ECOPHYSIOLOGICAL STUDIES OF *ORCHOMENOPSIS AFFINIS* (HOLMES) (LYSIANASSIDAE AMPHIPODA) IN AN INTERMITTENTLY ANOXIC FJORD

by

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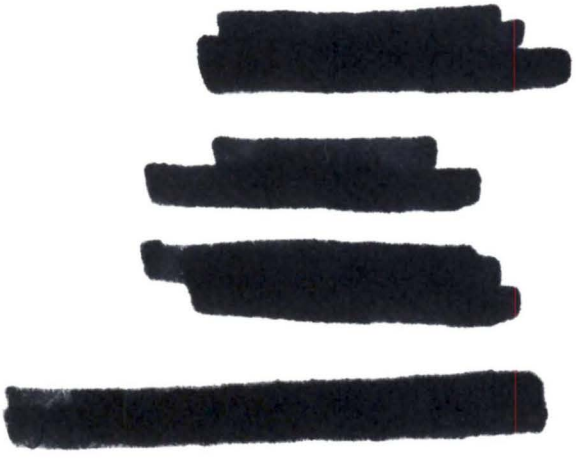

Supervisor: Dr. J. L. Littlepage

ABSTRACT

This study was undertaken in order to understand the physiological adaptations and ecology of Orchomenopsis affinis (Holmes) (Lysianassidae, Amphipoda) in Saanich Inlet, an intermittently anoxic fjord on Vancouver Island, British Columbia, Canada. Field sampling, submersible observation and laboratory experiments were carried out from November, 1985 to April, 1987.

O. affinis was found in abundance under oxygen deficient conditions, especially in the anoxic and sulfide-rich layer. O. affinis can survive under anoxic conditions for at least 25 hours and tolerate concentrations of sulfide up to 3 mM. The survival of O. affinis to temperature and salinity changes are 0 to 19 ^{o}C and 20 to 50 ^{o}/oo respectively.

O. affinis shows respiratory independence under the oxygen range from 0.5 to 10.0 mg/l. Respiratory dependence occurs when oxygen concentration is lower than 0.5 mg/l. Respiratory rates are lowest under low temperature and high salinity.

The vertical distribution of O. affinis indicates that more than 70% of the population is associated with the sediment-water interface during the day and about 15% of the population clings to the sea floor at night.

Animals migrate vertically to oxygen rich layers to eliminate the oxygen debt which accumulates under anoxic conditions.

O. affinis feeds by scavenging on or in the sediment beneath the anoxic water layer. Because of its obligatory vertical migration, it has the ecological role of transporting energy to the oxygenated layer, thereby establishing a unique food chain. This phenomenon is named Biological Upwelling.

The advantages to O. affinis in occupying the anoxic zone are: (1) greater availability of food, (2) refuge from predation, and (3) energy conservation through relatively lower metabolic rates in deep and colder water.

Though our knowledge of ecophysiological adaptations and ecological significance has increased, biochemical adaptation of this animal to sulfide and its metabolic pathways under aerobic and anaerobic conditions remain unknown.

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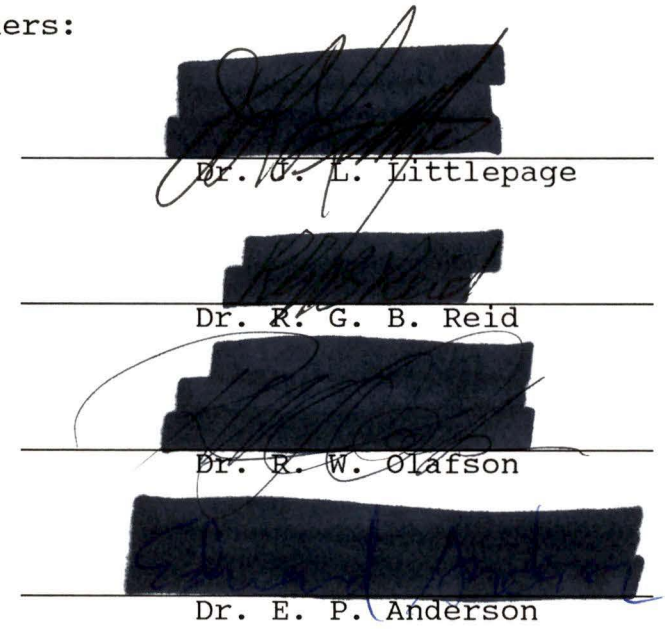

