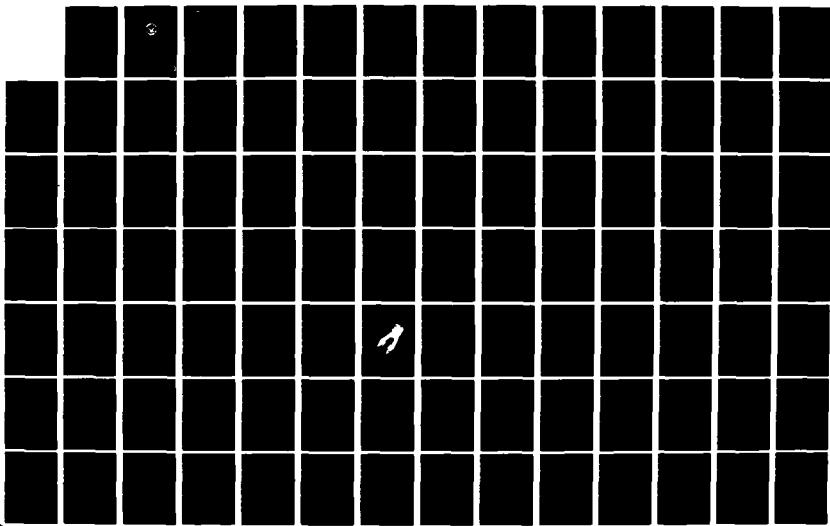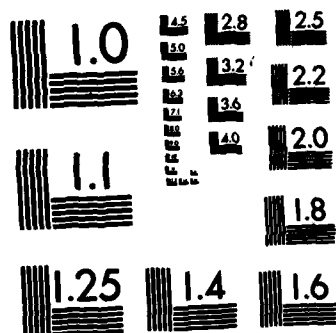OVERWINTERING STRATEGIES OF THE CALANOID COPEPOD
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THESIS

OVERWINTERING STRATEGIES OF THE
CALANOID COPEPOD CALANUS PLUMCHRUS
IN A PERIODICALLY ANOXIC BRITISH
COLUMBIA FJORD

by

Michael Bruce Cowen

October 1982

Thesis Advisor: E. C. Haderlie

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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

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Overwintering Strategies of the
Calanoid Copepod Calanus plumchrus in a Periodically
Anoxic British Columbia Fjord

by

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Submitted in partial fulfillment of the
requirements for the degree of

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ABSTRACT

A study was conducted to determine the excretion physiology and feeding behaviour of overwintering Calanus plumchrus V in Saanich Inlet, B.C. In December, no C. plumchrus V were found above 75m. 48% of the population was within 25m of the bottom. Oxygen concentrations below 75m declined steadily during the winter. By January, water below 150m was anoxic. Overwintering C. plumchrus V from Saanich Inlet would not eat under laboratory conditions. Seven species of cultured phytoplankton and Artemia sp. nauplii were offered as food. Mean ammonia excretion rates were 15.41 and 15.33 x 10-3 micro-gm atoms nitrogen per mg dry weight per day. These values are 10-20 times lower than those previously reported for overwintering copepods. It was calculated that C. plumchrus V had sufficient body nitrogen to survive at least 5 months at the observed rates of nitrogen excretion. It is concluded that C. plumchrus V in Saanich Inlet enter into diapause to survive low winter food levels. Feeding does not occur, protein metabolism is low and lipid reserves are not utilized.

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I. INTRODUCTION

Sound scattering layers in the sea have been known since the 1930's and intensive investigation in the last 20 years has done much to describe the biological nature of these layers. Most measurements of sound scattering have been made at acoustic frequencies below 30 KHZ where resonant scattering due to fish swimbladders and physonectid siphonophores form the most important contribution (Bary, 1966a and 1966b; Farquhar, 1977). More recently, the use of high frequency precision echosounders in the 30-300 KHZ range has allowed investigators to detect other faunal elements such as copepods, euphausids and pteropods in the water column (Sameoto, 1976; Hansen and Dunbar, 1971). When such organisms are concentrated in large numbers, the scattering often takes the form of a distinct layer.

Calanoid copepods form one of the dominant constituents of the zooplankton in the world oceans and play an important role in sound scattering at high frequencies. Castille (1975) speculated that copepods and phytoplankton were responsible for the acoustic volume reverberation he observed at 330 KHZ in the Western Pacific. Bary and Pieper (1971) working in Saanich Inlet, B.C. demonstrated that euphausids and large copepods were responsible for scattering observed at 107 and 197 KHZ. A 200 KHZ scattering layer in the North Pacific was found to correspond to large numbers of the large copepod <u>Calanus cristatus</u> (Barraclough <u>et</u> <u>al</u>., 1969). Hopkins <u>et</u> <u>al</u>. (1978) observed that sound scattering at 120 KHZ in a

Norwegian fjord was caused by euphausids, chaetognaths and calanoid copepods with the copepods comprising 72% of the biomass.

The investigation of sound scattering in the high frequency range of 30 to 300 KHZ assumes military significance when it is considered that most active homing torpedo transducers and mine countermeasure sonars operate in this frequency range. The French DUBM 21B IBIS and the British Type 2034 minehunting sonars operate at 100 and 110 KHZ respectively (Jane's Weapons Systems, 1981/82).

One of the necessary prerequisites to successful acoustic forecasting is to predict the occurrence, location and strength of biological sound scattering. Before this can be accomplished, detailed knowledge of the basic biology of each of the constituents of the scattering layers must be obtained. Specifically, it must be ascertained which physical ocean variables control the distribution of biological sound scatterers. It is to one aspect of this problem that this thesis is addressed.

In 1975, as part of the requirement for an Honours Degree at the University of Victoria, I initiated a study into several aspects of the physiology and ecology of two of the dominant zooplankters in Saanich Inlet, B.C.: the euphausid Euphausia pacifica and the calanoid copepod Calanus plumchrus. The laboratory data on E. pacifica was incorporated into my honors thesis. The laboratory and field data on C. plumchrus were not processed or evaluated, but were stored on magnetic tape at the University of Victoria awaiting future analysis. It is this raw data which forms the basis of my thesis.

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Calanus plumchrus is a very abundant calanoid copepod in the Northern Pacific Ocean and in the fjords of western British Columbia. It can reasonably be expected to form an important part of the sonic scattering layer in these areas. Fulton (1973a) reported that the stage V copepodite of Calanus plumchrus Marukawa (1921) (hereafter referred to as C. plumchrus V) did not feed during the last seven months of its life cycle. This con- clusion was based on two observations: 1) the absence of food material in the gut of either freshly caught or laboratory "fed" animals; 2) no faecal pellets were produced when the copepods were offered either Skeletonema sp. or Artemia sp. cultures as food. Fulton (1973-a) discounted the utilization of stored lipid as a possible food reserve during winter on the qualitative observation that the lipid sac of C. plumchrus "showed little or no reduction of oil reserves" between the months of September and December.

Littlepage and Rose (1974) demonstrated that C. plumchrus V collected in March actively fed on cultures of Isochrysis. Ammonia excretion approximately doubled when the copepods were starved for a period of 24 hours, indicating an increase in protein metabolism.

A study was initiated into the feeding behaviour of C. plumchrus V. The objective was fivefold: 1) determine if feeding could be induced in overwintering C. plumchrus V under laboratory conditions; 2) measure the ammonia excretion rates of C. plumchrus V and estimate the importance of protein metabolism as an energy source during periods of reduced primary production; 3) determine the vertical distribution of overwintering C. plumchrus V in Saanich Inlet and relate this to the environmental

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variables that might affect nutrition; 4) formulate a working hypothesis on the nature of overwintering nutrition in the stage V copepodites of <u>C</u>. <u>plumchrus</u>; 5) synthesize laboratory and field data to formulate a discussion on the contribution of <u>C</u>. <u>plumchrus</u> to sonic scattering in coastal areas.

II. LITERATURE REVIEW

A. DISTRIBUTION AND LIFE CYCLE OF CALANUS PLUMCHRUS

Calanus plumchrus has long been recognized as one of the most common copepods both in British Columbia coastal waters and in the North Pacific Ocean. Campbell (1934) stated that C. plumchrus "constitutes the preponderant, constant element of the zooplankton in the Strait of Georgia." Lebrasseur et al. (1969) and Parsons et al. (1969) noted that this copepod virtually dominated the zooplankton biomass in the Strait of Georgia during the spring and summer and was the major food source for young salmon entering the Strait en route to the open ocean. Taguchi and Ishii (1972) working in the Bering Sea and the northern North Pacific noted that "in summer immature (stage V) copepodites of these species (C. plumchrus and C. cristatus) constitute 50%-90% of the copepods caught in the euphotic layer." Marioka (1972) reported that C. plumchrus copepodite stage V "was by far the most abundant (copepod) at nearly all depths on all stations" in the western North Pacific while Taka et al. (1981) reported that C. plumchrus was the dominant copepod species in the Oyashio Current. Vinogradov (1968) cited by Marlowe and Miller (1975) stated that C. plumchrus and C. cristatus together dominate, in terms of biomass, the zooplankton in the Western Subarctic Domain (which includes ocean station PAPA).

Calanus plumchrus was first described by Brady (1833, cited by Campbell, 1934) under the name Calanus tonsus. The species is closely related to

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C. finmarchicus but is larger and lacks teeth on the anterior margin of the basal joint of the fifth leg (Campbell, 1934). C. plumchrus has been recorded in the North Pacific, southern South Pacific and the mid-Atlantic (Campbell, 1934). Its Pacific Ocean distribution coincides with that of the Pacific Subarctic water mass. It has been found as far south as 40 N and as far north as the Bering Sea.

The following summary of the life history of C. plumchrus has been condensed from Campbell (1934) and Fulton (1973): the final molt from the stage V copepodite to the mature adult form occurs between late December and mid-February. Breeding and egg laying take place below 300 meters (in the Strait of Georgia) from January to the end of March. Males die after copulation and the females after the completion of egg laying. Feeding does not occur during the adult life as the masticatory edges of the mandible are much reduced. The maxillae and the maxillipeds are smaller and have fewer filtering setae. Neither size of the brood nor the beginning of breeding depend on the presence or abundance of phyto-plankton (Heinrich, 1962).

The nauplii are positively phototropic and migrate to the surface waters at a rate of approximately 26 meters per day. Growth from the first naupliar stage to the Stage V copepodite requires about 74 days with peak abundance of Stage V's occurring in May. Intensive feeding at the surface by the copepodites results in the deposition of large quantities of lipids. Once lipid storage is complete, usually by early June, the copepods descend into deeper water. The entire population is below 100 meters by the end of July. From August to December there is a further slow migration into deeper water.

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B. PROTEIN AND LIPID METABOLISM IN CALANUS

Marine invertebrates utilize 3 forms of catabolism: (1) lipid-oriented; (2) polysaccharide-oriented; and (3) protein-oriented. In zooplankton, however, polysaccharide metabolism is very minimal (Mayzaud and Martin, 1975).

Lee et al. (1971a) reported that 59% of the total dry weight of C. plumchrus was lipid. Lee (1974) further reported that C. plumchrus V from Bute Inlet, B.C., was 47% lipid, with 90% of this total being in the form of storage lipids and 4% being incorporated as structural phospholipids. C. plumchrus V from the Bering Sea were shown to contain 53.5% protein, 38% lipids, 2.2% chitin, 0.9% carbohydrate and 5.4% ash (Ikeda, 1972). The very high proportion of storage lipids (wax esters and triglycerides), the relatively low proportion of these which are structural in nature (phospholipids), and the low levels of total body carbohydrate, strongly suggest that lipid is the major food reserve of these animals (Lee et al., 1971b).

Ikeda (1972) determined that 53.5% of the dry weight of C. plumchrus was protein. Assuming that ash, carbohydrate and chitin account for 8.5% of the total dry weight (Ikeda, 1972), the lipid analyses of Lee (1971 and 1974) would indicate that the total protein content of C. plumchrus ranges between 32% and 54%.

Nitrogen excretion rates can lead to useful generalizations concerning the importance of protein catabolism in the overall energy budget of an animal. Intensive investigation has demonstrated that calanoid copepods are primarily ammonotelic. Corner et al. (1965) concluded that ammonia

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accounted for a very high proportion of the total nitrogen excreted in
C. finmarchicus and C. helgolandicus. Corner and Newell (1967) found that
between 60% and 100% (mean = 74.3%) of the total excreted nitrogen in
both fed and starved copepods was in the form of ammonia. Small quanti-
ties of urea were also excreted but they could not find evidence for the
excretion of measurable amounts of amino acids. Johannes and Webb (1965)
reported that considerable quantities of amino acids were released by
mixed zooplankton cultures but the extremely high experimental densities,
roughly equivalent to 5,000 - 70,000 Calanus sp. per liter, make these
results suspect (Corner and Cowey, 1968). Butler et al. (1969) examined
the forms of nitrogen excreted by C. finmarchicus at different seasons
of the year and found that 78.3% of the total was excreted in the form
of ammonia. Corner et al. (1972) demonstrated that fed and unfed Calanus
sp. excreted respectively 87.5% and 90% of their total nitrogen as ammonia.
C. helgolandicus under either starving conditions or when fed barnacle
nauplii excreted between 89.95% and 91.23% of their total nitrogen as
ammonia with the remainder in the form of urea (Corner et al., 1976).
There was no evidence that a greater proportion of nitrogen was excreted
as urea with increasing food levels.

The extensive literature on copepod nitrogen excretion rates has been
reviewed by Corner and Davies (1971). The values of excretion rates,
in micro-grams of nitrogen/mg dry body weight/day, have ranged from
0.30 (Conover and Corner, 1968) to 38.1 (Corner et al., 1967) and are
summarized in Table XVI. The large variability reported in the literature
may be attributed to a wide range of factors including: differences in

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food levels, body sizes, experimental temperature, salinities, species and analytical techniques (Corner and Davies, 1971).

Conover and Corner (1968) were unable to detect any significant difference in nitrogen excretion rates between fed and starved animals. However, a number of workers (Corner et al., 1965; Conover and Newell, 1967; Butler et al., 1970; Corner et al., 1972; Corner et al., 1976 and Ikeda, 1977) have reported that nitrogen excretion is substantially higher in laboratory fed compared to starved animals.

Research into seasonal variation of Calanus sp. nitrogen excretion has yielded results consistent with those just described. Excretion rates were directly correlated with phytoplankton abundance, reaching the highest levels during the spring bloom, declining steadily during summer and fall and reaching their lowest levels in January and February during the period of lowest phytoplankton biomass (Conover and Corner, 1968; Butler et al., 1969; Butler et al., 1970). These results can be explained on the basis that nitrogen is excreted as a result of two processes: (a) deamination of assimilated food protein; the resulting carbon skeleton may be used to form lipid, a process which would be maximal during the period of rapid growth and lipid storage that occurs with the spring bloom (Butler et al., 1970) and (b) tissue protein catabolism, which would form the major source of excreted nitrogen during periods of low food levels (Corner et al., 1965).

Variable results have been reported from studies into the relative importance of lipids and proteins as sources of stored energy during periods of low food abundance. Conover (1962) tentatively suggested that

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C. hyperboreus utilized a "mixed substrate when food (was) available, shifting to a fat metabolism under starvation." Conover (1964, cited by Corner and Cowey, 1968) demonstrated that over a 14 week period of laboratory starvation, lipid accounted for most of the weight lost in C. hyperboreus. Conover and Corner (1968) noted that lipid was the primary energy source for C. hyperboreus during the fall. As fat reserves were reduced, protein was more heavily utilized with a corresponding increase in nitrogen excretion, though this was not observed until late in the winter. From November to March, 45% of the total body nitrogen was lost. During the same period, lipid levels dropped from 52% to 25% of the total dry body weight. C. hyperboreas collected from the Arctic Ocean on a monthly basis displayed a similar seasonal pattern (Lee, 1974). Lipids formed 75% of the total dry body weight in August after a summer of intense feeding and declined to 29% by the following June after a long winter in phytoplankton-deficient water. The above results were interpreted to suggest that the lipid was the primary energy store with protein reserves being utilized only when the lipids had been exhausted (Conover and Corner, 1968; Lee, 1974).

