cm. The crab control had a total of four bands, positioned between 4.3 cm and the boundary, while seven bands were found in the human hemoglobin, all situated between 2.4 and 5.2 cm.

The bands of *E. pacifica*, *C. challengeri* and *E. japonica*, from both Bute and Saanich Inlets, were compared. There was no discernable difference in either the position of the bands, or in the intensity of stain.

All spectrophotometric techniques attempted to quantify the pigments, failed.

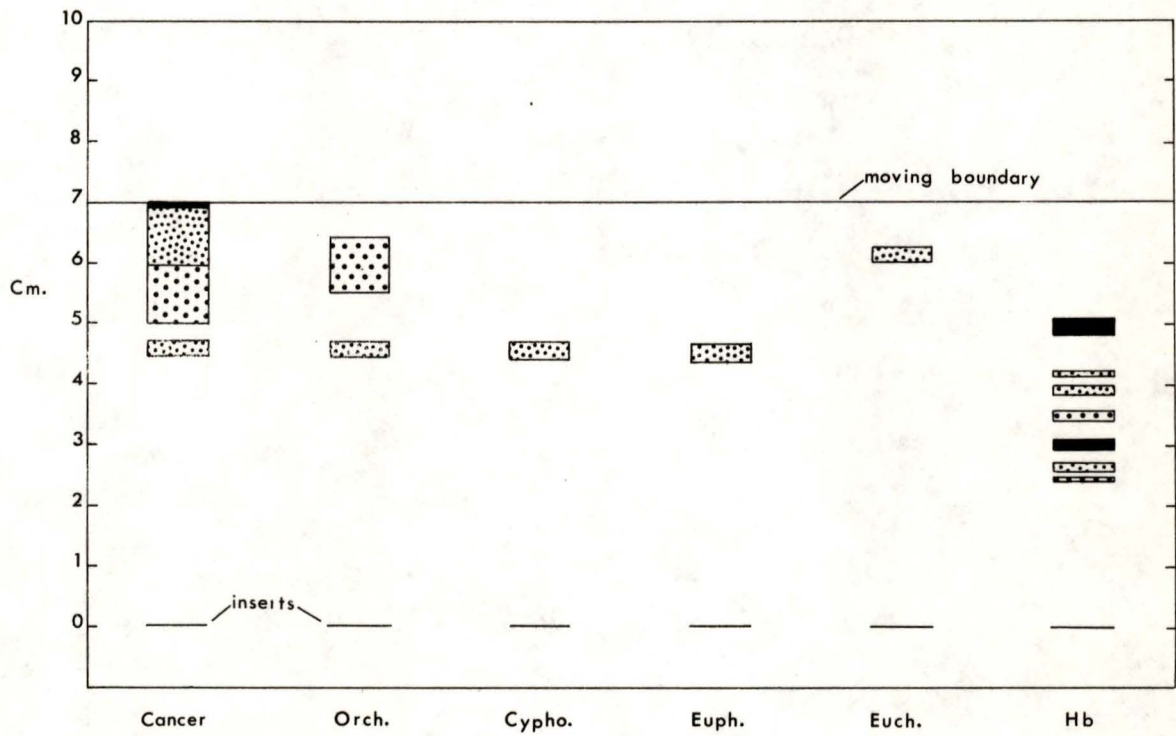


Fig.38. Electrophoretic Map of Blood Pigments.

DISCUSSION

I. Vertical Distribution and Migration.

The factors influencing the vertical distribution and migration of zooplankton have been reviewed by Raymont (1963), Banse (1964), and Mauchline (1969). In Saanich Inlet, the principal limiting factor determining the day depth of the organisms is the oxygen minimum layer. Richards (1965) has discussed the other consequential chemical components which build up in anoxic environments. Dissolved hydrogen sulphide and nitrite, two toxicants, appear to be the most important biproducts which could combine with the effect of low oxygen, to limit the zooplankton distribution (Vinogradov and Voronina, 1961). Carbon dioxide build-up is one other possible factor of importance. Fish (1968), in attempting to relate carbon dioxide and oxygen concentrations to zooplankton distribution, concluded that the effect of carbon dioxide was negligible, but that oxygen was of prime importance. Nitrite was not analyzed. However, Vinogradov and Voronina (1961) felt that nitrite could be of considerable importance. In the present study, hydrogen sulphide was analyzed, but was never recorded shallower than 150 meters (Table 4). This was considerably deeper than the day depth of the zooplankton populations and was, therefore, considered unimportant in this survey. The results indicated that the deeper the oxygen minimum layer, the deeper the organisms would migrate. The Bute Inlet observations verified this hypothesis. Lewis (1954), Boden and Kampa (1965), and Bary (1967), indicated that zooplankton migrated in response to isolumes. It is apparent that in Saanich Inlet these isolumes also produce migrations, but that the oxygen minimum layer prevents movement of the animals to

their "preferred" day depths.