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DEDICATION

This thesis is dedicated to

my father Axi Liu

(1922-1987)

INTRODUCTION

Orchomenopsis affinis (Holmes 1908), an amphipod crustacean, has been found in abundance in mid-depth and deep waters of the intermittently anoxic fjord Saanich Inlet (Fulton, 1968; Hoos, 1970; Mackie & Mills, 1983). Little is known about the ecophysiological adaptation and ecological significances of this species to the the intermittently anoxic and sulfide rich environment.

Extensive zones of oxygen deficiency are commonly found at intermediate depths in many oceans, in some coastal regions and in the deep parts of some fjords. Oxygen deficiency is also common in heavily polluted waters (Sverdrup et al., 1942; Richards, 1957; Wyrtki, 1962; Longhurst, 1967; Anderson & Devol, 1973).

Results from many ecological surveys show that dissolved oxygen concentration exerts a strong influence on the distribution of zooplankton and benthic organisms (Tulkki, 1965; Longhurst, 1967; Teal & Carey, 1967; Hoos, 1970; Belman, 1978; Brinton, 1979; Rosenberg, 1979; Jorgenson, 1980; Judkins, 1980; Bridges & Brand, 1980; Levings, 1980a; 1980b; Tunnicliffe, 1981; Devol, 1981; Mackie & Mills, 1983; Burd, 1983). Perhaps due to the long term stability of some oxygen minimum zones, some animals appear to have adapted to oxygen deficient conditions (Theede et al., 1969; 1973; Childress, 1971a; 1971b; 1975;

Rhoads & Morse, 1971; Schottler, 1979). Numerous authors have reported the existence of large populations of zooplankton in oxygen deficient layers (Schmidt, 1925; Jespersen, 1935; Sverdrup, 1942; Longhurst, 1967).

Adaptations of these species to low oxygen tensions have interested a number of authors. It has been reported that some animals maintain a high flow rate of water over their gills. The large gill surface area and the capacity to increase the ventilation volume in some animals is considerable and may be a significant factor in their ability to respire at very low oxygen levels (Gray, 1957; Childress, 1971b; Belman & Childress, 1976; Babula, et al., 1978; Burd, 1983).

Many previous workers have demonstrated that animals which were found in the oxygen deficient layers were generally good respiratory regulators (Teal, 1967; Thompson & Pritchard, 1969; Belman, 1976; Childress, 1975). Specimens of the mysid Gnathophausia ingens caught at depths with an average oxygen content of 0.2 ml/l to 0.5 ml/l could survive oxygen levels of 0.14 to 0.26 ml/l for at least 3 months (Childress, 1968). Childress (1975) reported that most species found in the oxygen minimum layer off California were capable of living entirely aerobically at an oxygen concentration of 0.2 ml/l.

Evidence indicates that aquatic organisms may utilize several metabolic pathways to obtain energy. These

processes can be aerobic or anaerobic (Hochachka & Somero, 1973; Davis, 1975; Zwaan, 1977; Reid & Brand, 1986). Many animals which are normally aerobic can survive many hours without oxygen by utilizing anaerobic means of energy production (Hochachka, 1980). Mangum and Van Winkle (1973) and Mangum and Burnett (1975) suggested that aerobic shutdown occurs when the oxygen gained by the animal from the medium failed to balance the oxygen utilized, thus triggering a reliance on energy production via anaerobic metabolic pathways.

It has been suggested that vertical migration is one of the most important adaptations found in low oxygen tolerant species (Teal & Carey, 1967). Animals migrate upwards to oxygen containing layers to repay the oxygen debt which was accumulated in their bodies when the pO_2 fell below the critical pressure at day depth (Childress, 1971a; 1971b; 1977; Belman, 1978).

Sulfide may be found in water, waste water and sludge as a result of microbial action on organic matter under anaerobic conditions and from certain industrial operations (American Public Health Ass., et al., 1971).