Orr (1934) found no significant change in the lipid levels of C. finmarchicus V during winter. However, in 1958, Marshall and Orr showed that overwintering Stage V C. finmarchicus lost a large proportion of their lipid content from autumn through January. Gatten et al., (1978) confirmed these results by recording a sharp decline in the total lipid of Stage V C. finmarchicus during the winter period.

There is some evidence to suggest that protein catabolism is an important energy source when food is scarce. Linford (1965) observed that lipid levels remained constant for C. helgolandicus starved for 8 days. Cowey and Corner (1963b) observed that 90% of the total weight lost by C. helgolandicus during 14 days of starvation was in the form of amino acids. Conover and Corner (1968) interpreted Harris' 1959 study as showing that Acartia sp. were catabolizing protein during a period of low in situ food levels. This was later confirmed by Mayzaud (1974) who showed that Acartia clausi utilized a predominantly protein catabolism during starvation. Mayzaud (1976) believed that some copepods can utilize both proteins and lipids. He stated that C. finmarchicus "appeared to be able to switch several times during the starvation period from a predominantly protein catabolism to a predominantly lipidic catablolism and vice versa." He felt that this overwintering strategy would help to conserve body protein which cannot be depleted below a certain level.

The relative importance of protein and lipid metabolism in C. plumchrus has been investigated. Fulton (1973a) concluded that there was no reduction of lipid reserves in animals retained for 3.5 months in filtered seawater. These results were based on visual observations of the size of the oil sac. Lee (1971) showed that lipids composed 59% of the total dry weight in female, adult C. plumchrus. It is known that adult C. plumchrus do not feed and that lipid reserves are totally exhausted during the egg laying process (Fulton, 1973). It must therefore be assumed that Lee's (1971) analyses were conducted immediately prior to egg laying. This

would indicate that overwintering $\underline{C}$. $\underline{plumchrus}$ V do not utilize their lipid reserves as a supplemental energy source.

Recently hatched $\underline{C}$. $\underline{plumchrus}$ from Saanich Inlet when starved under laboratory conditions demonstrated much lower ammonia excretion rates compared to fed animals (Ikeda, 1977). These results are similar to reports by Corner $\underline{et}$ $\underline{al}$. (1965), Corner and Newell (1967), Butler $\underline{et}$ $\underline{al}$. (1970), and Corner $\underline{et}$ $\underline{al}$. (1972) that starving $\underline{C}$. $\underline{finmarchicus}$ and $\underline{C}$. $\underline{helgolandicus}$ had the lower excretion rates when compared to fed animals. However, these findings contradicted those of Littlepage and Rose (1974) who investigated the possible role of protein catabolism as an energy reserve during laboratory starvation. They found that ammonia excretion levels in late winter Saanich Inlet $\underline{C}$. $\underline{plumchrus}$ V were approximately twice as high in starved as in fed copepods.

There are fundamental differences between the life cycles of $\underline{C}$. $\underline{plumchrus}$ and both $\underline{C}$. $\underline{finmarchicus}$ and $\underline{C}$. $\underline{helgolandicus}$ which might account for their differing responses to starvation. $\underline{C}$. $\underline{finmarchicus}$ and $\underline{C}$. $\underline{helgolandicus}$ start breeding only in the presence of the large quantities of phytoplankton that accompany the spring bloom (Heinrich, 1952). Egg production is severely inhibited by the absence of food (Marshall and Orr, 1955). Gatten $\underline{et}$ $\underline{al}$. (1980) states that "egg production (in $\underline{C}$. $\underline{helgolandicus}$) is specifically dependent on the level of lipid in the phytoplankton and its assimilation by the copepods." $\underline{C}$. $\underline{plumchrus}$ is one of the few copepods that does not feed as an adult and where egg production depends entirely on stored energy reserves (Campbell, 1934). Littlepage and Rose (1974) hypothesized that non-utilization of lipids (Lee, 1971; Fulton, 1973)

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during winter is primarily a reproductive modification allowing for retention of lipid stores for reproduction. Utilization of body proteins, as indicated by increased ammonia excretion in "starving" animals would serve to supplement low in situ food levels.

C. THE PROBLEM OF OVERWINTERING NUTRITION

Overwintering, herbivorous zooplankton that do not vertically migrate and live below the euphotic zone are faced with the problem of obtaining sufficient food in the virtual absence of living plant material. The following is a brief survey of the literature concerning modes of alternative nutrition that have been demonstrated or are potentially available to a herbivore.

The problems associated with overwintering nutrition have been recognized by Digby (1954), Marshall and Orr (1958), Adams and Steele (1966) and Butler et al. (1970). All of these workers have predicted that a switch to a carnivorous habit and/or detrital feeding would be the most likely adaptation to low phytoplankton levels. Calanus sp. has been shown to be at least partly carnivorous. Marshall (1928, cited by Adams and Steele, 1966) noted that between 27% and 48% of the copepods examined had crustacean remains in their guts. Anraku and Omori (1963) demonstrated that C. finmarchicus would eat Artemia sp. nauplii in the absence of plant food but would selectively filter phytoplankton in a mixed culture. Conover (1966) similarly demonstrated that Calanus sp. would capture and eat Artemia sp. nauplii. Mullin (1966) showed that 19 species of Indian Ocean copepods would readily eat Artemia sp.

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The omnivorous copepod C. pacificus fed disproportionately on the prey in greatest relative abundance when given a choice of phytoplankton or copepod nauplii in the laboratory (Landry, 1981). This "switch" from herbivory to carnivory in response to a shortage of phytoplankton would be of significant value during the overwintering period. Corner et al. (1974 and 1976) demonstrated that total levels of body nitrogen and phosphorus could be sustained indefinitely in C. helgolandicus when fed living and dead nauplii of the barnacle Elminius modestus. These researchers concluded that Calanus sp. probably survives the winter in the Clyde Sea by feeding carnivorously, being unable to derive adequate nutrition from either detritus or organic aggregates.

The role of detritus as a zooplankton food source has been the subject of much speculation. Riley (1959 cited by Corner and Cowey, 1964) observed that large quantities of detritus were present in Long Island Sound and that zooplankton assimilated more nitrogen than was found in the phytoplankton. Corner and Cowey (1964) interpreted these results as evidence for detrital feeding. Parsons and Strickland (1962) attributed only 0.2% of the total dry plant organic matter in the northeast Pacific Ocean to living plant matter. Biochemical analyses have established the nutritive value of detritus by demonstrating the presence of a wide range of amino acids and carbohydrates (Parsons and Strickland, 1962; Cowey and Corner, 1962, 1963a,b; Corner et al., 1974).

Many authors (Digby, 1954; Marshall and Orr, 1958; Parsons and Strickland, 1962; Jorgenson, 1962; Adams and Steele, 1966; Mullin, 1966; Martin, 1968; Butler et al., 1970 and Raymont, 1971) have speculated that

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detritus plays an important role in the nutrition of zooplankton. Among the first to investigate the possible use of detritus by copepods were Paffenhofer and Strickland (1970). They observed feeding on both senescent and fresh, lightly disintegrated C. helgolandicus faecal pellets. However, when offered natural detritus, C. helgolandicus appeared "unable or unwilling to make use of any of the 'structureless' detritus." Paffenhofer and Strickland (1970) concluded by stating that selectivity was probably more a function of physical shape than nutritive value.

The use of faecal pellets as a food source was demonstrated by Paffenhofer (cited by Marshall, 1973 as a personal communication) when he raised Calanus sp. from copepodite III to adult on a diet of faecal pellets. He concluded that detritus was of little or no food value except in the form of faecal pellets or bacterial aggregates. Vinogradov (1962) theorized a similarly important role for faecal pellets. He postulated that vertically migrating zooplankters feed at surface, but only partially digest their food. A portion of this food would be later released as faecal pellets when the animals descended and would serve as food for deep living non-migratory zooplankton.

The unsuitability of detritus as a food source has been demonstrated by Corner et al. (1974). A test diet of natural suspended matter at a concentration five times the winter Clyde Sea levels failed to sustain either body nitrogen or phosphorus in C. helgolandicus over a period of five days. The copepods fed on the detritus and produced faecal pellets, but both fed and unfed control animals lost 27% of their nitrogen and 33% of their phosphorus, indicating that natural detritus was ingested but

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was of no or little nutritive value. The estuarine copepods Eurytemora
affinis and Scottolana canadensis do not survive well or produce eggs
when feeding on detritus that has been autoclaved but thrive on detritus
which is rich in bacteria and ciliated protozoans (Heinle et al., 1977).

Some forms of bacteria are capable of sustaining growth in freshwater
cladocerans and molluscs (Jorgenson, 1962). Bacteria in the free state,
because of their small size, are probably not an important part of the
copepod diet (Marshall, 1973). However, a great many marine bacteria are
epiphytic, growing on the surface of particulate matter or can occur in
aggregates large enough to be caught in filtering setae (Raymont, 1971).
Information on bacterial biomasses is scarce due to the difficulty of
separating epiphytic bacteria from their substrates. Seki and Kennedy
(1969) concluded that bacterial aggregates in the Strait of Georgia were
present during winter in quantities equivalent to the total biomass of
phytoplankton and were potential sources of food for filter feeders. The
role of bacteria in zooplankton nutrition has not been clearly elucidated.

Approximately 90% of the organic carbon in the ocean is present in
the form of dissolved compounds (Holm-Hansen, 1971). Direct uptake of
dissolved organic matter through the arthropod epidermis has been dis-
counted as improbable (Corner and Cowey, 1964). However, (Chapman, 1975)
indicates that dissolved glucose can be actively taken up by overwintering
C. plumchrus and concentrated to four times the ambient level over 24
hours. The significance of this uptake in the overall nutrition of the
animal has not been determined.

Baylor et al. (1962) and Sutcliff et al. (1963) discovered that organic particles could be formed in the laboratory by bubbling air through natural seawater. It was found that the growth of Artemia sp. could be supported by aggregates formed in this manner (Baylor and Sutcliffe, 1963). Studies undertaken in Long Island Sound (Riley et al., 1963), the North Atlantic Ocean (Riley et al., 1964) and the Sargasso Sea (Riley et al., 1965) indicated the presence of large quantities of organic aggregates similar to those produced in the laboratory. It was hypothesized that this material originated by adsorption of dissolved organic matter on subsurface bubbles, detritus or bacterial clumps (Riley, 1970). Sheldon et al. (1967) concluded that particle formation was not restricted to the surface interface but could occur spontaneously at greater depths. The formation of organic aggregates and their subsequent consumption by zooplankton has been an attractive but largely unproven mechanism for utilizing the vast reserves of dissolved organic matter present in the ocean (Paffenhofer and Strickland, 1970).

Corner et al. (1974) demonstrated that water removed from the Clyde Sea in winter would not yield organic aggregates unless enriched with soluble extracts of plant cells. Furthermore, copepods fed this enriched "sea foam" lost about 21% of their total body phosphorus in five days. They concluded that organic aggregates alone could not sustain overwintering Calanus sp.

It has been suggested that Calanus sp. may greatly reduce their metabolism during periods of food scarcity. Beyer (1962) concluded that copepods "hibernated" over winter. Marshall and Orr (1958) also

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considered "hibernation" as a possible adaptation to low food levels. They noted that winter respiration rates were much lower than peak spring rates but concluded that real "hibernation" did not occur: the population lived in an "economical way" by using little oxygen, living in deep water and not undertaking vertical migration. Conover (1962) and Conover and Corner (1968) similarly demonstrated greatly reduced winter respiration rates. The latter authors likened this metabolic slowdown and ability to arrest normal development to insect diapause. A similar conclusion was reached by Hallberg and Hirche (1980) who discovered that over-wintering C. finmarchicus and C. helgolandicus have a much reduced mid-gut epithelium, low digestive enzyme activities, very low respiration rates and "arrested development" whicn they considered as "an expression of a physiological condition that closely resembles the diapause of fresh water cyclopoids and insects."

Cowey and Corner (1963b) tested the hypothesis that Calanus sp. survives the entire winter without feeding. High levels of nitrogen excretion and mortality after 14 days of laboratory starvation led them to conclude that copepods must eat regularly in order to survive. The experiments were repeated in 1970 (Butler et al.) when it was found that total body reserves of nitrogen and phosphorus significantly decreased during periods of starvation. Although daily food requirements were calculated to be less than those during summer (as a result of reduced metabolism) it was concluded that Calanus sp. must feed during the winter. Nutrition was supplemented by the metabolism of body lipids and proteins. Approximately 50% of total body nitrogen and 25% of the total phosphorus

were metabolized by overwintering _Calanus_ sp. between the months of
October and February (Butler _et al._, 1970).

Harding (1974) examined the guts of a large number of deep sea cope-
pods collected from depths below 1000 meters and concluded that they fed
on a combination of detrital material (faecal pellets, cysts, organic
aggregates, diatom tests, etc.), sinking carcasses of larger animals and
dissolved organic materials. None of the zooplankton Harding investigated
were calanoid copepods of the species previously mentioned in this review.

III. METHODS

A. FIELD SAMPLING

Zooplankton samples were collected biweekly from October to January, 1974-75 at Station E (Lat. 48 31'N., Long. 123 30'W.) in Saanich Inlet, British Columbia (Fig. 1 and 2). The maximum depth at this location is 206 meters. Horizontal tows using a Nitex 223 one-meter net with closed cod-end were conducted at depths between 170 and 195 meters. The zoo-plankton were sorted into several plastic buckets (10 liter capacity) which were stored on ice for transport back to the laboratory. Calanus plumchrus were removed and stored at 9 C at a density of 100 per 10 liter bucket in sea water collected from 100 meters and twice filtered through a 0.45-micron membrane filter. Aliquots were removed from the buckets every 12 hours for the first three days after capture and examined for faecal pellets.

Positive identification of C. plumchrus was made using the keys and detailed species descriptions provided in Brodskii (1950), Fulton (1973b), Campbell (1934) and Tanaka (1956).

Vertical distributions of chlorophyll-a, salinity, temperature and dissolved oxygen were determined monthly (Oct. to Jan.) at the sampling station. Nansen bottles equipped with reversing thermometers were used to measure temperature and collect water samples for dissolved oxygen and salinity determinations. The oxygen samples were fixed with manganous sulphate and alkaline iodide on shipboard. A PVC Niskin sampler was used

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to collect water for chlorphyll analysis and later experimental use. A vacuum filter apparatus was used on shipboard to filter 3.0 liter water samples through Gelman glass fiber type A filters for chlorophyll determinations. MgCO3 was added prior to the filtration of the samples to prevent acid hydrolysis of the chlorophyll (Strickland and Parsons, 1968). Filters were stored on ice in blackened jars containing silica gel and then frozen at -20 C upon return to the laboratory. Small water samples from several depths below 75 meters were preserved with a solution of acetic acid and iodine for later identification of the phytoplankton present.

Salinity was measured with a Bissett and Berman Hytech M Model 6220 Salinometer. Dissolved oxygen was determined using a modification of the Winkler titration method of Strickland and Parsons (1968) described in Drinnan and Littlepage (1971). Samples were analyzed one to four weeks after fixation.

Chlorophyll-a concentrations were determined with a modification (Drinnan and Littlepage, 1971) of the trichrometric method of Strickland and Parsons (1968). The absorbances of the chlorophyll extracts were measured in 10-cm small volume cuvettes on a Perkin Elmer (Model 46) Spectrophotometer. The SCOR/UNESCO equations (Strickland and Parsons, 1968) were used to convert absorptions to chlorophyll-a concentrations.

Vertical distribution of C. plumchrus V was determined by means of a series of vertical hauls employing a horizontally rigged Nitex 223 one-meter net with a wire mesh flow-through cod-end. The net was quickly lowered to the desired depth (75, 100, 125, 150, 175, or 200 meters) and

immediately returned to the surface where the animals were preserved in formalin. Animals were counted and population densities computed in June, 1981.