Orchomenella obtusa occurred at all depths and was considered to be the most tolerant species present in Saanich Inlet. The aggregations of *Calanus plumchrus* and *Pseudocalanus minutus* were present at 125 meters continually and at 150 meters occasionally, throughout the study period. These two species were assumed to be the next most tolerant species. The remaining zooplankton all had their populations centered slightly above, or just within, the oxygen minimum layer, suggesting that these species are the least resistant to the low oxygen concentrations, having been most influenced by its presence.

II. Oxygen Tolerance Tests.

The vertical distributions of the Saanich Inlet zooplankton reflect the trends observed in the oxygen tolerance tests. In general, the longer the organisms survived the tests, the deeper they occur in Saanich Inlet, and the more time they spend in the minimum layer.

The abilities of *Orchomenella obtusa* and *Calanus plumchrus* to remain within the oxygen minimum continually, as suggested by their daily vertical distribution, was supported by their responses to conditions of low oxygen. In the lab both species survived for 25 hours at 0.39 ml/l. Fish (1968) noted that *Orchomenella obtusa* could tolerate at least 36 hours in these conditions in the field. *Calanus plumchrus* has not been observed by anyone in the field, but its ability to tolerate 25 hours of low oxygen in the lab, and the field observations of its distribution, suggests that it too could survive for at least this long in the field.

The oxygen tolerance test results for *Parathemisto pacifica* proved unexpected. The center of the population of this amphipod tended to avoid the oxygen minimum layer completely, suggesting an inability of the animal to tolerate low oxygen levels. However, it was observed to survive as long as 17 hours in the lab, and at least 12 hours in the field.

The 50% survival time of *Metridia lucens* was very similar in both Bute and Saanich Inlets. This suggests that no adaptation to oxygen deficient environments occurs in this species.

Euchaeta japonica, and *Cyphocaris challengeri* had very similar 50% survival times in Saanich Inlet. Their distribution in relation to the oxygen minimum was also similar, indicating that they are responding equally to the limiting factor. In Bute Inlet, both species survived for considerably shorter, but identical, times than they did in Saanich. Therefore, it seems that these crustacea have adapted to conditions of low oxygen in Saanich Inlet.

Euphausia pacifica survived for the shortest period of time in relation to the other zooplankton tested. This was also reflected in their day depth of between 75 and 100 meters, the shallowest of the species analyzed. Furthermore, they rarely entered the oxygen minimum. Thus it was not surprising that in the lab animals from both Bute and Saanich had a 50% survival time of less than one hour. However, in the field a 50% survival time of two hours was recorded in Saanich Inlet, suggesting that the lab treatment was somehow damaging this species.

III. Respiration Determination.

One would expect that the low oxygen conditions imposed on the zooplankton of Saanich Inlet would result in a depression of the respiration rate of the zooplankton in this area, as compared to the rate in locations where this stress is not present. This trend was apparent in three of the four species compared, but only one animal, *Parathemisto pacifica*, had a statistically significant lower rate in Saanich Inlet than in Bute Inlet.

The results from the respiration study suggest that several factors may be influencing the oxygen consumption rates of the zooplankton analyzed. Therefore, respiration rate alone may not be a good criterion to consider when attempting to relate zooplankton responses with environmental factors, such as oxygen deficient water. In some instances, the data correspond very nicely to "the expected", but in other cases, the reverse was observed. Conover (1960) noted that some species had a more variable respiration rate than others. This "inherent variability", could, when trying to relate several species to environmental conditions, mask the basic trends. Raymond (1959) felt that comparison of respiration rates from different areas would be complicated by such factors as size, degree of maturity, and generation. Conover (1960) after finding significantly different respiration rates between geographical areas separated by 100 miles, but with similar hydrographic conditions, concluded that food availability, food diversity, and the position of the zooplankton in the food chain, would influence the respiration rate of the study species.

Cyphocaris challengeri was the only species that did not follow any of the hypothesized patterns. In the oxygen tolerance tests, this amphipod could tolerate low oxygen conditions in Saanich Inlet for considerably longer periods than it could in Bute. Thus, in theory, one would expect the respiration rate to be lower in Saanich Inlet than it would be in Bute. However, the respiratory rate of the Saanich Inlet animals was found to be significantly higher than it was in Bute, the reverse of what would be expected. As suggested by Conover, this result could possibly be due to other factors, in this case, its position in the food chain. In Saanich, the population of this species is small, and it has to compete with those of *Orchomenella obtusa* and *Parathemisto pacifica*, the dominant amphipods. In Bute Inlet, on the other hand, *C. challengeri* has by far the largest population, while *O. obtusa* is absent, and *P. pacifica* numbers are greatly reduced. However, *C. challengeri*'s seasonal respiration pattern is also totally different from the expected, and from the observed trends, in the remaining species. Why the respiration rate of this amphipod would be lowest in the summer, and highest in the winter, is not apparent.