In the sea, the disappearance of oxygen is often correlated with the formation of hydrogen sulfide (Theede et al., 1969). For many animals, the lack of oxygen and/or the presence of hydrogen sulfide proves fatal (Brongersma-Sanders, 1957; Theede, 1973). However, some

marine invertebrate animals can live in sulfide-rich habitats, including the tube worms and other invertebrates which have been found in the deep-sea hydrothermal vents (Felbeck, 1983) and the gutless clam Solemya reidi which occurs in sewage outfall and pulpmill effluent zones (Reid, 1980).

Intensive biochemical studies have been carried out on the sulfur metabolism of these species. Animal-bacteria symbiosis was described by Felbeck et al. (1981). However, since most of the experiments have been done on symbiotic organisms with guts that are reduced or absent, little is known about the physiological adaptations and physiological tolerances of anoxic and sulfide resistant non-symbiotic animals that depend on feeding and digestion. The resistance of various communities in the Black Sea and North Sea to both anoxia and anoxia plus hydrogen sulfide have been investigated by Theede et al. (1969). Results indicated that the resistance of species to oxygen deficiency is greater than that to oxygen deficiency combined with the presence of hydrogen sulfide.

Crustacean species showed the least resistance to sulfide. In their review paper, Fenchel and Riedl (1970) pointed out that the entire Arthropoda group was missing from the sulfide containing sandy bottom zone. However, ecological surveys have found that a brachyuran crab, Bythograea themydron is endemic to the hydrothermal vents.

It encounters concentrations of hydrogen sulfide of up to 318 uM (Vetter, et al., 1987). This thesis reports the presence of a lysianassid amphipod at anoxic and sulfide-rich layer in Saanich Inlet.

Feeding strategy is another important adaptation which may limit animal distribution and survival. Generally speaking, food fall in the open ocean is a relatively rare event and deep living animals often suffer from food shortage (Stockton & DeLace, 1982). Dahl (1979) described strategies that scavenging amphipods utilize for survival: quick response in location of the food source, high food intake rate, low metabolic rate during periods of inactivity (torpor), and ability to survive prolonged starvation.

These animals may use chemoreceptors and mechanoreceptors for detecting their food (Wilson, 1970; Crisp, 1974). Hessler et al. (1978) and Thurston (1979) suggested that chemosensory attraction is the main way animals detect their food. Data accumulated from submersible observations, time-lapse camera and baited free-vehicles show many large mobile animals live in deep water (Barham et al., 1967, Isaacs, 1969; Dayton and Hessler, 1972; Grassle, et al., 1975). However, very few laboratory experiments have been carried out on deep water animals because of the technical difficulties involved (Hessler et al., 1978). The limit of physiological

information on deep midwater organisms regarding feeding rates, food retention time and assimilation efficiencies is a serious gap in our knowledge that prevents our proper understanding of the ecological function of these communities (Angel, 1984).

Zooplankton have evolved various feeding strategies. Marshall and Orr (1955) reported that the resting copepodite V of Calanus finmarchicus did not feed in the deep water. McLaren (1963) suggested the vertical migratory species fed in the upper layer when they migrated upward in the evening.

Some scavenging zooplankton, commonly amphipods, may also feed on materials found on the bottom of the deep-sea (Fuzessery & Childress, 1975; Hessler et al., 1978; Stockton & Delaca, 1982). Studies on the effect of bait size and sampling time on the attraction of the lysianassid amphipods Anonyx sarsi and Orchomenella pinguis in middle Saint Lawrence Estuary, Sainte-Marie (1986) found that numbers of lysianassids attracted to traps increased with increasing bait size and both species were most active at night. Some studies have shown that swimming and feeding activity of shallow water lysianassids occurs mostly in darkness (Bregazzi, 1973; Stepien & Brusca, 1985). Darkness may offer protection against visually orientated predators (Hobson & Chess, 1976; Alldredge & King, 1980). But light intensity is

reduced in deeper waters. Lysianassids can swim and feed at any time (Sainte-Marie, 1986). However, there are no reported instances of zooplankton feeding under anoxic conditions.