C. plumchrus and water samples were collected on November 1, 1974 from a station in the Strait of Georgia midway between Nanaimo and Vancouver, B.C. (49 15.8'N., 123 44.2'W.) (Fig. 1). A Nansen cast was made to determine salinity, temperature and dissolved oxygen levels at a depth of 400 meters (sonic depth = 414 meters). A Niskin sampler was used to collect water from 400 meters for chlorophyll analysis, phytoplankton and detritus identification and later experimental work.

A "Bongo" vertical closing net (Koeller, 1975) was used to collect zooplankton on two hauls. The depth intervals sampled were 350 to 410 meters and 330 to 400 meters. C. plumchrus were isolated from each haul and stored on ice in plastic buckets for transport back to the laboratory where they were transferred to 0.45-micron double filtered, 400-meter water.

B. LABORATORY EXPERIMENTS

Seven different phytoplankton cultures were used in the feeding experiments and are listed in Table I. The approximate dimensions of each phytoplankter as measured with an optical micrometer are also included.

All cultures were grown under fluorescent light at 9 to 12 C in the growth medium described by Guillard and Ryther (1962). Water obtained from a depth of 100 meters in Saanich Inlet was twice filtered through 0.45-micron Millipore filters and autoclaved prior to addition of nutrients and

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vitamins. The growth of the cultures was monitored by daily cell counts
with a Model B Coulter Counter (Table I).

1. Feeding

In the first eight feeding experiments, C. plumchrus were offered
phytoplankton cultures. In Experiment 9, freshly hatched Artemia sp.
(brine shrimp) nauplii were supplied. Experiment 10 was conducted when
it became evident that a control was required to ensure that lack of
feeding by C. plumchrus was not caused by the experimental design and
laboratory conditions. Calanus pacificus was chosen as the control animal
and was offered all seven phytoplankton cultures and Artemia sp. nauplii.

The general laboratory procedures were similar in all phyto-
plankton feeding experiments and are described below and in Figure 3.
However, each experiment differed from the others in such parameters as
the number of replicates, copepod densities, duration of experiment,
species, age and concentration of cultures. These parameters have been
summarized for each experiment in Tables II and III.

Phytoplankton cultures were stored in the dark for 5 to 10 hours
to ensure that cell division would be reduced prior to the start of the
experiment. Logarithmic phase cultures were used in all experiments
except Number 6 where age was an experimental variable. The cultures were
diluted to the desired concentration with 0.45-micron double filtered
seawater.

The general experimental design was as follows:

Control I   filtered seawater (f.s.w.) only
Control II   f.s.w. + copepods

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Control III   f.s.w. + phytoplankton

Experimental   f.s.w. + phytoplankton + copepods

920 ml glass jars were used as the feeding vessels and filled with 800 ml of one of the above four combinations. The number of replicates and the plankton species and concentration(s) used in the three controls and the experimental jars are summarized in Table II for each of the feeding experiments.

The "f.s.w. only" jars were designed to monitor any increases in particle concentrations during the experiment due to reaggregation of particles (Sheldon et al., 1967). The "f.s.w. + copepods" jars gave an indication of any increase in particle counts due to the animals, e.g., faecal pellets or the release of particulate matter associated with the external surfaces of the copepods. Changes in the phytoplankton population due to cell division or mortality were monitored by the "f.s.w. + phytoplankton" controls. The copepod feeding rates were determined by the differences in phytoplankton concentrations before and after the feeding period as corrected by the 3 sets of controls.

All animals were "starved" in 0.45-micron filtered seawater for a minimum of 4 days prior to the start of the experiment. Ten animals were selected at random and the fifth legs examined to ensure positive identification of Calanus plumchrus V (Fig. 4).

The copepods were carefully removed from the storage buckets, filtered onto a section of coarse plankton netting, rinsed several times with filtered seawater and placed in the feeding jars. The particle concentrations were determined with a Coulter Counter using a 100-micron

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apperture tube. A minimum of five counts were made in each jar. The instrumental parameters used to count each phytoplankter are summarized in Table I.

The jars were then strapped to the feeding wheel and rotated at 6 r.p.m. for 22 to 75 hrs at 9 C in the dark. Rotation prevented settling the phytoplankton cells and limited growth of bacteria on the walls of the container (Zobell and Anderson, 1936). In Experiments 2, 4 and 6 the jars were not placed on the feeding wheel but were carefully inverted once every 10 hours. This eliminated the possibility that rotation might disturb the animals to such an extent as to discourage feeding. The exper-iments were conducted in the dark to reduce or eliminate phytoplankton cell division and to simulate in situ light regimes of overwintering C. plumchrus.

At the end of the feeding period, the animals were removed and the final particle concentrations determined. 90-ml aliquots were removed from each of the jars containing copepods, preserved with 10 ml of ethanol and placed in phytoplankton settling chambers. After 48 hours, an inverted microscope was used to search for faecal pellets. Five copepods from each jar were rinsed and dissected for a gut content analysis.

In Experiment 4, chlorophyll-a analyses were performed to determine if feeding had occurred. 100-ml aliquots from each of the "f.s.w. + phyto-plankton" and "f.s.w. + copepods + phytoplankton" jars were filtered onto glass fibre filters and analyzed for chlorophyll-a content.

In Experiments 8 and 10, Olisthodiscus sp. cells previously killed by freezing were offered as food to both C. plumchrus and C. pacificus. The same experimental procedures used with live cells were followed.

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In Experiment 6, cultures in 3 different phases of growth formed the supplied food. "Early log phase" cells were obtained from cultures that had not reached the point of inflection in their growth curve. "Late log phase" cells were collected when the growth rate was beginning to decline after the point of inflection. "Stationary phase" cells were obtained from 3 week old cultures.

Freshly hatched Artemia sp. nauplii were supplied at several concentrations to both C. plumchrus and C. pacificus in Experiment 9. 800 ml of 0.45-micron filtered seawater were added to each of the feeding jars and the Artemia introduced. After the contents of the jars had been well mixed, aliquots were removed with volumetric pipettes, passed through grided Millipore filters and the number of Artemia sp. counted. The volume of the aliquots taken varied with the density of Artemia sp. and are listed in Table X. Tests showed that random variation among aliquots was less than 10%. It was therefore decided that two aliquots, one removed before and the other after the feeding period, would be sufficient to detect any gross concentration changes. Fifteen copepods were added to each jar. The feeding vessels were stored in the dark for 36 hours after which aliquots were removed, filtered and counted.

2. Ammonia Excretion

The ammonia excretion rates of C. plumchrus V were measured in Experiments 11 and 12. Sixteen liters of 0.45-micron filtered seawater were well mixed in 5-gallon carboys. 40 mg/l of streptomycin sulphate and 40 mg/l of penicillin-G were added to reduce bacterial growth (Butler et al., 1969).

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In experiment 11, six 920 ml jars served as controls with no animals added. In the remaining jars, 5, 10, 20, 30, 40, 60 or 100 animals were added. Two replicates at each concentration were made. In Experiment 12, six jars were designated as controls with between 18 and 21 animals added to each of the remaining 20 containers.

Care was taken to ensure that exposure of the water to atmospheric ammonia was kept to a minimum. When such exposure was unavoidable, all samples were exposed for an equal duration. Copepods were stored in the dark for a minimum of 7 days prior to the start of each experiment.

After storage in the dark for approximately 30 hours, ammonia concentration in all the jars was determined by the buffered indophenol blue technique developed by Koroleff (1970). The complexing reaction is specific for ammonia and has a useful range of between 0.005 and 100 micro-gram Atoms per liter (Koroleff, 1970).

Three 60 ml aliquots were removed from each of the jars with a volumetric pipette and placed in 60 ml glass stoppered reagent bottles. 2.0 ml of phenol-sodium nitroprusside solution were added, followed by 2.0 ml of hypochlorite solution (Koroleff, 1970). After mixing, the reagent bottles were stored in the dark for a minimum 12 hour development period. Light absorption was measured in 10 cm cells at 630 nm with a Perkin-Elmer (Model 46) spectrophotometer. Calibration standards were prepared by diluting a stock solution of ammonium chloride to produce standard solutions of 0.1, 0.2, 1.0 and 2.0 micro-gm atoms N/liter. 60 ml aliquots of these standards were treated in the same manner as the experimental aliquots and mean calibration constants were calculated from the absorbances. Less than 5% variability occurred among replicates.

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IV. RESULTS

A. FIELD SAMPLING

The vertical distribution of Calanus plumchrus in Saanich Inlet is summarized in Table IV and Figure 5. No animals were observed in the top 75 meters of the water column. 89% of the total population was below 100 meters with 48.1% within 25 meters of the bottom.

Physical oceanographic data collected in Saanich Inlet between the months of October and January 1974-75 are summarized in Tables V to VIII and Figures 6 to 10. Oxygen concentrations below 100 meters declined steadily with time.

Anoxic conditions existed in January with only 0.15 ml/1 oxygen present at 150 meters and none detectable at 200 meters. Hoos (1970) similarly reported that "throughout most of the year, the oxygen concentration below 100 meters was less than one milliliter per liter, and at 175 meters was undetectable." Chlorophyll-a was never detected below 30 meters. The density structure of the water column as determined by the vertical changes in sigma-t indicated that the water below 75 meters was essentially isopycnal during the study period with a small positive density gradient extending to the bottom. By January, all sigma-t values below 75 meters were almost identical.

The physical data from the Strait of Georgia are displayed in Table IX. Unlike Saanich Inlet, the deep waters (400 meters) of the strait were not oxygen deficient (3.04 ml/1). No chlorophyll-a could be detected at 400 meters.

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Microscopic examination of preserved water samples collected from between 75 and 200 meters in the Strait of Georgia indicated the presence of substantial quantities of detritus. Except for the occasional large centric diatom frustulle, no intact phytoplankton cells were observed.

In summary, the majority of the population of C. plumchrus in Saanich Inlet was restricted to the bottom 100 meters of the water column in isopycnal water that was devoid of oxygen and living plant matter but rich in detritus.

B. LABORATORY EXPERIMENTS

1. Feeding

All attempts to induce laboratory feeding in C. plumchrus failed. Seven different phytoplankton cultures representing a wide range of sizes, shapes and taxonomic categories were offered as food. Concentrations and the age of the cultures were varied, as were the copepod densities, the length of each experiment and the duration of prior starvation. Freshly hatched Artemia sp. larvae and dead phytoplankton cells were similarly rejected.

The results of these experiments are listed in Appendix Tables A-I to A-X. No decrease in cell concentrations was observed in any of the "f.s.w. + phytoplankton + copepods" jars. In nearly all cases, a slight increase in particle concentrations occurred. This was attributed to reaggregation of particulate matter (Sheldon et al., 1967) as indicated by small increases in particle counts in the "f.s.w. only" controls and/or the release of particles clinging to the external surfaces of the copepods

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as suggested by slightly increased particle counts in the "f.s.w. + copepods" controls. No faecal pellets were observed in any of the 100 ml aliquots removed from each jar at the termination of the experiment or in aliquots removed following initial capture of the zooplankton. No evidence of recognizable phytoplankton remains were found in any of the dissected copepod guts.

An independent t-test indicated that there was no significant difference ($P < 0.05$) between the chlorophyll-$\underline{a}$ concentrations in experimental (f.s.w. + phytoplankton + copepods) jars and control (f.s.w. + phytoplankton) jars. A paired t-test demonstrated that there was no significant difference ($P < 0.05$) between the Artemia sp. concentrations before and after the introduction of copepods.

To test the hypothesis that laboratory conditions and experimental procedures were responsible for the lack of feeding, Calanus pacificus was collected and subjected to the same laboratory and experimental conditions as $\underline{C}$. plumchrus. This copepod is morphologically similar to $\underline{C}$. plumchrus, though smaller and with a slightly different life cycle (Brodskii, 1950). Feeding was observed in all seven algae cultures, the Artemia sp. nauplii and the dead phytoplankton cells (Tables X and XI). It was concluded that the absence of feeding in $\underline{C}$. plumchrus was not an artifact of the experimental method.

Ingestion rates for $\underline{C}$. pacificus were calculated using the formula of Esais and Curl (1972):

I.R. = ((Cc-Cg)V)/NT)

where: I.R. = ingestion rate in cells per copepod per hour

Cc = concentration before feeding (cells/ml)

Cg = concentration after feeding

V = jar volume in ml

T = time in hours

N = number of copepods in the jar

All "before" and "after" concentrations were corrected for changes in the control jars.

The volume of water swept clear by each copepod (the filtration rate) was calculated using the formula of Gauld (1951):

$$F = V(\log(Co) - \log(Ct))/(Nt\log(e))$$

where: F = filtration rate in mls swept clear per day per copepod

V = volume of jar in mls (800 ml)

Co = concentration before feeding (cells/ml)

Ct = concentration after feeding (cells/ml)

t = duration of experiment in days

N = the number of copepods in the jar

The above calculation assumes that the concentration of cells decreases exponentially with time and that F is constant over the period of the experiment. However, it is known that filtering rate (F) varies with cell concentration (Gauld, 1951) so the assumption of a constant filtration rate is only valid for small changes in Co-Ct.

The filtration and ingestion rates and the percent of available phytoplankton removed each day are summarized in Table XII. General trends indicate that smaller phytoplankton cells at higher concentrations were removed faster than larger cells at lower concentrations.

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The ingestion rate of _Artemia_ sp. as a function of the initial _Artemia_ sp. concentration is displayed graphically in Figure 11. The ingestion rate increased with increasing number of prey and showed no signs of approaching a saturation value.

2. Ammonia Excretion

The mean calibration factor determined at each concentration of the standard ammonium chloride solutions and the mean of these F values for both Experiments 11 and 12 are listed in Table XIII. Summaries of the ammonia excretion rates in these two experiments are presented in Tables XIV and XV.

The excretion rates were calculated using the following formula:

$$E = ((A1 - A2)(F)(V))/(WT)$$

where: E = mean excretion rate in microgram atoms N per mg. dry weight per day

$A1$ = spectrophotometric absorbance of indophenol blue in experimental jars: mean of 3 replicates

$A2$ = mean absorbance of the 6 control jars

F = mean calibration factor to convert absorbances to concentrations

V = total volume of water = 0.8 liter

W = total dry weight of copepods in milligrams

T = duration of experiment in days

The excretion rates, expressed as micro-gram atoms N per animal per day, were calculated by multiplying the mean copepod weight per jar by the excretion rate expressed as micro-gm atoms N per mg dry weight per day.

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Days to exhaustion of total body nitrogen were calculated by dividing total body nitrogen by the excretion rate expressed as micro-gm per animal per day. Total body nitrogen was taken to be 7% of the dry weight (Omori, 1969). For the purposes of this index, it was assumed that there would be no protein uptake from feeding and that 100% of body nitrogen would be available to metabolism.

The mean excretion rates (with 95% confidence limits) for Experiment 11 were $15.41 \pm 2.92 \times 10\text{-}3$ micro-gm atoms N per mg dry weight per day and for Experiment 12 were $15.33 \pm 0.84 \times 10\text{-}3$ micro-gm atoms N per mg dry weight per day. A regression analysis of ammonia excretion on the density of animals in each jar in Experiment 11 indicated that excretion rates did not vary with the number of animals per jar ($P < 0.05$).

$\underline{C}$. $\underline{plumchrus}$ stored in plastic buckets tended to remain vertically oriented in motionless suspension. Observations in a larger 200 liter container over a 3-week period confirmed that $\underline{C}$. $\underline{plumchrus}$ would remain motionless for long periods of time. No movement of feeding or swimming appendages was observed. $\underline{C}$. $\underline{pacificus}$, $\underline{C}$. $\underline{glacialis}$, and $\underline{C}$. $\underline{cristatus}$ under similar circumstances swam constantly.