Excluding the *Cyphocaris challengeri* results for the remainder of the discussion, the observed results were near those expected. Respiration rates, although only statistically significant for *Parathemisto pacifica*, were higher in the summer months than in the winter, in all of the species. This is probably related to their daily vertical migrations through the warm surface waters which are prevalent in the summer. *Orchomenella obtusa* had very minimal seasonal fluctuations in respiration rate. The fact that it never migrated into the warmer water above

75 meters, but remained in the more stable environment below, could explain these results.

This hypothesis would also hold for the copepod *Calanus plumchrus*. Its respiration rate, although not determined in this study, was analyzed by Topping in 1966. He found no seasonal fluctuations in the respiration rate of this copepod, and concluded that this species did not migrate to any great extent. This hypothesis has been confirmed for *Calanus hyperboreus* by Conover (1968), and in the present study for *C. plumchrus*.

Parathemisto pacifica and *Euchaeta japonica* had considerably higher respiration rates in Bute Inlet than they did in Saanich Inlet, but only the *Parathemisto pacifica* values were statistically significantly different. This demonstrates the possible effect of the oxygen minimum layer on the respiration rate of these Saanich Inlet animals. In addition to the depressed respiration rate in the Saanich Inlet *Euchaeta japonica*, this species could tolerate the low oxygen conditions better in Saanich Inlet than in Bute, suggesting a correlation between these two factors. Unfortunately it was impossible to observe whether this relationship was present in *Parathemisto pacifica*, due to the shortage of this amphipod in Bute Inlet. The respiration rate of *Parathemisto pacifica* from Saanich Inlet was significantly lower than it was for the same species from Bute. Therefore, if this animal followed the same pattern as that observed for *E. japonica*, *P. pacifica* would have survived for considerably shorter period of time in Bute.

The respiration rate for *Euphausia pacifica* from both areas was almost identical. The species also had very similar oxygen tolerance responses in both areas. This suggests that *Euphausia pacifica* does

not alter its metabolic patterns to survive in Saanich Inlet. The vertical distribution data also indicated that the euphausiid remained on the edge of the oxygen minimum or above, at all times, and thus may aggregate at a depth where the oxygen concentration would not alter its respiratory rate. Paranjape (1967 a & b) found a mean respiration rate for Saanich Inlet *Euphausia pacifica* of 0.8 $\mu\text{l}/\text{mg}/\text{hr}$ in the summer. This rate was considerably lower than values observed by authors in more southerly locations (Lasker, 1966, Small and Hebard, 1966). Paranjape concluded that the respiration rate was being depressed by the oxygen minimum layer present in the inlet. The present study found a mean August respiration rate of 0.804 $\mu\text{l}/\text{mg}/\text{hr}$ for *Euphausia pacifica*, identical to that of Paranjape (1967 a & b). Since the respiration rate for the euphausiid in Bute Inlet was almost identical to that observed in Saanich in November, one can only conclude that the low respiration rate appears to be characteristic of this geographical area, and is not influenced by the presence or absence of an oxygen minimum layer.

IV. Respiratory Blood Pigment Analysis.

The object of the blood analysis was to isolate and to quantify the respiratory pigments present in the zooplankton species, and then to attempt to relate these results to their observed vertical distributions, oxygen tolerance levels, and respiration rates. Unfortunately quantification of the results was not achieved and there, this parameter cannot be discussed further.

Waterman (1960) and Barnes (1963), state that the higher crustacea have hemocyanin as their respiratory pigment. Wieser (1965) analyzed

the hemocyanins of 15 species of amphipods and isopods. Mauchline, 1969, indicated that no properties of the respiratory pigments of euphausiids have been determined. The electrophoresis performed in the present study showed that the two species of amphipods and *Euphausia pacifica* had a similar band of pigment concentrated at between 4.5 and 4.7 cm above the level of the inserts. *Cancer magister* also had one band situated at this level. Thus it appears that all three of these species possess hemocyanin as their respiratory pigment. The literature also states that the lower crustacean, including copepods, often possess hemoglobin as their respiratory pigment (Barnes, 1963). Hoshi and Sugano (1965) showed that the cladoceran *Moina macrochaeta* had more hemoglobin under oxygen deficient conditions than it did in oxygen rich environments. In the present study, the electrophoretic band produced for *Euchaeta japonica* does not correspond to any of the human hemoglobin bands. However, since a great variety of hemoglobins exist, this does not necessarily mean that the pigment present is not hemoglobin. The fact that a pigment band was found at all would suggest that a hemoglobin, of a type other than that found in human blood, is present in this species.

SUMMARY

1. Twenty-seven species of zooplankton, encompassing 6 phyla were recorded from the oxygen minimum layer, but only 3 species, *Orchomenella obtusa*, *Calanus plumchrus*, and *Pseudocalanus minutus*, migrated into the minimum to any great extent.
2. The depth of the daytime zooplankton aggregation was directly related to the depth of the minimum layer. The deeper the minimum, the deeper the zooplankton extended.
3. The zooplankton aggregation was usually more dispersed on days of low light intensity than on clear days.
4. Laboratory oxygen tolerance tests on the 7 species of zooplankton produced similar results to those of the *in situ* experiments done on the same species.
5. *Calanus plumchrus*, and *Orchomenella obtusa* were observed to survive at 0.40 ml/l for 25 hrs in Saanich Inlet, but were not tested from Bute Inlet.
6. *Euchaeta japonica* had a 50% lab survival time of 4 hrs in Saanich Inlet, and 1 hr and 20 minutes in Bute Inlet. The respiration rate of *E. japonica* was biologically significantly lower in Saanich than in Bute, suggesting a relationship between respiration and low oxygen tolerance levels. Furthermore, seasonal differences in the respiration rate were observed from Saanich, with a considerably higher rate in the summer than in the winter.
7. *Metridia lucens* had a similar 50% survival time of 6 hrs from both sampling areas, suggesting that no physiological adaptation had

occurred for this species.

8. *Parathemisto pacifica* had a 50% survival time of 7 hrs in Saanich Inlet but was not tested from Bute. *P. pacifica* had a significantly lower respiration rate in Saanich than in Bute, and has a significantly higher rate in the summer than in the winter.
9. *Cyphocaris challengeri* had a 50% lab survival time of 4 hrs in Saanich and 1 hr and 20 minutes in Bute Inlet, indicating a higher tolerance capability in Saanich Inlet. Respiration rates did not produce the expected results, as the rate was significantly lower in Bute than in Saanich. Furthermore, the rate was significantly higher in the winter than in the summer in Saanich Inlet.
10. *Euphausia pacifica* could survive for only short periods of time in low oxygen concentrations in both inlets (20% survival after one hour). The respiration rates determined from the two areas were not significantly different either, suggesting that *E. pacifica* does not appear to adapt to the minimum conditions, but avoids the layer.
11. Quantification of the respiratory blood pigments were not attained. Two bands of blood pigment were discerned for *O. obtusa* and one band for *E. pacifica*, *E. japonica*, *C. challengeri*, and *P. pacifica*.

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APPENDIX

APPENDIX TABLE I. Vertical Distribution in No/M³

July 8-9, 1969.

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengerii</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	0.12	-----	-----	-----	-----	-----
125 m.	0.09	-----	-----	-----	-----	78.69
100 m.	0.13	11.69	5.39	0.30	0.42	4.54
75 m.	-----	2.75	0.45	13.25	0.32	-----
50 m.	-----	0.53	0.01	0.01	-----	-----
25 m.	-----	0.03	-----	-----	-----	-----
Dusk						
150 m.	0.21	-----	-----	-----	-----	-----
125 m.	3.39	1.57	-----	-----	0.19	130.56
100 m.	0.10	37.12	2.88	0.83	8.67	4.32
75 m.	-----	1.90	0.59	0.33	5.13	0.15
50 m.	-----	-----	-----	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Midnight						
150 m.	0.11	-----	-----	-----	-----	-----
125 m.	0.48	0.90	-----	-----	-----	142.62
100 m.	0.07	3.92	1.23	-----	0.64	0.74
75 m.	0.07	3.74	0.80	-----	0.80	-----
50 m.	0.03	3.57	0.67	0.27	0.68	-----
25 m.	-----	4.02	2.59	9.86	10.94	-----
Dawn						
150 m.	0.82	-----	-----	-----	-----	-----
125 m.	0.39	0.18	-----	-----	0.12	120.89
100 m.	1.25	2.50	5.73	0.03	1.92	2.11
75 m.	0.06	15.11	0.83	0.27	1.87	-----
50 m.	-----	11.91	0.36	1.73	0.03	-----
25 m.	-----	-----	-----	0.06	-----	-----

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APPENDIX TABLE I (cont'd.). Vertical Distribution in No/M³

July 29-30, 1969.