V. DISCUSSION

To detect measurable changes in zoologically influenced parameters
(e.g., ammonia, oxygen or phytoplankton concentrations) it is often
necessary to use zooplankton at concentrations several orders of magni-
tude greater than in situ levels. In this study, efforts were made to
use the lowest concentration of copepods concomitant with the detection
limits of the analytical techniques. Hoos (1970) reported a maximum
density of C. plumchrus V in Saanich Inlet of 0.28 copepods/liter.
Concentrations of between 6.3 and 125 copepods/liter were used in this
research. These densities are significantly higher than in situ levels,
but represent a considerable improvement over the densities of between
1000 and 1400 copepods/liter used in some earlier research (Butler et al.,
1969, 1970; Corner et al., 1965, 1967; Corner and Newell, 1967).

It is not possible to duplicate the in situ environment in the labora-
tory. Conditions of light, temperature, oxygen concentration, salinity,
etc., can only be approximated to varying degrees. The processes of cap-
ture and experimentation may greatly alter a copepod's behavioral and
physiological responses. The results of laboratory research must therefore
be interpreted in the light of these limitations.

The first adult C. plumchrus were observed on February 7 in Saanich
Inlet. By March 6, all C. plumchrus had molted into the adult stage VI.
Campbell (1934) observed that the molt between stage V and adult occurred
in early January. Fulton (1973) described the same event as occurring
between late December and early February. In both cases, the final molt

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occurred at least one month earlier than was observed during this study. It was unlikely that Littlepage and Rose (1974) were working with C. plumchrus V during March. Adult females dominate the population at this time of year but do not feed. A similar copepod species, such as C. glacialis, may have been the animal studied (Littlepage, 1982, pers. comm.).

C. plumchrus V did not feed under laboratory conditions at any time during this study. Feeding experiments were conducted several times each month between September and February with both Artemia sp. and phytoplankton offered as food. Experimental conditions were varied extensively in order to minimize any circumstances that might have discouraged feeding. C. pacificus fed under all experimental conditions. On the basis of these results, it is hypothesized that C. plumchrus does not feed during the last five months it spends as an overwintering stage V copepodite.

Fulton (1973) proposed a similar hypothesis on the basis of a single 4 day feeding experiment in September, using only Artemia sp. and Skeletonema sp. as food sources and on the absence of digested material in the gut of freshly caught and dissected copepods. There was no indication, however, that adequate controls were used to ensure that handling and laboratory conditions were not responsible for lack of feeding. Gut content analyses are not reliable in determining if feeding has occurred because the "trauma" associated with capture often causes violent expulsion of gut contents (Marshall, 1973). The best evidence for the absence of feeding during winter supplied by Fulton (1973) was of an indirect nature. He demonstrated that C. plumchrus V could survive for 3.5 months without food in aseptically filtered seawater. However, the ability to survive

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without food does not necessarily imply that feeding does not occur
in situ.

Gardner (1972) also suggests that C. plumchrus V does not feed during
winter. He states that "the animals (C. plumchrus) were not fed during
the experiment as feeding in the C-V drops off considerably in the fall
(Gardner, preliminary observations)". Nowhere does he state the nature
of these "preliminary observations" and thus critical comments on their
validity are not possible.

Zooplankton normally inhabiting a portion of the water column devoid
of viable phytoplankton cells may be "acclimated" to feeding on detritus
or small zooplankters. Healthy phytoplankton cultures would represent
an atypical food at that time of year and may not be consumed. However,
during early summer, stage V copepodites do eat large quantities of phyto-
plankton and there is no morphological evidence suggesting that the ability
to filter out algal cells ceases as the animal descends into deeper water.
Calanus is a filter feeder and is not able to exercise a great deal of
control over the material it captures (Marshall, 1973). If C. plumchrus
does feed on detritus and/or small zooplankton, there is no a priori evi-
dence that it would not eat phytoplankton cells when offered, even though
these were absent in the natural environment.

Ammonia excretion rates determined in this study indicate that nitrogen
metabolism in C. plumchrus is very much less than in other overwintering
copepods. Less than 0.34% of the total body nitrogen was excreted daily
compared to values of between 1.34% and 15.5% described in the literature
(Table XVI). The "days to exhaustion of total body nitrogen" index

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calculated in Table XVI represents an estimate of maximum survival time
at the measured excretion rate. This index assumes that nitrogen excretion
rates are constant and that protein is not replenished by feeding. Death
would occur substantially before 100% of the body nitrogen had been
exhausted.

Conover and Corner (1968) found that overwintering C. hyperboreus
lost 45% of total nitrogen between November and March. Assuming these
results can be extrapolated to other calanoid copepods, C. plumchrus
could sustain a similar 45% loss without deleterious effects. Arbitrarily
assuming that a further 5% loss would be fatal, between 165 and 183 days
would be required for C. plumchrus to sustain a critical 50% loss of
nitrogen. It is evident that C. plumchrus has sufficient protein reserves
to sustain the animal at the observed rates of nitrogen metabolism for
several months without replenishment from external sources.

Integration of data from this study and from previous published litera-
ture has led to the hypothesis that the metabolic rate of overwintering
C. plumchrus in Saanich Inlet is substantially lower than that reported
for other species of Calanus. The concept of "hibernation" or "diapause"
as originally discussed by Marshall and Orr (1958) and the attendant reduc-
tions in all aspects of metabolism is suggested as an adaptive solution to
the problem of overwintering nutrition. The following is a summary of the
evidence used to arrive at this conclusion.

Corner et al. (1974) demonstrated that active carnivory was the only
form of nutrition capable of sustaining nitrogen and phosphorus levels in
overwintering Calanus. If overwintering C. plumchrus V has metabolic

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requirements similar to those of C. helgolandicus, carnivorous feeding
would be the expected mode of nutrition. C. plumchrus V would not ingest
Artemia sp. nauplii, which are actively eaten by most calanoid copepods
(Mullin, 1966; Marshall, 1973). The absence of feeding in overwintering
C. plumchrus V and its requirement in C. finmarchicus and C. helgolandicus
(Corner et al., 1974) constitutes indirect evidence that the metabolic
rate of the former species must be lower than that of the latter.

Evidence for a greatly reduced metabolic rate can be inferred directly
from data concerning lipid reserves and nitrogen excretion. Lipid metab-
olism in C. plumchrus is very low, as demonstrated by the retention of
from 50% to 60% (0.41-0.47mg) of its total body weight as lipid throughout
the overwintering period (Lee, 1971).

Nitrogen excretion data indicate that protein metabolism in C. plumchrus
V is at least an order of magnitude lower than that reported for other over-
wintering copepods. Calculations based on the observed ammonia excretion
rates suggested that C. plumchrus V would not exhaust body protein during
6 months of starvation. This conclusion was confirmed by Fulton (1973)
who demonstrated that C. plumchrus V could survive 3.5 months of starvation
and then molt successfully into the adult. Overwintering C. helgolandicus
suffered losses of 20% and 22% of body nitrogen and phosphorus respectively
after only 5 days without food (Corner et al., 1974).

Oxygen concentrations in the deeper water of Saanich Inlet steadily
declined during the winter until essentially anoxic conditions existed
below 150 meters by January (Table VIII, Fig. 10). Approximately 55% of
the C. plumchrus V population resided in this oxygen minimum layer (Fig. 5).

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Aerobic metabolism would of necessity be at very low levels. The deep waters of the Strait of Georgia were not oxygen deficient (Table IX) and metabolic rates would not be limited by the in situ oxygen concentration.

The observation that C. plumchrus V remained suspended in the water column, motionless, may suggest energy conservation. All other copepods subjected to similar circumstances exhibited continuous swimming. The large lipid sac in C. plumchrus V may serve as a flotation device.

According to Mansingh (1971) diapause is the most highly evolved system of dormancy able to overcome cyclic, long-term and extreme environmental conditions. However, diapause has until recently only been used in reference to insect overwintering strategies. Elgmork and Nilssen (1978) made a detailed comparison between the sequential stages of insect diapause and the dormant stages of fresh water cyclopoids which bury themselves in the bottom sediment before the lake freezes over. They concluded that the two overwintering processes were physiologically equivalent. The biochemical link between insect diapause and the physiological state of overwintering marine copepods was established by Hirche (1978). He could not detect any trypsine (a digestive enzyme) activity in overwintering calanoid copepods (species not identified) in a Swedish fjord. Amylase activity was at a very low level. Microscopic examination of the mid-gut epithelium showed strongly reduced microvilli (Hallberg and Hirche, 1980). Hirche concluded that these copepods were unable to digest food. He also observed that overwintering copepodite stage V's retained in the laboratory were floating motionless with their antennae stretched backwards along the body, an observation which matches the laboratory behavior of C. plumchrus.

Copepods from the Swedish fjord did not produce faecal pellets and would not feed on algae cultures of _Thalassiosira fluviatilis_ and _Scripsiella faroensis_ (Hirche, 1978). Hirche concluded that these copepods survived the low food conditions present in the fjord during winter by entering into a dormant state virtually identical to insect diapause. These conclusions were reiterated in 1980 by Hallberg and Hirche working on overwintering C. _finmarchicus_ and C. _helgolandicus_ captured from another Swedish fjord. They observed a very much reduced mid-gut epithelium associated with very low digestive enzyme activity. Again, diapause was offered as an explanation.

It would appear from the results of this study that _Calanus plumchrus_ has also met the challenge of low winter food levels by adopting a dormant physiological state very similar to insect diapause. This conclusion supports earlier speculation by Gardner (1972) who first suggested that the behavioral pattern of C. _plumchrus_ could be described in terms of a diapause. He used Hoar's (1966) rather broad definition of diapause as a "condition characterized by an abrupt onset of dormancy, followed by resumption of growth and terminating in metamorphosis, rapid growth or reproductive activity". Gardner (1972) did not investigate the extent or physiological nature of this overwintering dormancy. He did suggest that C. _plumchrus_ would derive a considerable energy bonus by feeding in near-surface waters during early summer and then descending to deeper, cooler waters to assimilate the food and to rest during the fall and winter period. The concept of diel and seasonal vertical migration serving as an energy conservation mechanism was first proposed by McLaren (1963) to

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explain why the deep scattering layer frequently migrates towards the surface at night and descends to depth by day.

In recent years, a substantial amount of research has been conducted into the biology of the zooplankton that inhabit the extensive oxygen minimum zones that exist in most of the world's oceans at intermediate depths. A large, permanent oxygen minimum layer exists in the Northern Pacific Ocean between 5 N and Alaska and at depths ranging from 100m to 2000m (Dietrich et al., 1975). The geographical range of C. plumchrus also includes the North Pacific (north of 40 N) but an extensive litera-ture search indicates that it has not been found in the oxygen minimum layer.

Longhurst (1967) found that the zooplankton in the Eastern Pacific oxygen minimum layer off Mexico was dominated by the resting stage V cope-podites of C. helgolandicus (= pacificus). He suggested that oxygen deficient layers were suitable locations for resting stocks owing to their low temperatures which would "favor the low metabolic rate presumably needed to over-winter for a period of more than six months."

Judkins (1980) reported half a dozen different species of calanoid copepod residing in the oxygen minimum layer off Peru. Species found included C. chilensis, Eucalunus inermis, and Paracalanus parvus.

Childress (1968 and 1975) measured the oxygen consumption rates of 28 species of midwater crustaceans including four copepods that lived in low oxygen layers off southern California. He discovered that most of the species examined could maintain a constant oxygen consumption rate over a broad range of ambient oxygen partial pressures down to the lowest

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pressure to which they were usually exposed in their natural habitat. He suggested that anaerobic metabolism would be very unlikely because the food level in an oxygen minimum layer "is apparently too low to allow animals to live actively, hunt food, grow and reproduce using the low energy yield of anaerobic metabolism". Childress (1975) concluded that the majority of zooplankton living in oxygen minimum zones do so aerobically.

The research of Longhurst, Judkins and Childress demonstrates that calanoid copepods can and do thrive at very low oxygen levels. The relative absence in the literature of references to C. plumchrus living in oxygen minimum zones may be attributable to a lack of concurrent zooplankton and oxygen sampling at intermediate depths (down to 2000m) in the North Pacific. All of the above researchers did their sampling south of C. plumchrus's range. Alternatively, it may be possible that C. plumchrus simply does not inhabit the North Pacific oxygen minimum zone.

My experimental results indicate that C. plumchrus is fully adapted to life at low oxygen levels. However, my study was conducted in a restricted basin (Saanich Inlet) which has a transitory oxygen minimum zone. In contrast, the oxygen minima in the subtropical Pacific are large scale and permanent features. Devol (1981) investigated zooplankton respiration rates in two British Columbia fjords (Saanich and Princess Louise Inlets) which both have transitory oxygen minimum zones. In sharp contrast to the abundance of life found in open ocean minima, he discovered virtually no zooplankton of any kind inhabiting the oxygen minimum zone. Specifically, he found the majority of the zooplankton,

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including C. plumchrus hovering in the oxycline immediately above the oxygen minimum. Devol explained this important difference in terms of the long term stability of open ocean oxygen minima providing a constant environment for the evolution of unique aerobic respiration mechanisms. This is contrasted by the isolated and transient nature of low oxygen zones in largely enclosed basins which would require an organism to deal with drastic seasonal changes in oxygen concentration. Devol suggests that few organisms have evolved a physiology capable of dealing with this harsh environment.

Devol's (1981) results appear to contradict my findings in that he did not observe C. plumchrus in Saanich Inlet inhabiting the oxygen minimum zone. However, Devol conducted his sampling in April, June, and July while mine was done in October through January. Based on the observations presented in this thesis, I would suggest that C. plumchrus migrates into the oxygen minimum zone sometime during the August to September time-frame, which is the interval separating Devol's and my sampling periods. This is in keeping with the generally accepted life cycle of C. plumchrus as reviewed earlier in this paper.

Fjords present several unique acoustic forecasting problems related to the great temporal and spatial variability in their physical oceanography. Heavy winter precipitation and highly seasonal river runoff combine to produce large scale changes in the sound speed profile. Many basins, including Saanich Inlet, undergo a dramatic "flushing" in the fall when the physical properties of the water change substantially in a few weeks. Man-made sources of ambient noise are frequent and of

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relatively high intensity. The biological contributions to both ambient noise and sonic scattering are also much more variable and hence, less predictable, than in the open ocean.

Acoustical transmission loss prediction models which are valid in highly convoluted coastal regions (e.g., British Columbia and the NATO Northern flank) must take into account the seasonal variation in biological scattering. C. plumchrus constitutes one of the single largest components of zooplankton biomass in B.C. coastal waters and, as such, is an important source of high frequency (60 KHZ and up) sonic scattering. The seasonal change in vertical distribution and population density of C. plumchrus has a substantial impact on sonic scattering intensities. The population is concentrated in surface waters during the spring and early summer and in deep water during winter. Oxygen minimum layers present during winter in many B.C. coastal fjords seem to offer a particularly attractive habitat.

High frequency mine counter-measures sonars and acoustic homing torpedos operating in surface waters during summer will be influenced by the strong C. plumchrus induced volume reverberation and scattering. Deep running torpedos and variable-depth minehunting sonars operating in the oxygen minimum layers will also experience back scattering from C. plumchrus. Dense copepod aggregations attract large schools of fish, notably the Pacific salmon, which make a very substantial contribution to volume reverberation and backscattering in the 2-20 KHZ range (Urick, 1975). Most naval search and attack sonars operate at these frequencies and thus, indirectly, are affected by the seasonal distribution of C. plumchrus.

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Bottom deployed acoustic torpedo "mines" would also be influenced by copepod scattering. The USN CAPTOR system (enCAPsulated TORpedo) is designed to be deployed on the bottom of a strategically important strait and consists of an encapsulated MK 46 torpedo and both active and passive sonar detection systems (Janes Weapons Systems, 1981-82). The torpedo is automatically launched upon detection of an enemy submarine. If such a system were to be deployed in a British Columbia fjord, its operational depth could coincide with the winter oxygen minimum layer and its accompanying population of $\underline{C}$. plumchrus.

All acoustical forecasting schemes involve solving the sonar equation. Components of the active sonar equation include biologically induced transmission loss and volume reverberation. Future research in this field should be directed towards specifically measuring copepod induced sonic scattering and reverberation in coastal waters with the aim of forecasting scattering and reverberation levels with variable geographical location, season and depth. The predicted levels could then be fed into the sonar equation to produce better estimates of operational sonar detection ranges.