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengeri</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	0.09	-----	-----	-----	-----	-----
125 m.	12.51	29.79	0.29	1.23	7.62	202.47
100 m.	0.14	27.72	4.98	11.24	4.70	18.48
75 m.	-----	2.50	0.29	8.74	-----	1.47
50 m.	-----	0.05	-----	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Dusk						
150 m.	0.08	-----	-----	-----	-----	0.03
125 m.	8.83	8.06	0.74	0.16	11.12	281.60
100 m.	-----	18.72	1.72	8.80	0.45	2.98
75 m.	-----	3.62	0.42	0.48	-----	1.22
50 m.	-----	2.30	-----	26.44	0.03	-----
25 m.	-----	0.07	-----	0.20	-----	-----
Midnight						
150 m.	0.10	0.03	-----	-----	-----	3.62
125 m.	5.60	1.70	-----	-----	1.47	186.88
100 m.	0.30	3.08	0.20	0.68	0.07	-----
75 m.	0.13	12.73	1.07	11.47	0.33	-----
50 m.	-----	14.11	0.81	8.31	3.34	-----
25 m.	-----	21.69	2.90	32.10	7.86	-----

APPENDIX TABLE I (cont'd.). Vertical Distribution in No/M³

August 26-27, 1969

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengeri</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	0.16	0.00	-----	-----	-----	-----
125 m.	1.79	4.35	4.96	14.14	15.04	84.48
100 m.	1.28	57.98	4.80	49.28	3.20	4.61
75 m.	0.20	30.69	0.34	15.39	-----	-----
50 m.	-----	-----	0.02	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Dusk						
150 m.	0.31	-----	-----	-----	-----	-----
125 m.	3.23	13.53	0.83	0.83	1.38	122.40
100 m.	-----	15.26	5.31	54.59	5.44	1.79
75 m.	-----	20.80	2.73	4.07	0.17	-----
50 m.	-----	27.46	0.08	4.00	-----	-----
25 m.	-----	7.61	-----	1.21	-----	-----
Midnight						
150 m.	0.27	0.64	-----	-----	-----	28.75
125 m.	0.62	8.83	0.50	-----	0.61	18.69
100 m.	0.64	29.70	0.45	32.38	1.09	1.79
75 m.	0.10	13.57	0.99	16.23	1.02	-----
50 m.	0.04	13.44	0.93	10.76	1.76	-----
25 m.	-----	39.68	4.48	22.52	4.10	-----
Dawn						
150 m.	0.19	0.04	-----	-----	-----	0.35
125 m.	3.96	8.96	1.18	0.22	6.43	75.78
100 m.	2.18	4.32	4.77	0.58	3.23	0.50
75 m.	4.70	27.90	4.54	2.72	2.34	-----
50 m.	0.02	1.10	0.10	0.19	4.48	-----
25 m.	-----	0.06	-----	-----	-----	-----

APPENDIX TABLE II: Percent Vertical Distribution

July 8-9, 1969.

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengerii</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	36.05	-----	-----	-----	-----	-----
125 m.	25.87	-----	-----	-----	-----	94.55
100 m.	38.08	77.90	92.23	2.21	92.98	5.45
75 m.	-----	18.33	7.67	97.75	7.02	-----
50 m.	-----	3.55	0.10	0.04	-----	-----
25 m.	-----	0.22	-----	-----	-----	-----
Dusk						
150 m.	5.78	-----	-----	-----	-----	-----
125 m.	91.62	3.87	-----	-----	1.37	96.69
100 m.	2.60	91.46	82.93	71.85	61.96	3.20
75 m.	-----	4.67	17.07	28.15	36.66	0.11
50 m.	-----	-----	-----	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Midnight						
150 m.	15.05	-----	-----	-----	-----	-----
125 m.	63.92	5.55	-----	-----	-----	99.49
100 m.	8.52	24.27	23.30	-----	4.90	0.51
75 m.	8.52	23.18	15.13	-----	6.13	-----
50 m.	4.00	22.11	12.60	2.63	5.21	-----
25 m.	-----	24.89	48.97	97.37	83.76	-----
Dawn						
150 m.	4.60	-----	-----	-----	-----	-----
125 m.	21.71	0.60	-----	-----	3.01	98.28
100 m.	70.36	8.41	82.59	1.53	48.75	1.72
75 m.	3.34	50.88	12.14	12.71	47.40	-----
50 m.	-----	40.12	5.27	82.61	0.84	-----
25 m.	-----	-----	-----	3.15	-----	-----

APPENDIX TABLE II (Cont'd.) Percent Vertical Distribution

July 29-30, 1969

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengeri</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	0.69	-----	-----	-----	-----	-----
125 m.	98.20	49.60	5.22	5.80	61.85	91.03
100 m.	1.11	46.16	89.57	52.99	38.15	8.31
75 m.	-----	4.16	5.21	41.21	-----	0.66
50 m.	-----	0.08	-----	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Dusk						
150 m.	0.85	-----	-----	-----	-----	-----
125 m.	99.15	24.60	26.69	0.44	95.88	0.01
100 m.	-----	57.14	59.73	24.40	3.87	98.52
75 m.	-----	11.05	14.58	1.33	-----	1.04
50 m.	-----	7.02	-----	73.28	0.26	0.43
25 m.	-----	0.20	-----	0.55	-----	-----
Midnight						
150 m.	1.66	0.06	-----	-----	-----	-----
125 m.	91.28	3.19	-----	-----	-----	1.90
100 m.	4.89	5.77	4.02	1.30	11.25	98.10
75 m.	2.17	23.86	21.49	21.82	0.50	-----
50 m.	-----	26.45	16.27	15.81	2.53	-----
25 m.	-----	40.66	58.23	61.07	25.56	-----
					60.16	-----

APPENDIX TABLE II (Cont'd.) Percent Vertical Distribution

August 26-27, 1969.

	<i>O. obtusa</i>	<i>P. pacifica</i>	<i>C. challengerii</i>	<i>E. pacifica</i>	<i>E. japonica</i>	<i>C. plumchrus</i>
Noon						
150 m.	4.56	-----	-----	-----	-----	-----
125 m.	52.34	4.86	48.97	17.90	82.46	96.37
100 m.	37.38	62.33	47.39	62.35	17.54	3.63
75 m.	5.72	33.00	3.40	9.75	-----	-----
50 m.	-----	-----	0.24	-----	-----	-----
25 m.	-----	-----	-----	-----	-----	-----
Dusk						
150 m.	9.00	-----	-----	-----	-----	-----
125 m.	91.00	17.20	9.30	1.36	19.69	-----
100 m.	-----	19.40	59.41	89.33	77.83	98.56
75 m.	-----	26.43	30.35	6.66	2.49	1.44
50 m.	-----	27.28	0.94	0.66	-----	-----
25 m.	-----	9.68	-----	1.99	-----	-----
Midnight						
150 m.	16.13	0.91	-----	-----	-----	58.55
125 m.	37.28	12.59	6.75	-----	7.11	37.82
100 m.	38.23	42.33	6.10	39.56	12.48	3.63
75 m.	5.74	19.34	13.51	19.82	11.97	-----
50 m.	2.63	19.16	12.64	13.10	20.57	-----
25 m.	-----	5.66	61.00	27.52	47.87	-----
Dawn						
150 m.	3.13	0.09	-----	-----	-----	0.35
125 m.	56.40	21.15	11.18	18.66	53.60	99.00
100 m.	35.51	10.20	45.02	13.43	26.93	0.65
75 m.	4.70	65.85	42.90	63.43	19.47	-----
50 m.	0.26	2.57	0.91	4.48	-----	-----
25 m.	-----	0.15	-----	-----	-----	-----

APPENDIX TABLE III. *Euphausia pacifica* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
19/8/69	1	5.35	2.725	0.509
	1	2.96	1.775	0.600
	1	18.30	-----	0.198
	1	14.10	4.875	0.346
	1	4.48	3.150	0.703
20/8/69	1	3.44	4.067	1.182
	1	3.00	3.233	1.182
	1	2.42	1.771	0.7315
	1	11.53	7.981	0.692
	1	2.48	1.470	0.591
	1	4.63	5.410	1.185
	1	4.53	3.133	0.692
	1	3.44	3.095	0.899
	1	2.33	3.000	1.290
	1	3.77	1.770	0.469
18/9/69	1	5.60	2.820	0.504
	1	7.22	4.260	0.590
	1	6.12	4.440	0.726
	1	10.45	5.298	0.507
	1	11.54	5.820	0.504
	1	4.39	4.269	0.970
	1	16.31	7.470	0.458
	1	6.40	4.260	0.666
	1	6.75	6.360	0.942
	13/11/69	1	5.71	2.400
1		2.52	0.900	0.357
1		4.05	1.525	0.377
14/11/69	1	5.71	2.400	0.420
	1	3.19	2.013	0.631
	1	10.13	5.138	0.507
	1	11.18	5.625	0.503
	1	5.76	3.850	0.688
	1	3.64	2.100	0.577
17/02/70	1	4.50	2.48	0.55
	1	3.16	2.53	0.799
	1	3.16	2.325	0.736
	1	2.08	1.275	0.613
	1	2.86	1.675	0.586
	1	2.86	1.63	0.568