VI. SUMMARY

1. A study was initiated into the feeding behaviour and excretion physiology of the stage V copepodite of _Calanus plumchrus_ in Saanich Inlet with the goal of formulating a hypothesis on the nature of over-wintering nutrition.

2. In December, no _C. plumchrus_ V were observed above 75m; 48% of the total population were within 25m of the bottom of the Inlet.

3. Oxygen concentrations below 75 meters in Saanich Inlet declined steadily during the winter months; by January, anoxic conditions existed from 150m to the bottom.

4. No chlorophyll-_a_ could be detected below 30m.

5. All attempts to induce feeding in _C. plumchrus_ under laboratory conditions failed. Feeding was demonstrated in _C. pacificus_ under similar conditions and it was concluded that _C. plumchrus_ V did not feed _in situ_ during the winter.

6. Nitrogen excretion in _C. plumchrus_ was measured with the ammonia detection technique of Koroleff (1970). The mean excretion rates in the two experiments were: 15.4×10^{-3} and 15.3×10^{-3} micro-gm atoms of nitrogen per mg dry weight per day.

7. The nitrogen excretion rates were 10-20 times lower than those previously reported for calanoid copepods.

8. It was calculated that _C. plumchrus_ had sufficient body protein to sustain itself at the observed nitrogen excretion rates for a minimum of 5 months.

9. Laboratory observations of the behaviour of C. plumchrus in large volumes of water indicate that this copepod may often be suspended motionless in the water column.

10. It was hypothesized that C. plumchrus V meets the problem of reduced winter food levels by entering a state of "quasi-hibernation" or diapause characterized by a reduction of all metabolic functions.

11. C. plumchrus is a significant source of high frequency sonic scattering. Predicting zooplankton scattering intensity as a function of season, geographical location and depth is an important goal in acoustic forecasting. A significant step towards attaining this capability would be to conduct extensive temporal and spatial field measurements of copepod scattering and reverberation in coastal waters.
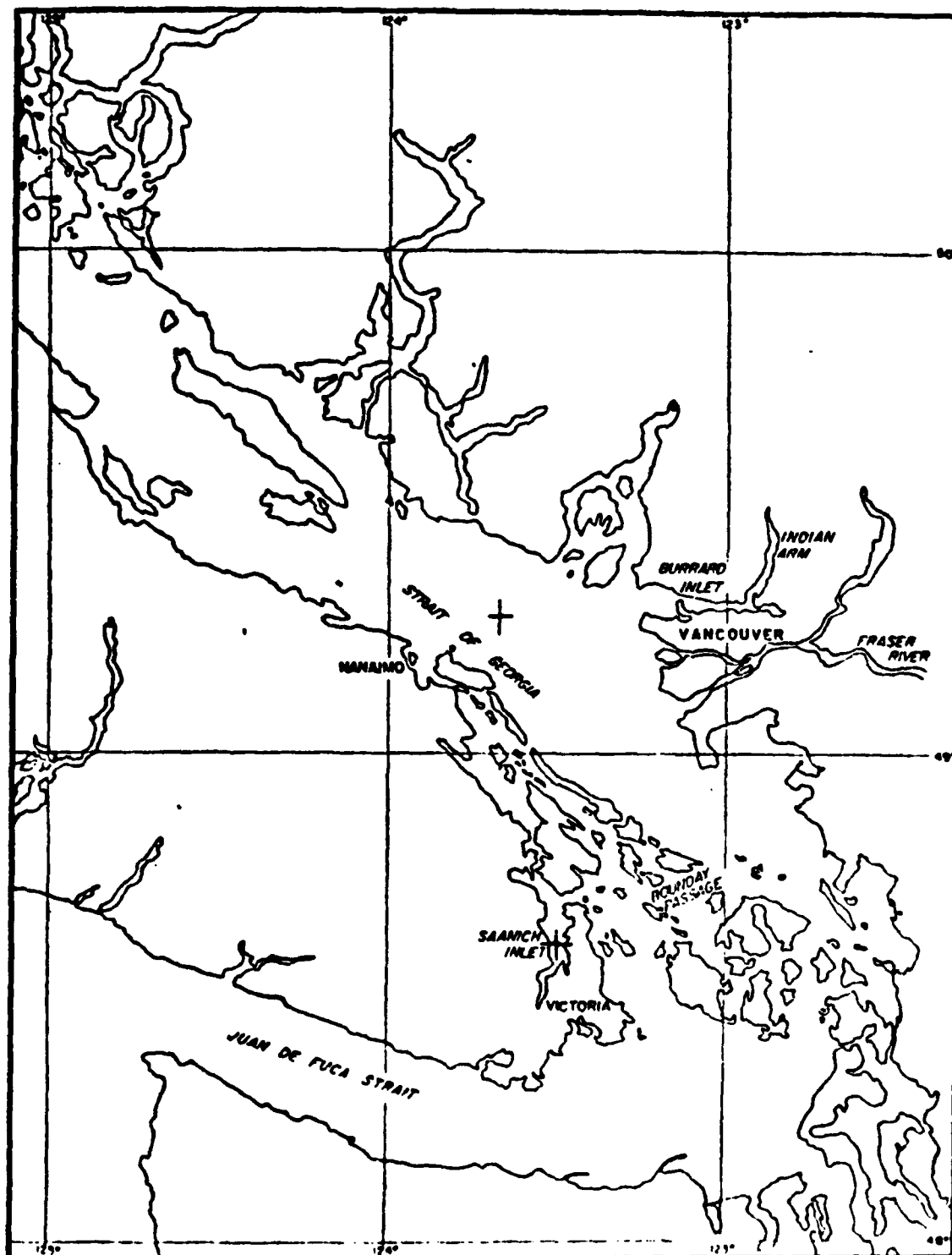
Figure 1. Map showing location of the two sampling stations (+)
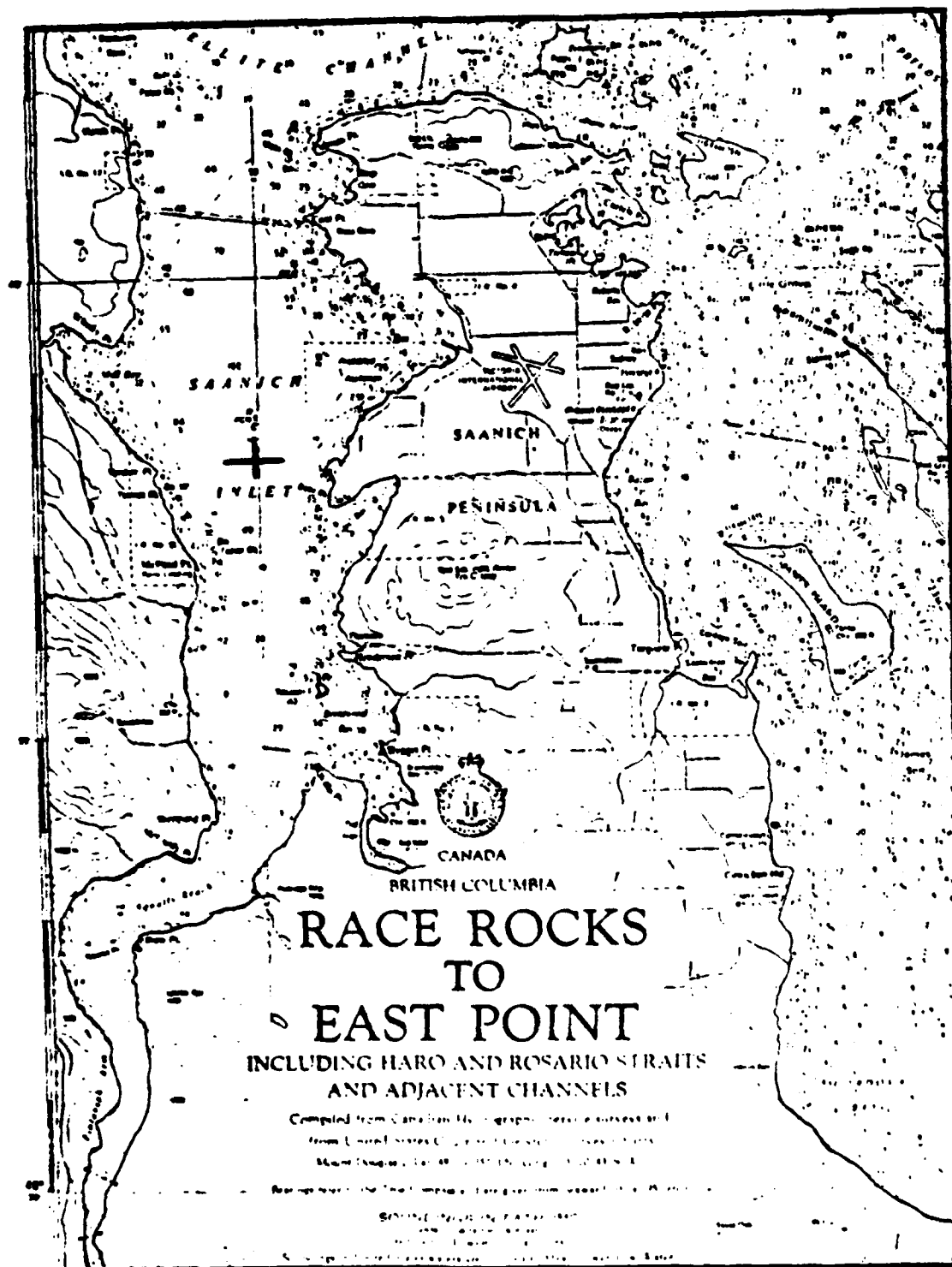
Figure 2. Chart showing location of Station E in Saanich Inlet (+)

Zooplankton haul ⟨ Saanich Inlet / St. of Georgia

Sorting

Storage at 9°C in f.s.w. for minimum of 4 days

Plankton Cultures

in dark 4-8 hrs.

Copepods rinsed – resuspended in feeding jars

a	f.s.w. only
b	f.s.w. + plankton
c	f.s.w. + copepods
d	f.s.w. + copepods + plankton

Coulter Counter

Feeding wheel – in dark – 22-76 hrs.

faecal pellet search ——— Copepods removed – gut content analysis

Coulter Counter

Chlorophyll analysis

Figure 3. Experimental flowchart

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Figure 4.   Representative fifth leg of _Calanus plumchrus_ V.