APPENDIX TABLE III. (cont'd) *Euchaeta japonica* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$	
04/8/69	3	1.41	1.117	0.792	
	3	0.87	0.883	1.015	
	3	1.29	1.025	0.795	
05/8/69	3	0.70	0.867	1.238	
	3	0.80	0.600	0.750	
	3	1.13	0.992	0.878	
07/8/69	3	1.27	0.804	0.633	
	3	1.78	0.663	0.372	
	3	1.59	0.738	0.464	
11/8/69	3	0.93	1.250	1.344	
	3	0.80	0.858	1.073	
	3	1.15	0.908	0.790	
12/8/69	3	0.40	0.363	0.906	
	3	0.49	0.467	0.952	
	3	0.95	0.542	0.570	
	3	0.45	0.408	0.907	
	3	0.48	0.217	0.451	
	3	0.67	0.517	0.771	
	3	0.51	0.458	0.899	
	3	0.87	0.467	0.536	
	3	0.72	0.500	0.694	
	3	1.77	1.017	0.574	
19/8/69	3	0.65	0.758	1.167	
	3	0.89	0.783	0.880	
	3	0.96	0.240	0.250	
21/8/69	3	1.12	0.440	0.393	
	3	1.45	0.210	0.145	
	3	1.44	0.310	0.215	
	3	1.03	0.360	0.350	
	3	0.93	0.250	0.269	
	3	1.38	0.615	0.446	
	3	1.50	0.815	0.543	
	3	0.85	0.305	0.359	
	13/11/69	3	1.44	0.786	0.546
		3	1.44	0.813	0.564
3		1.57	0.771	0.491	
3		1.38	0.954	0.691	
3		1.31	0.792	0.604	
3		1.29	0.588	0.455	
3		1.45	0.888	0.612	
3		1.07	0.496	0.463	
3		1.58	0.946	0.599	

sol

APPENDIX TABLE III. (cont'd.) *Euchaeta japonica* Respiration Data

Date	No.	Dry Wt(mg)	μ l/animal/hr	μ l/mg/hr
14/11/69	3	0.98	0.894	0.912
	3	1.21	0.796	0.658
	3	1.25	0.821	0.657
	3	1.23	0.958	0.779
	3	1.26	1.192	0.946
	3	1.17	0.750	0.641
17/02/70	3	1.28	0.756	0.59
	3	1.02	0.644	0.626
	2	0.86	0.59	0.688
	3	1.14	0.7	0.614
	3	1.24	0.89	0.72
	3	1.09	0.72	0.66

APPENDIX TABLE III. (cont'd.) *Parathemisto pacifica* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
31/7/69	3	1.46	1.718	1.170
	3	.73	1.100	1.503
	3	.86	1.167	1.365
	5	.61	1.340	2.182
04/8/69	3	.49	.742	1.514
	3	.63	1.250	1.975
	3	1.73	2.158	1.248
05/8/69	3	1.22	1.946	1.595
	3	.62	.983	1.578
	3	1.32	1.658	1.256
07/8/69	3	1.34	1.250	.993
	3	.80	1.475	1.844
	2	.79	1.275	1.614
11/8/69	3	.45	1.008	2.241
	3	.65	1.225	1.885
	3	.95	1.092	1.149
19/8/69	2	.96	1.138	1.185
	3	1.21	1.125	.930
21/8/69	3	2.02	2.380	1.178
	3	2.34	1.740	.744
	3	1.87	2.080	1.112
	3	2.78	1.430	.514
	3	2.20	1.590	.723
	2	1.69	.630	.373
	3	2.25	1.360	.604
	3	1.64	1.005	.613
	3	1.72	1.800	1.050
13/11/69	2	4.08	3.863	.947
	3	1.56	1.592	1.020
	3	1.53	1.292	.844
	3	3.74	3.892	1.041
	3	1.53	1.550	1.013
	4	1.44	1.538	1.068
14/11/69	3	1.56	1.717	1.100
	3	1.72	2.192	1.274
	3	.79	1.042	1.319
	3	1.27	1.192	.938
	3	1.55	1.392	.898
	3	.93	1.050	1.129
	3	2.23	2.129	.955
	3	1.42	1.363	.960
	3	1.80	1.913	1.063

APPENDIX TABLE III. (cont'd.) *Parathemisto pacifica* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
17/02/70	2	3.07	2.76	0.90
	3	3.12	3.25	1.04
	3	3.31	3.575	1.08
	3	2.34	2.458	1.05
	3	1.82	1.59	0.875
	3	3.03	3.058	1.01