Figure 5. The vertical distribution of <u>Calanus</u> <u>plumchrus</u> in Saanich
Inlet at 1300 hrs, December 19, 1974. "Percent" refers to
the percentage of the total <u>C</u>. <u>plumchrus</u> V in the water
column present in each 25 m interval.
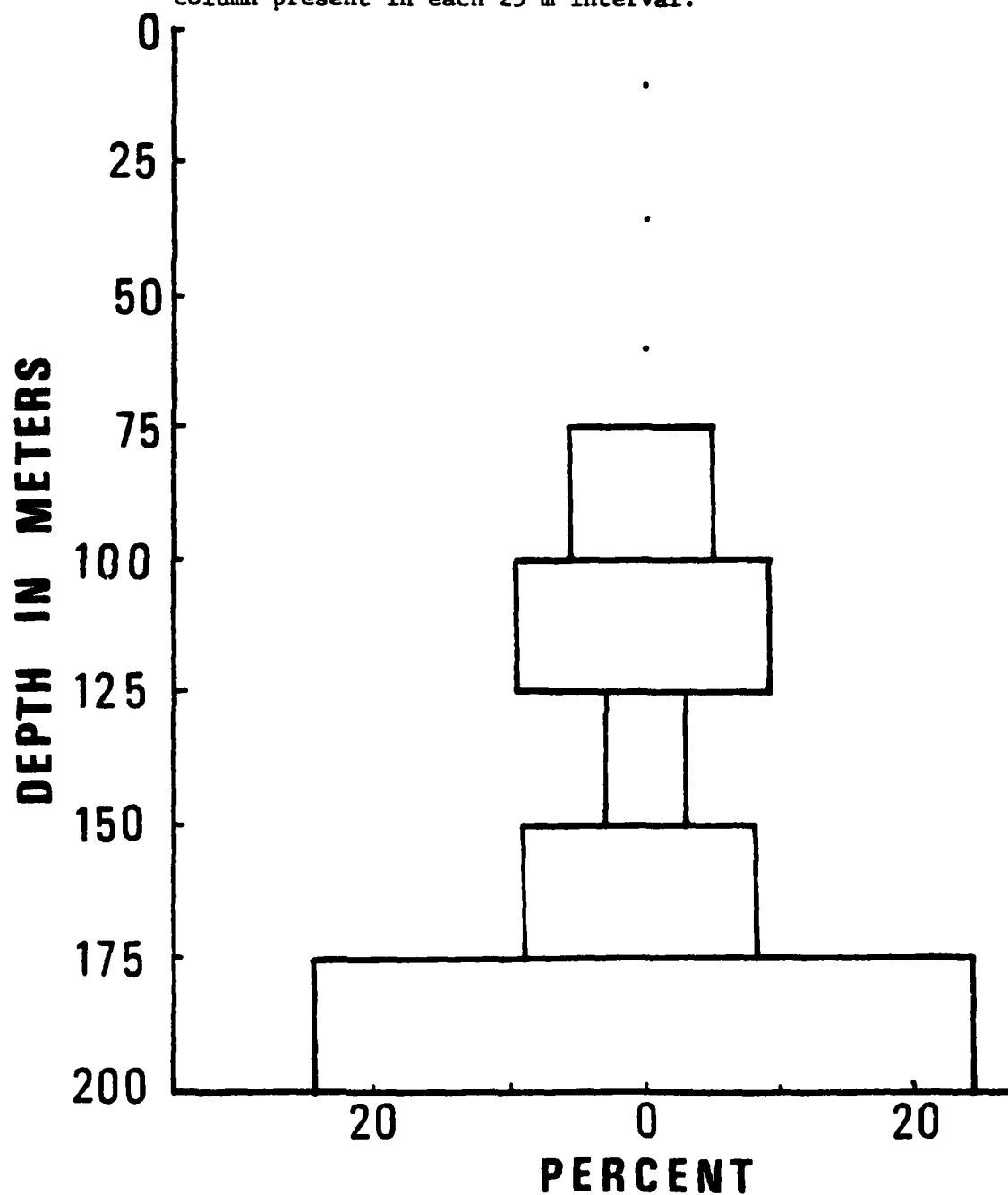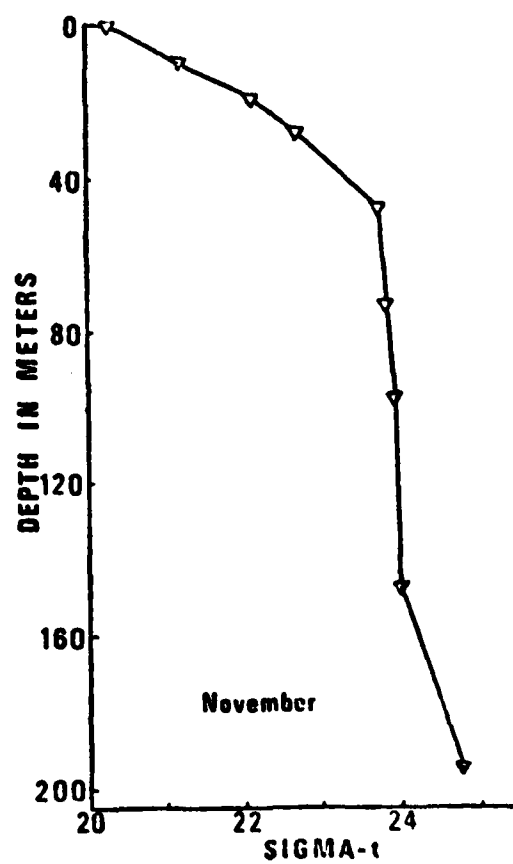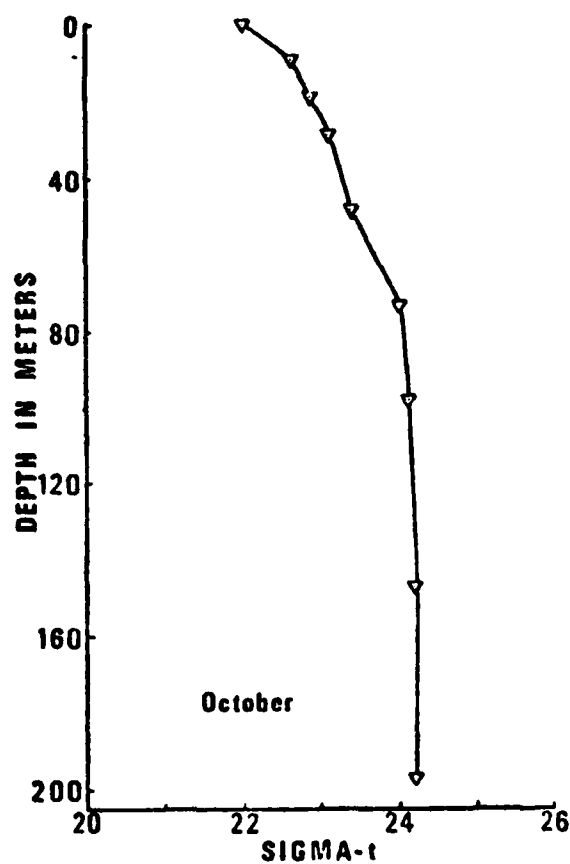
Figure 6. The vertical distribution of Sigma-t in Saanich Inlet during October and November.
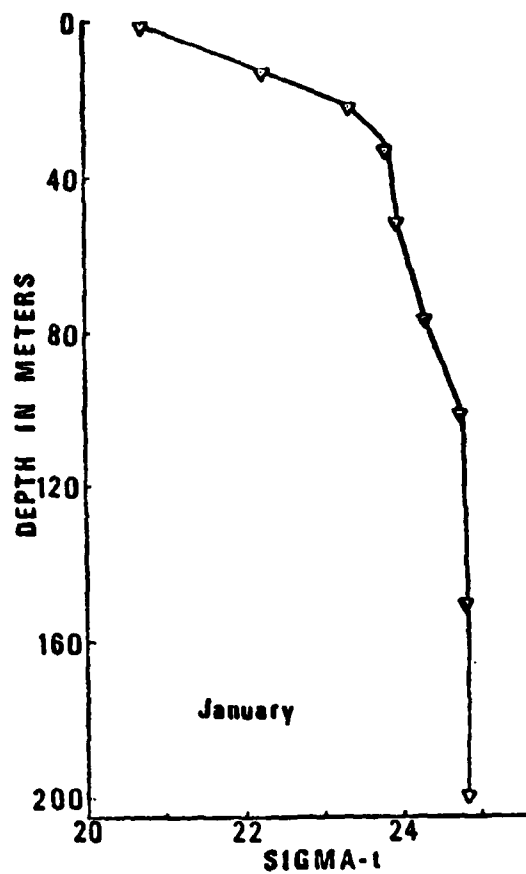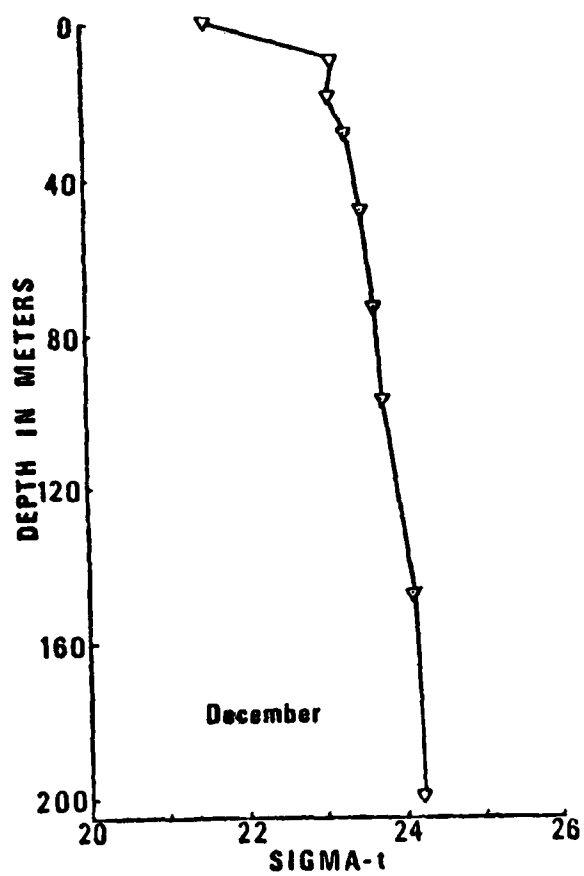
Figure 7. The vertical distribution of Sigma-_t_ in Saanich Inlet
during December and January.
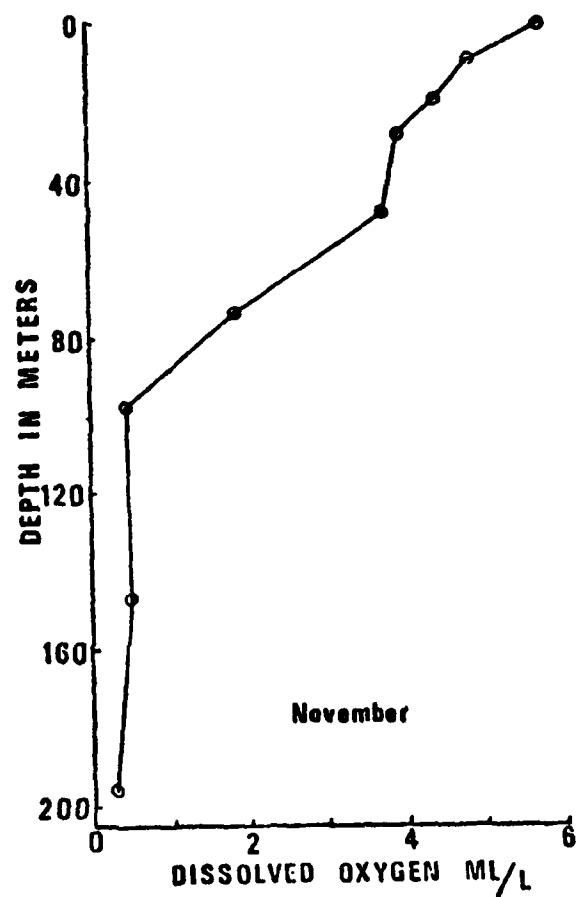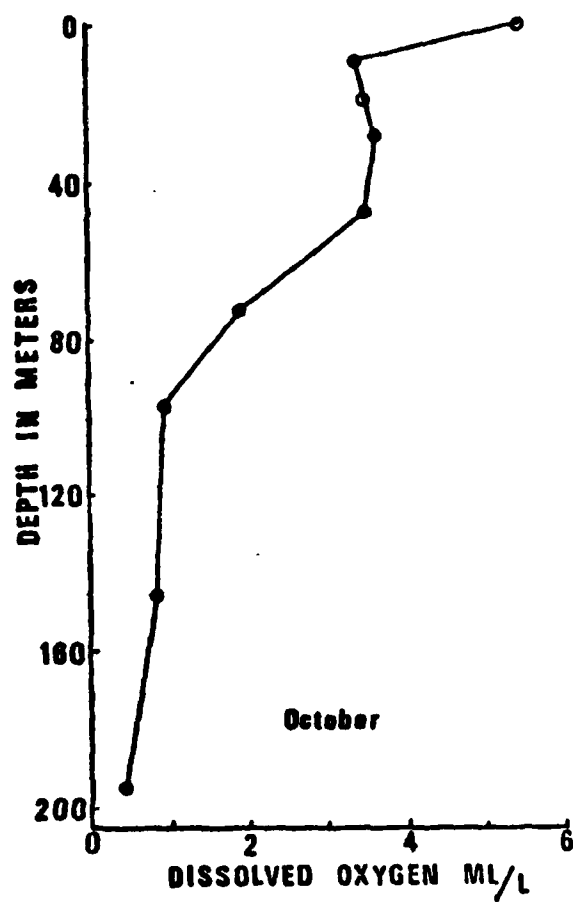
Figure 8. The vertical distribution of dissolved oxygen in Saanich
Inlet during October and November.
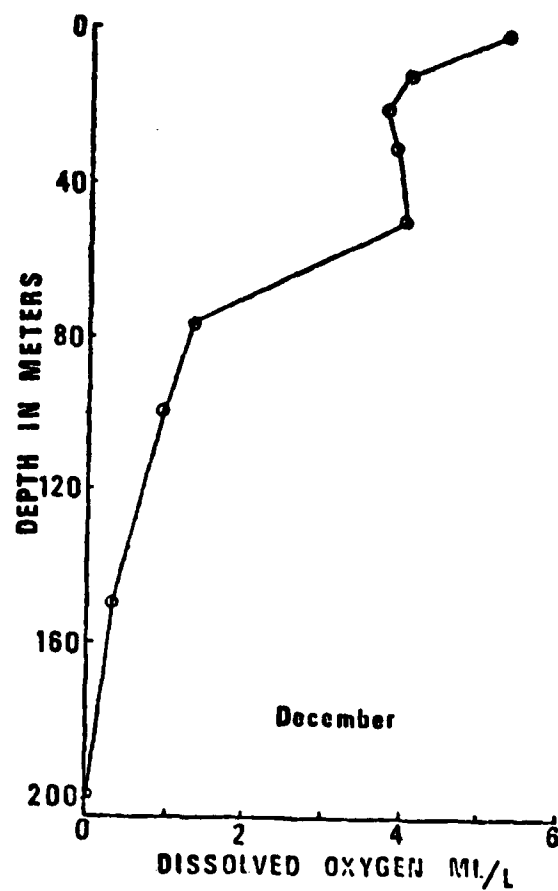
Figure 9. The vertical distribution of dissolved oxygen in Saanich Inlet during December.
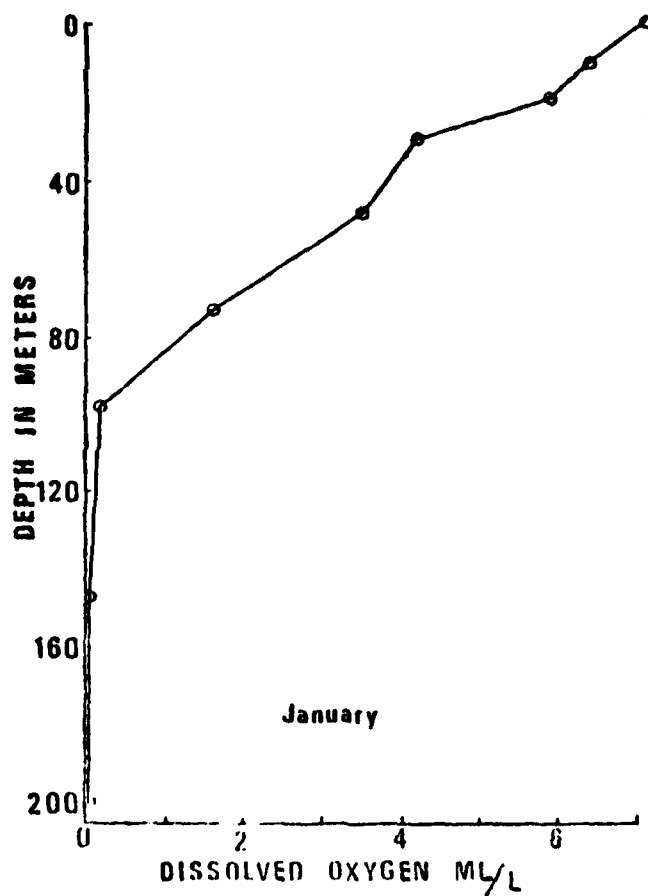
Figure 10.   The vertical distribution of dissolved oxygen in Saanich

Inlet during January.
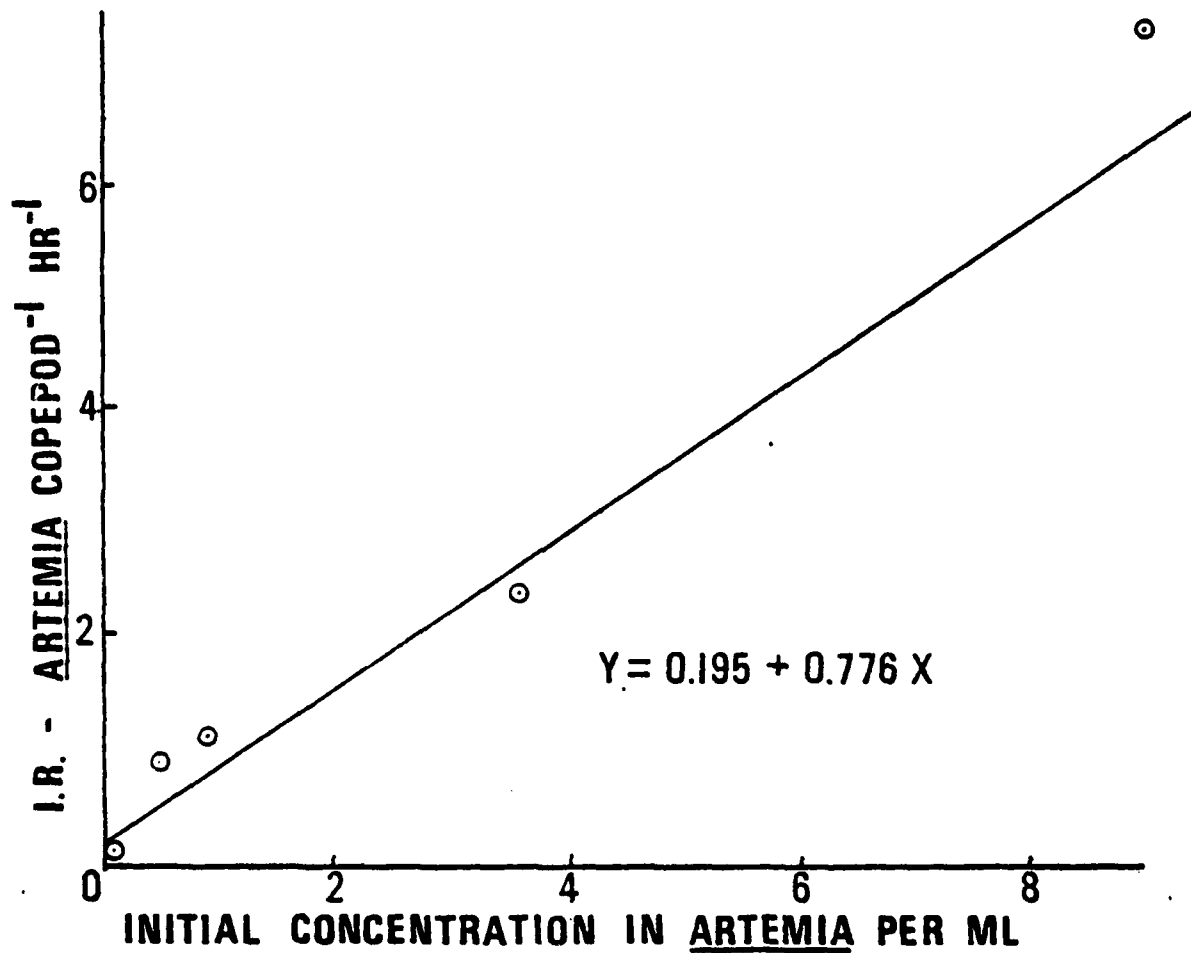
Figure 11.   Regression of mean C. pacificus ingestion rate (I.R.) on

initial Artemia sp. concentration.

TABLE I. Phytoplankton Dimensions and the

Coulter Counter Parameters Used to

Determine Phytoplankton Concentrations

Culture	Length (microns)	Width (microns)	Sensitivity	Thresholds
Thalassiosira fluviatilis	15-20	10	1	20-100
Nitzschia sp.	22-30	5-6	0.25	20-100
Isochrysis sp.	4-5	spherical	0.0825	20-100
Peridinium sp.	20-25	15-20	2.8	20-100
Chroomonas salina	12-15	8-10	0.25	15-100
Olisthodiscus sp.	20-25	concave disk	1	25-100
Cymbomonas sp.	10-15	spherical	0.50	20-100

TABLE II. Summary of Experimental Parameters

Experiment	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10
Culture	Iso.*	Iso.	Thal.	Thal.	Nitz.	Nitz.	Peri.	Olis. Cym. Chro.	Art.	all 7 cultures
Growth phase of culture	log	log	log	early log	log	variable	late log	log	—	log
Hours culture pre-adapted in dark	6	8	8	10	8	6	8	7	9	10
Range of plankton conc. cells/ml	250– 20,000	750	100– 23,000	1000	100– 16,000	600 3200	50– 6000	250– 2000	.08– 40	250–500
No. of copepods per jar	20	5-100	20	5-100	20	15	18	20	15	20
Previous days starvation	4	14	5	7	8	10	5	8	6	7
Experiment Duration-hrs.	36	72	24	30	41	75	41	22	36	33
Rotation-rpm	6	0	6	0	6	0	6	6	0	6
Origin of copepods	S	S	G	S	G	S	S	S	S	S

*Abbreviations: Iso. = Isochrysis   Thal. = Thalassiorsira   Nitz. = Nitzschia   Chro. = Chroomonas
Art. = Artemia   Peri. = Peridinium   Olis. = Olisthodiscus
Cym. = Cymbomonas   S = Saanich Inlet   G = St. of Georgia

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TABLE III. Summary of the Experimental Design:

Plankton Concentrations, Copepod Densities, and

Number of Replicates in Each Experiment

Exp't No.	Phytoplankton and Copepod Densities	Replicates
#1	250, 700, 1400, 2000, 4400 8200, 20,000 cells/ml. 20 animals/jar	2 blanks 3 water + copepods 1 water + plankton 2 water + plankton + copepods for each concentration total = 26 jars
#2	750 cells/ml 5, 10, 20, 50, 100 animals/jar	2 blanks 1 water + copepods 1 water + plankton 1 water + plankton + copepods for each concentration total = 22 jars
#3	100, 200, 400, 800, 1600 3400, 6800, 23,000 cells/ml. 20 animals/jar	same as Experiment - 1 total = 29 jars
#4	1000 cells/ml. 5, 10, 20, 50, 100 animals/jar	same as Experiment - 2 total = 23 jars
#5	100, 200, 400, 800, 1800, 3200 7400, 16,000 cells/ml.	same as Experiment - 1 total = 29 jars
#6	600, 3200 cells/ml. "early log," "late log" and "stationary" phase cells at each concentration 15 animals/jar	3 blanks 3 water + copepods 1 water + plankton 2 water + plankton + copepods for each of the 3 cell ages at the 2 concentrations

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TABLE III. Continued

Exp't No.	Phytoplankton and Copepod Densities	Replicates
#7	50, 100, 200, 500, 1000, 3000, 6000 cells/ml. 18 animals/jar	same as Experiment - 1 total = 26 jars
#8	*Chroomonas*: 500, 2000 cells/ml. *Olisthodiscus*: 300, 1600 *Cymbomonas*: 300, 1800 frozen *Olisthodiscus* 2000 20 animals/jar	1 water + copepods 1 water + plankton 2 water + plankton + copepods for each concentration total = 28 jars
#9-A	*Artemia:* 0.081, 0.45, 0.97, 2.06, 4.03, 7.54, 15.8, 39.3 per ml.	1 jar at each concentration
#9-B	.081, 0.52, 0.89, 3.62, 8.96 per ml.	total = 13 jars
#10	*Isochrysis*: 700 cells/ml. *Nitzschia*: 600 *Thalassiosira*: 600 *Chroomonas*: 800 *Olisthodiscus*: 500 *Peridinium*: 250 *Cymbomonas*: 500 frozen *Olisthodiscus*: 500	same as Experiment - 8 total = 32 jars

TABLE IV. The Vertical Distribution of

C. plumchrus V in Saanich Inlet

between 1300–1400 hrs. 19 Dec. 1974

Sampled Depth Intervals	Number of animals counted	Depth Interval	No. of Animals/m^3	Percentage of total
0–75 m	0	0–75 m	0	0%
0–100	48	75–100	1.22	11.1%
0–125	128	100–125	2.04	18.5%
0–150	152	125–150	0.61	5.5%
0–175	232	150–175	1.83	16.6%
0–200	432	175–200	5.30	48.1%

TABLE V.   Station E. Summary

Physical Data 17 Oct. 1974

Depth (m)	Temp C	Salinity ‰	Sigma-t	O_2 ml/l	chlorophyll-a mg/m^3
0	13.20	29.42	22.07	5.50	0.25
10	11.30	29.78	22.69	3.41	1.81
20	10.91	29.96	22.89	3.62	0.11
30	10.67	30.19	23.17	3.70	-
50	10.16	30.53	23.46	3. 65	-
75	9.22	31.10	24.06	1.98	-
100	9.00	31.19	24.16	1.00	0.0*
150	9.02	31.31	24.25	0.90	0.0*
20C	9.00	31.31	24.26	0.50	0.0*

*undetectable

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TABLE VI.   Station E Summary

Physical Data 18 Nov. 1974

Depth (m)	Temp C	Salinity ‰	Sigma-t	O_2 ml/l	chlorophyll-A mg/m^3
0	8.55	26.22	20.35	5.85	.085
10	8.62	27.35	21.22	4.92	.089
20	8.75	28.61	22.19	4.50	.025
30	9.53	29.48	22.75	3.96	0.0*
50	9.57	30.82	23.79	3.83	0.0*
75	9.46	30.92	23.88	1.88	0.0*
100	9.21	30.99	23.98	0.50	0.0*
150	9.00	31.04	24.04	0.55	0.0*
200	9.00	30.96	24.77	0.35	0.0*

*undetectable

TABLE VII.   Station E Summary

Physical Data 19 Dec. 1974

Depth (m)	Temp C	Salinity ‰	Sigma-$\underline{t}$	O_2 ml/l	chlorophyll-$\underline{a}$ mg/m^3
0	8.23	27.83	21.63	5.36	0.10
10	8.96	29.96	23.25	4.07	0.85
20	8.94	30.08	23.24	3.83	0.0*
30	8.85	30.17	23.39	3.96	0.0*
50	8.80	30.36	23.55	4.13	0.0*
75	8.65	30.52	23.69	1.35	0.0*
100	8.92	30.71	23.79	1.00	0.0*
150	8.93	31.22	24.20	0.34	0.0*
200	8.93	31.28	24.24	undetectable	0.0*

*undetectable

TABLE VIII. Station E Summary

Physical Data 16 Jan. 1975

Depth (m)	Temp $^{\circ}C$	Salinity %	Sigma-$\underline{t}$	O_2 ml/1	chlorophyll-$\underline{a}$ mg/m^3
0	7.41	26.53	20.74	7.21	0.20
10	8.00	28.59	22.28	6.53	0.93
20	7.59	30.01	23.44	6.00	0.0*
30	8.10	30.32	23.88	4.31	0.0*
50	7.00	30.63	23.98	3.56	0.0*
75	7.05	31.06	24.34	2.21	0.0*
100	6.98	31.11	24.38	0.25	0.0*
150	7.00	31.12	24.39	0.10	0.0*
200	7.00	31.12	24.39	undetect-able	0.0*

*undetectable

TABLE IX. Strait of Georgia Summary

Physical Data 1 November 1974

Depth (m)	Temp °C	Salinity	Sigma-$\underline{t}$	O_2 ml/l	chlorophyll-$\underline{a}$ mg/m^3
400	8.92	31.25	24.22	3.04	0.00

TABLE X. Experiment 9-B. The Ingestion of *Artemia*

sp. nauplii by *Calanus pacificus*

Initial Artemia Concentration	Volume of Aliquots	Number of Artemia in aliquot		*Ingestion Rate (Artemia copepod^{-1}hr.$^{-1}$)
		time 0	time 0 + 24 hrs.	
.081 per ml.	--	65	25	0.11
0.52	75 ml.	39	8	0.92
0.89	75	67	29	1.13
3.62	50	181	128	2.36
8.96	25	224	141	7.37

*I.R. = $\dfrac{\text{(Initial concentration)}-\text{(final concentration) x 800 mls.}}{\text{(volume of aliquot)(15 copepods)(24 hrs.)}}$

TABLE XI. Mean Coincidence Corrected Particle Counts for Experiment – 10. *C. pacificus*

Conc. Cells/ml.	water + plankton		water + copepods		water + plankton + copepods replicate-1		replicate-2	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Isochrysis								
700 Before	360	10.1	15	4.1	370	13.1	365	14.9
After	370	5.6	22	3.7	90	7.9	78	6.5
Nitzschia								
600 Before	320	14.9	8	2.5	329	17.2	332	19.2
After	328	16.2	14	4.5	118	11.1	155	12.3
Thalassiosira								
600 Before	345	18.2	4	2.5	341	17.2	359	16.7
After	359	14.3	9	6.3	162	10.3	118	12.2
Chroomonas								
800 Before	375	11.5	19	5.6	392	14.9	371	10.3
After	399	12.4	27	7.9	125	17.2	194	16.1
Olisthodiscus								
500 Before	263	18.9	4	2.3	276	17.1	279	14.3
After	281	16.1	8	4.5	141	15.2	195	18.6
Peridinium								
500 Before	129	11.1	0	0	137	14.3	146	14.3
After	141	6.9	0	0	91	6.9	109	11.7
Cymbomonas								
500 Before	279	15.6	9	3.5	285	13.4	261	11.7
After	291	12.9	14	3.4	181	19.2	202	16.9
dead Olisthodiscus								
500 Before	260	11.9	7	3.5	275	13.2	265	17.1
After	251	16.2	10	2.9	125	16.5	154	12.3

TABLE XII. The Ingestion Rates of *C. pacificus*

Feeding on Different Phytoplankton Cultures in Experiment - 10

Culture	Filtration Rate ml. copepod^{-1}day^{-1}		Ingestion Rates cells copepod^{-1}hr.$^{-1}$ ± 95% confidence limits*		Percent available food removed per day	
	(1)	(2)	(1)	(2)	(1)	(2)
Isochrysis	71.8	80.9	987 ± 60	956 ± 60	80.0	83.0
Nitzschia	48.4	35.6	750 ± 73	637 ± 77	68.4	57.5
Thalassio-sira	35.5	58.3	660 ± 75	867 ± 76	58.1	72.4
Chroomonas	64.7	36.0	996 ± 61	673 ± 65	76.3	54.4
Olisthodis-cus	41.5	19.6	523 ± 81	353 ± 82	56.9	38.0
Peridinium	22.0	16.3	200 ± 61	163 ± 67	43.8	33.6
Cymbomonas	21.7	14.6	403 ± 81	253 ± 70	42.5	29.1
dead *Olisthodis-cus*	37.1	26.0	540 ± 77	410 ± 70	58.9	46.4

*Method for calculating confidence limits is described in the Appendix: page 85.

TABLE XIII. Summary of Calibration Factors (F)

Determined from Ammonia Standardization Runs

Ammonia Concentration μgm-At NH_3/ℓ	Experiment 11 F	Experiment 12 F
0.1	3.22	2.70
0.2	4.34	4.17
0.4	4.21	6.45
1.0	4.95	5.59
2.0	5.31	2.65
mean	4.41	4.31

TABLE XIV. A Summary of the Ammonia Excretion

Rates of *Calanus plumchrus* V from Experiment – 11

No. of Animals per jar	Mean copepod weight (mg.)	µgm-At N mg dry weight^{-1} day^{-1} (X10^{-3})	µgm-At N animal^{-1} day^{-1} (X10^{-3})	Days to exhaustion of total body nitrogen	% of total body nitrogen excreted per day
5	.900	18.26	16.43	274	0.36
6	.752	6.67	5.05	749	0.13
8	.988	11.37	11.23	440	0.23
10	.870	22.00	19.14	227	0.44
20	.915	16.55	15.14	303	0.33
20	.793	9.77	7.75	514	0.19
27	.782	17.11	13.38	292	0.34
30	.784	17.65	13.83	282	0.35
39	.812	17.45	14.17	287	0.35
35	.345	9.43	7.96	532	0.19
50	.797	18.36	14.63	271	0.37
56	.349	24.72	20.98	202	0.49
107	.740	14.15	10.47	352	0.28
113	.814	12.26	9.97	406	0.25
mean	.780	15.41	12.87	366	0.30
95% con-fidence limits	.104	2.92	2.57	86.2	0.06

TABLE XV. A Summary of the Ammonia Excretion

Rates of *Calanus plumchrus* V from Experiment - 12

No. of Animals per jar	Mean copepod weight (mg.)	μgm-At N mg dry weight^{-1} day^{-1} (X10^{-3})	μgm-At N animal^{-1} day^{-1} (X10^{-3})	Days to exhaustion of total body nitrogen	% of total body N excreted per day
20	.715	15.21	10.86	329	0.30
20	.759	19.00	14.42	264	0.38
18	.908	14.00	12.71	357	0.28
19	.800	15.20	12.16	329	0.30
21	.781	17.76	13.87	281	0.36
20	.881	15.19	13.38	329	0.30
20	.827	13.39	11.07	373	0.27
18	.938	12.58	11.80	398	0.25
19	.826	14.08	11.63	354	0.28
20	.925	14.31	13.24	350	0.28
21	.834	16.24	13.54	308	0.32
20	.838	16.78	14.06	297	0.33
20	.933	13.82	12.89	362	0.27
21	.852	14.30	12.18	348	0.28
20	.939	13.22	12.41	377	0.26
20	.832	17.40	14.47	286	0.35
20	.873	15.74	13.74	318	0.31
20	.792	17.83	14.12	279	0.36
21	.806	16.81	13.54	298	0.33
20	.915	13.72	12.55	363	0.27
$\bar{x}$	.849	15.33	12.93	330	0.34
95% confidence limits	0.030	0.841	0.506	17.6	0.04

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TABLE XVI. Summary of

Calanus sp. Nitrogen Excretion Rates

Reference	Species	µgm At–N mg dry wt. $^{-1}$ copepod day^{-1}	% of total body N excreted per day	days to exhaustion of total body N
Exp't 11	C. plumchrus V	0.0154	0.30	366
Exp't 12	C. plumchrus V	0.0153	0.34	330
Taguchi and Ishi (1972)	C. plumchrus V	0.227	3.44	29
Corner and Newell (1967)	C. helgolandicus (adult)	0.238	4.75	21
Butler et al. (1969)	C. finmarchicus V	0.172	15.5	6.5
	C. helgolandicus V	0.076	6.8	15
Conover and Corner (1965)	C. hyperboreus V	0.059	1.34	75
Corner et al. (1965)	C. finmarchicus V	0.55	7.71	13
Butler et al. (1970)	C. helgolandicus V	0.114-0.700	2.3-14.0	7-44
Littlepage and Rose (1973)	C. plumchrus V	0.46 -0.90	9.2-18	5.5-10.9

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Key to Tables A-I - A-VIII

1: Concentration (cells/ml) column: refers to the approximate cell concentration in each jar.

2: $\bar{x}$: mean particle counts: the mean of 5 separate counts by the Coulter Counter Volume sampled in each count - 0.5 mls except for Experiment 7 where Volume = 2.0 mls.