Ampipod

APPENDIX TABLE III. (cont'd.) *Cyphocaris challengeri* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$	
31/7/69	3	2.62	1.717	0.655	
	3	2.02	0.783	0.388	
	3	2.35	1.858	0.791	
04/8/69	3	4.11	3.267	0.795	
	3	5.24	1.867	0.356	
	3	3.46	2.858	0.826	
05/8/69	3	3.34	3.525	1.055	
	3	4.73	3.525	0.745	
	3	3.19	2.058	0.645	
07/8/69	3	2.57	1.054	0.410	
	3	1.64	0.889	0.541	
11/8/69	3	3.35	1.496	0.447	
	3	0.79	1.021	1.292	
	3	2.63	2.492	0.948	
19/8/69	3	2.53	1.683	0.665	
	3	2.70	1.258	0.466	
	3	3.30	1.233	0.374	
20/8/69	3	3.93	1.258	0.320	
	3	3.65	4.400	1.206	
21/9/69	3	5.40	2.470	0.457	
	3	5.74	2.210	0.385	
	3	5.05	2.050	0.406	
	3	3.37	3.110	0.923	
	3	4.70	2.460	0.523	
	3	4.93	2.640	0.536	
	13/11/69	3	2.88	2.030	0.706
		3	4.83	2.708	0.561
3		4.50	2.667	0.593	
3		2.47	2.125	0.860	
3		1.76	1.783	1.013	
3		3.23	1.942	0.601	
3		4.39	2.963	0.675	
3		2.48	1.496	0.603	
14/11/69	3	4.55	2.996	0.658	
	3	4.70	1.617	0.344	
	3	1.97	3.192	1.620	
	3	3.18	4.125	1.297	
	3	3.06	2.942	0.961	
	3	1.58	1.460	0.923	
17/02/70	3	1.96	2.583	1.318	
	3	1.91	1.84	0.96	
	3	1.96	2.675	1.36	
	3	2.08	1.44	0.693	

*amphipod*APPENDIX TABLE III (Cont'd.) *Orchomenella obtusa* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
24/7/69	5	5.99	1.945	0.325
	4	5.57	2.394	0.430
04/8/69	3	6.56	1.933	0.295
	3	6.65	2.508	0.377
	3	7.23	2.867	0.396
05/8/69	3	9.95	2.833	0.285
	3	6.22	2.542	0.409
	3	4.74	2.167	0.457
07/8/69	3	6.00	0.608	0.101
	3	6.66	1.233	0.185
	3	7.77	1.317	0.170
11/8/69	3	6.68	1.775	0.266
	3	5.57	1.242	0.223
	3	8.57	1.900	0.222
12/8/69	3	4.97	1.442	0.290
	3	6.34	2.250	0.355
	3	6.39	2.158	0.338
	3	5.84	2.033	0.348
	3	7.80	2.325	0.298
	3	6.71	1.383	0.206
21/8/69	3	4.00	0.885	0.221
	3	3.72	0.865	0.233
	3	7.95	1.665	0.209
17/2/70	3	5.02	1.84	0.367
	3	6.44	1.98	0.308
	3	4.50	1.39	0.309

*Amp pack*APPENDIX TABLE III. (Cont'd) Bute Inlet *Parathemisto pacifica* Respiration Data

Date	No.	Dry Wt(mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
29/10/69	1	0.44	0.6	1.364
	2	0.42	0.364	0.863
	3	1.18	1.575	1.335
	3	1.09	1.45	1.330
	3	0.89	1.408	1.582
	3	0.30	1.150	3.833
31/10/69	3	0.62	0.958	1.546
	3	1.11	1.575	1.419
	3	0.48	0.808	1.684
	3	0.53	0.692	1.305
	3	0.53	0.733	1.384
	3	0.66	0.908	1.376

Bute Inlet *Cyphocaris challengeri* Respiration Data*myp*

29/10/69	3	5.78	2.775	0.480
	3	6.05	3.042	0.503
	3	4.63	2.542	0.549
	3	3.61	2.025	0.561
	3	3.36	2.608	0.776
	3	3.51	1.90	0.541
31/10/69	3	4.78	2.617	0.547
	2	4.34	1.10	0.253
	3	3.34	2.258	0.676
	4	4.47	2.825	0.632
	3	4.67	2.075	0.444
	3	4.25	1.942	0.457
	3	4.33	2.33	0.539
	3	3.11	1.388	0.446
3	3.90	1.804	0.463	

Bute Inlet *Euphausia pacifica* Respiration Data*Euphausia*

29/10.69	1	4.53	2.15	0.475
	1	9.01	4.75	0.527
	1	12.67	5.8	0.458
	1	10.09	5.15	0.510
	1	4.60	2.525	0.549
	1	13.27	5.95	0.448

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APPENDIX TABLE III. (Cont'd.) Bute Inlet *Euchaeta japonica*
Respiration Data

Data	No.	Dry Wt (mg)	$\mu\text{l}/\text{animal}/\text{hr}$	$\mu\text{l}/\text{mg}/\text{hr}$
29/10/69	3	1.16	0.671	0.578
	3	1.17	0.746	0.638
	3	1.14	0.688	0.603
	3	0.89	0.708	0.796
	3	0.62	0.75	1.048
	3	0.99	0.875	0.884
	3	0.75	0.646	0.861
	3	0.92	0.963	1.046
	3	1.13	1.096	0.970
	31/10/69	3	1.81	1.217
3		1.57	1.183	0.549
3		1.55	1.108	0.448
3		1.83	1.110	0.672
3		1.56	1.30	0.754
3		0.93	1.017	0.715

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