3: S = standard deviation of variation

   $= \dfrac{\bar{x}}{S} \times 100\%$

4: B = particle concentration BEFORE start of experiment

   A = particle concentration AFTER duration of experiment

TABLE A-I. Mean Particle Counts for Experiment - 1

Concentration cells/ml.		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate - 2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
250	B	125	4.1	3.3	139	3.3	2.4	140	4.1	2.9
	A	135	3.9	2.9	147	6.2	4.2	150	3.6	2.4
700	B	352	4.1	1.16	380	1.6	0.42	362	4.2	1.2
	A	380	2.8	0.74	395	3.9	0.91	370	3.7	1.0
1400	B	660	9.8	1.5	685	5.8	0.85	675	4.9	0.72
	A	690	6.2	0.90	693	7.3	0.92	690	7.8	1.13
2000	B	1005	12.1	1.2	1009	11.7	1.1	1107	9.6	0.87
	A	1065	14.4	1.3	1090	10.1	0.93	1131	10.2	0.90
4400	B	2198	18.5	0.84	2105	35.7	1.70	2135	17.6	0.82
	A	2231	21.7	0.97	2175	21.8	1.00	2162	26.1	1.2
8200	B	4091	30.5	0.74	4110	39.9	0.97	4129	31.0	0.75
	A	4123	29.2	0.70	4139	45.0	1.08	4152	22.0	0.53
20,000	B	9725	55.2	0.56	9865	80.7	0.31	9809	52.3	0.53
	A	9800	61.9	0.63	9879	71.9	0.73	9839	41.9	0.43
Blank	B	32	4.6	14.3	38	7.2	18.9			
	A	40	9.2	23.0	52	3.9	7.5			
Water + copepods	B	80	3.2	4.0	72	2.9	4.1	83	4.6	5.5
	A	89	4.5	5.1	81	1.2	1.5	90	3.9	4.3

TABLE A-II. Mean Particle Counts for Experiment - 2

density copepods/jar		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate - 2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
5	B	410	5.7	1.39	420	9.9	2.35	429	8.3	1.93
	A	421	6.8	1.61	431	8.1	1.88	436	7.6	1.74
10	B	407	5.1	1.25	431	7.2	1.67	420	8.7	2.07
	A	429	7.4	1.72	462	6.5	1.41	441	8.1	1.83
20	B	408	8.0	1.96	431	6.3	1.46	418	4.8	1.15
	A	416	7.0	1.68	440	5.9	1.34	427	9.1	2.13
50	B	435	8.2	1.88	450	7.6	1.68	461	8.2	1.78
	A	447	9.1	2.00	473	4.5	0.95	470	9.5	2.02
100	B	462	9.7	2.09	476	9.3	1.95	480	10.1	2.10
	A	483	8.2	1.69	483	7.9	1.63	500	12.3	2.46
Blank	B	20	4.5	22.5	17	6.8	40.0			
	A	27	3.9	14.4	43	7.2	16.7			
		water + 5 copepods			water + 10 copepods			water + 10 copepods		
	B	61	4.7	7.7	70	7.8	11.4	72	3.9	5.4
	A	69	9.2	13.3	75	5.2	6.93	80	6.2	7.8
		water + 50 copepods			water + 100 copepods					
	B	85	13.1	15.4	121	4.2	3.5			
	A	109	12.7	11.6	145	15.9	10.9			

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TABLE A-III. Mean Particle Counts for Experiment - 3

Concentration cells/ml		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate - 2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
100	B	55	5.5	10.0	57	6.7	12.0	50	4.1	8.0
	A	57	4.2	7.4	60	5.9	9.8	55	6.0	10.9
200	B	100	6.6	6.6	101	4.2	4.2	112	2.0	1.8
	A	105	7.1	6.8	109	3.2	2.9	115	4.1	3.6
400	B	223	6.2	2.8	231	3.5	1.5	229	4.8	2.1
	A	230	5.9	2.6	239	2.3	0.96	240	1.9	0.79
800	B	421	7.1	1.68	430	8.1	1.88	427	7.0	1.64
	A	436	6.5	1.49	445	5.5	1.23	439	6.9	1.57
1600	B	829	8.3	1.00	849	7.9	0.93	835	3.6	0.43
	A	841	7.6	0.90	861	8.1	0.94	845	6.2	0.73
3400	B	1729	8.1	0.46	1721	7.3	0.42	1791	12.1	0.67
	A	1751	6.9	0.39	1735	4.9	0.28	1805	11.2	0.62
6800	B	3391	25.8	0.76	3290	30.1	0.91	3301	20.7	0.68
	A	3410	31.9	0.93	3340	19.1	0.57	3390	29.7	0.88
23,000	B	11,621	71.8	0.62	11,729	91.7	0.78	11,895	101.1	0.85
	A	11,821	89.1	0.75	11,931	61.5	0.52	12,013	121.9	1.01
Blank	B	8	4.1	51	12	4.3	36			
	A	13	2.9	22.3	14	3.1	22.1			
Water + copepods	B	10	5.0	50	11	3.1	28			
	A	11	6.0	60	13	4.0	31			

TABLE A-IV. Mean Particle Counts for Experiment - 4

Density copepods/jar		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate - 2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
5	B	521	5.7	1.09	532	5.2	0.97	527	3.7	0.71
	A	539	6.2	1.15	540	4.9	0.91	549	5.4	0.75
10	B	533	4.3	0.81	529	6.9	1.30	551	10.1	1.83
	A	552	5.1	0.92	549	7.3	1.33	572	6.9	1.20
20	B	562	6.0	1.06	565	6.5	1.15	570	14.9	2.61
	A	579	5.8	1.00	578	3.2	0.55	598	20.1	3.36
50	B	528	4.9	0.93	508	7.0	1.37	517	2.9	0.56
	A	541	7.2	1.32	521	6.0	1.15	541	5.9	1.09
100	B	543	3.5	0.64	527	7.7	1.46	549	3.4	0.62
	A	549	4.7	0.85	538	9.2	1.71	562	7.2	1.28
Blank	B	13	4.1	31.5	12	4.9	40.8			
	A	15	3.6	24.0	17	7.8	45.8			
		water + 5 copepods			water + 10 copepods			water + 20 copepods		
	B	9	2.5	27.7	15	4.7	31.3	17	3.9	22.9
	A	12	3.5	29.2	21	6.5	30.9	19	4.2	22.1
		water + 50 copepods			water + 100 copepods					
	B	30	7.8	26.0	45	4.3	9.5			
	A	31	7.0	22.6	60	9.2	15.3			

TABLE A-V. Chlorophyll-a Concentrations of the

Feeding Jars in Experiment - 4 at the end of the

Feeding Period

	Chlorophyll concentrations in mg/m^3		
water only	water + copepods	water + plankton (5 jars)	water + plankton + copepods (10 jars)
0.00	0.00	1.99	1.92, 1.76
0.00	0.00	2.23	2.02, 2.31
		2.00	2.23, 2.18
		2.36	1.89, 1.86
		1.95	2.19, 2.24

Statistical analysis: Independent t test (Sokal and Rohlf 1969)

Ho: there is no difference between the chlorophyll-a concentrations of

the "water + plankton" jars and the "water + plankton + copepods"

jars.

Calculated $t = +0.657$ $t_{.05(13)} = 2.16$

The null hypothesis is therefore accepted.

TABLE A-VI. Mean Particle Counts for Experiment – 5

Concentration cells/ml.		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate-2		
		$\bar{x}$	s	c.v.	x	s	c.v.	$\bar{x}$	s	c.v.
100	B	70	3.2	4.5	65	6.2	9.5	68	5.0	7.4
	A	85	5.7	6.7	72	4.4	6.1	73	5.8	7.9
200	B	123	4.9	3.9	120	2.1	1.7	125	6.8	5.4
	A	141	5.3	3.8	136	7.8	5.7	141	9.2	6.5
400	B	209	6.2	2.9	203	8.2	4.0	210	4.3	2.0
	A	219	7.9	3.6	223	6.9	3.1	215	9.9	4.6
800	B	410	9.8	2.4	426	10.2	2.4	419	3.2	0.76
	A	425	8.7	2.1	430	6.9	1.6	439	11.5	2.62
1800	B	891	11.5	1.3	888	6.7	0.75	900	10.8	1.18
	A	898	15.2	1.7	899	9.1	1.01	921	2.9	.31
3200	B	1550	8.9	0.57	1600	9.2	0.57	1582	13.3	0.84
	A	1565	11.7	0.74	1631	3.9	0.24	1602	11.2	0.69
7400	B	3701	21.5	0.58	3692	23.6	0.64	3681	39.7	1.08
	A	3729	10.9	0.29	3709	41.2	1.11	3695	49.8	1.35
16,000	B	8091	62.1	0.76	8001	47.6	0.59	8111	39.6	0.48
	A	8129	79.3	0.98	8219	82.7	1.0	8293	101.9	1.2
Blanks	B	19	4.5	23.7				13	3.9	30
	A	25	6.2	24.8				17	2.9	17
Water + copepods	B	27	4.7	17	32	4.3	13.4	20	7.7	38.5
	A	41	3.8	93	51	6.1	11.9	29	6.0	20.7

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TABLE A-VII. Mean Particle Counts for Experiment - 6

Age and Concentration		water + phytoplankton			water + phytoplankton + copepods					
					replicate - 1			replicate - 2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
600 cells/ml										
early log	B	329	18.0	5.47	333	7.9	2.4	340	13.9	4.08
	A	331	16.2	4.89	351	14.1	4.01	362	17.8	4.91
late log	B	341	18.9	5.54	372	16.2	4.35	376	14.3	3.80
	A	351	17.1	4.87	389	23.1	5.93	392	19.1	4.87
Stationary	B	333	20.3	6.09	356	10.8	3.03	360	19.8	5.50
	A	342	21.2	6.19	379	17.6	4.64	392	20.9	5.33
3200 cells/ml										
early log	B	1629	16.2	0.99	1651	10.9	0.66	1662	12.3	0.74
	A	1633	15.1	0.92	1679	7.6	0.45	1693	18.9	1.11
late log	B	1641	17.7	1.07	1661	12.4	0.74	1652	4.4	0.26
	A	1662	15.0	0.90	1673	9.9	0.59	1683	13.3	0.79
Stationary	B	1639	15.4	0.94	1649	19.2	1.16	1677	7.52	0.45
	A	1649	13.2	0.80	1659	14.9	0.89	1694	16.8	0.99
Blank	B	17	6.2	36	21	4.3	20.	10	7.2	72
	A	25	3.9	15	30	6.9	23	31	9.1	29
Water + copepods	ʟ	28	6.2	22	17	3.5	21	21	7.2	24
	A	35	4.5	13	29	6.9	24	33	7.4	22

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TABLE A-VIII. Mean Particle Counts for Experiment – 7

Volume Counted – 2.0 ml.

Concentration cells/ml.		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate-2		
		x̄	s	c.v.	x̄	s	c.v.	x̄	s	c.v.
50	B	107	6.2	5.8	113	4.9	4.3	111	6.5	5.8
	A	110	3.5	3.2	119	7.2	6.0	122	3.9	3.2
100	B	239	4.5	1.9	241	6.9	2.8	250	8.8	3.5
	A	245	7.2	2.9	249	2.2	0.9	265	7.7	2.9
200	B	419	8.2	1.9	425	13.5	3.17	417	6.2	1.5
	A	438	11.3	2.6	436	12.9	2.95	439	15.3	3.48
500	B	1062	25.6	2.41	1075	31.2	2.90	1069	22.2	2.07
	A	1095	20.7	1.89	1100	19.8	1.80	1075	16.4	1.52
1000	B	1982	35.2	1.77	2001	29.3	1.46	1995	35.2	1.76
	A	2012	41.2	2.04	2222	33.6	1.51	2005	37.9	1.89
3000	B	6252	61.5	0.98	6200	31.8	0.51	6236	81.2	1.30
	A	6281	71.2	1.13	6250	59.6	0.95	6341	61.0	0.96
6000	B	12,052	89.2	0.74	12,079	90.1	0.75	13,000	65.3	0.50
	A	12,095	110.1	0.91	13,025	129.1	0.99	13,129	89.5	0.68
Blank	B	0	0	0	1	0.5	50	0	0	0
	A	0	0	0	3	1.5	50	2	.5	25
Water + copepods	B	0	0	0	1	0.5	50	0	0	0
	A	2	1.5	75	2	1.5	75	0	0	0

TABLE A-IX. Mean Particle Counts for Experiment – 8

Concentration cells/ml.		water + phytoplankton			water + phytoplankton + copepods					
					replicate-1			replicate-2		
		$\bar{x}$	s	c.v.	$\bar{x}$	s	c.v.	$\bar{x}$	s	c.v.
Chroomonas										
500	B	275	7.2	2.6	280	14.2	5.07	265	17.6	6.64
	A	289	11.2	3.9	292	12.1	4.14	278	8.2	2.94
2000	B	1025	10.3	1.0	1003	12.3	1.23	1018	8.2	0.80
	A	1052	8.7	0.82	1028	15.6	1.52	1037	11.7	1.13
Olisthodiscus										
300	B	151	6.9	4.6	138	5.2	3.8	142	10.2	7.2
	A	162	12.3	7.6	145	8.9	6.1	149	7.4	4.9
1600	B	821	10.1	1.23	829	9.3	1.12	838	6.3	.75
	A	830	12.1	1.46	842	14.2	1.68	851	9.9	1.16
Cymbomonas										
300	B	167	12.1	7.24	173	9.2	5.3	180	14.7	8.2
	A	175	11.3	6.45	185	13.1	7.1	193	8.3	4.3
Frozen *Olisthodiscus*										
2000	B	982	9.6	.95	1002	10.1	1.0	1010	6.9	0.68
	A	998	8.3	.83	1020	11.3	1.1	1023	7.8	0.76
		water + copepods (Sensitivity – ½)			water + copepods (Sensitivity – 1)			water + copepods (Sensitivity – ½)		
	B	20	4.9	24	6	2.5	42	12	2.3	19.2
	A	35	5.8	17	8	3.3	41	18	4.9	27.2

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TABLE A-X. Experiment 9-A.

The effect of *C. plumchrus* on the concentration

of *Artemia* larvae over a 24 hour period

Initial *Artemia* Concentration (animals per ml.)	Volume of Aliquot (in mls.)	Number of *Artemia* in aliquot	
		time 0	time 0 + 24 hrs.
0.081	* --	65	71
0.45	75	34	36
0.97	75	73	70
2.06	75	155	148
4.03	50	202	221
7.54	25	189	180
15.8	12	190	201
39.3	5	196	190

*concentration was not determined by the removal of aliquots. Instead, a known number (65) animals were added to the jar.

Statistical analysis: Paired t-test (Sokal and Rohlf, 1969).

Ho: the number of Artemia did not change over 24 hrs.

calculated t = -0.468 $t_{.05(7)}$ = 2.368.

The null hypothesis is accepted.
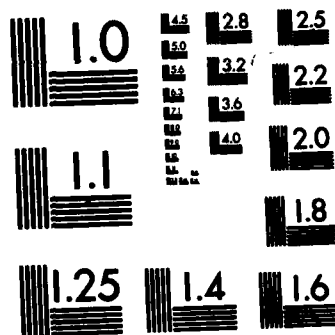
MICROCOPY RESOLUTION TEST CHART

NATIONAL BUREAU OF STANDARDS-1963-A

Method of calculating 95% confidence limits for Ingestion rates in

Table XII (Gregory, 1981; pers. comm.).

$$\bar{x} \pm t_{(.05)(n-1)} \, S_{\bar{x}_1 - \bar{x}_2 + \bar{x}_3 - \bar{x}_4 + \bar{x}_5 - \bar{x}_6}$$

where: $\bar{x}$ = mean change in the number of cells per 0.5 ml

and: $S_{\bar{x}_1 - \bar{x}_2 + \bar{x}_3 - \bar{x}_4 + \bar{x}_5 - \bar{x}_6}$ (the standard error)

$$= \frac{2 \, Sp}{n}$$

where: n = number of counts made on Coulter Counter to determine each

mean concentration.

Sp is a pooled estimate of the variance

$$Sp = \frac{\overline{S_1^2 + S_2^2 + S_3^2 + S_4^2 + S_5^2 + S_6^2}}{6}$$

where: $S_1^2 \ldots S_6^2$ are the variances of the mean concentration before

and after the 24 hr. feeding period in the 2 control jars and

the experimental jar, with each variance based on 5 separate

counts with the Coulter Counter.

Confidence limits for Ingestion Rate

$$= \frac{\text{(above calculated limits)}(800 \text{ mls/jar})}{(24 \text{ hrs.})(20 \text{ copepods/jar})} \times 2$$

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