Fjords which commonly have oxygen depleted deep water if isolated by sills, are among the most productive habitats with actual and potential significance in commercial and sports fisheries (Brattegard, 1979). Saanich Inlet, a small fjord located on the southeast side of Vancouver Island, British Columbia, Canada, has been investigated by many marine scientists (Herlinveaux, 1962; Richards, 1965; Hoos, 1970; Anderson & Devol, 1973; Emerson, et al., 1979; Thomson, 1981; LeBlond, 1983). Saanich Inlet is an intermittently anoxic fjord with a maximum depth of 236 m and a sill depth of 70 m. The water below 100 m is isolated and experiences seasonal anoxia and flushing (Richards, 1965; Anderson and Devol, 1973). Water behind and below the shallow sill is stagnant from late winter to summer which results in oxygen depletion and hydrogen sulfide accumulation. Anoxia and sulfide concentrations up to 40 uM have been recorded in stagnant bottom waters (Emerson, 1979). This situation changes when dense oxygenated water originating from upwelling on the Washington-Oregon coast reaches the sill and flushes into the basin of the Inlet in late summer or early autumn displacing the less dense resident water (Waldichuk, 1957;

Anderson & Devol, 1973; Emerson, 1979). A midwater oxygen minimum may be found occasionally during the flushing period.

Several planktonic crustaceans occur in the oxygen depleted layer of Saanich Inlet (Fish, 1968; Hoos, 1970). Of these, Orchomenopsis affinis can survive longer than other local species under low oxygen conditions (0.39 ml/l) (Fish, 1968). Hoos (1970) and Mackie and Mills (1983) showed that the vertical migration and distribution of zooplankton in Saanich Inlet was correlated to their tolerance of low oxygen conditions.

Because of the high mobility of lysianassid species, only a few can be caught by traditional samplers: dredges, corers, grabs, plankton nets and trawls. Chevreux (1900) first successfully trapped deep-sea amphipods during the cruises of Prince Albert I of Monaco. He noted that all deep-sea amphipods caught in baited traps belong to the Family Lysianassidae. At least 16 genera and 28 species were collected in baited traps, 16 species of them in one single catch. Since the introduction of the baited camera in the late 1960's and increased use of baited traps in the early 1970's, deep-sea demersal scavenger studies have made great progress and presented spectacular results (Hessler et al., 1972; Shulenberger & Hessler, 1974; Shulenberger & Barnard, 1976; Hessler et al., 1978; Dahl, 1979; Thurston, 1979). Direct observations from

submersibles have also increased knowledge of deep sea fauna (Barham et al., 1967; Grassle et al., 1975; Mackie & Mills, 1983).

Observations of feeding behavior of Eurythenes gryllus made by Ingram and Hessler (1983), showed that E. gryllus occured singly when not at bait. Near an odor source all species tend to choose bait with other amphipods on it, neglecting similar bait nearby. When given a choice of traps, individual E. gryllus prefer to enter traps containing individuals of similar age and sex. They suggested that locating a food item in amphipods is probably based more on information received from other amphipods than on food odor. It is unknown how this communication works.

Deep sea scavengers constitute a major element of the deep-sea fauna and occupy certain special ecological niches. It has been suggested that the mobile scavenging animals play an especially important role in the dynamics of deep benthic communities (Issacs, 1969; Dayton & Hessler, 1972; Hessler & Jumars, 1974; Shulenberger & Hessler, 1974; Haedrich & Rowe, 1977).

Though many studies have been done on the taxonomy and distribution of lysianassid amphipods (Barnard, 1969), little is known about metabolism and physiological adaptations of these scavenging animals to environmental conditions. In order to get some basic information on

their physiological adaptations, a study was undertaken on Orchomenopsis affinis, an amphipod living in oxygen poor bottom waters of Saanich Inlet.

The purpose of the present study is to determine: (1) physiological tolerances and metabolic responses of Orchomenopsis affinis to variations in environmental factors, (2) activity patterns and feeding behavior, and (3) ecological function of O. affinis in the fjord ecosystem. Investigation of these factors will increase our ecological knowledge of scavengers in intermittently anoxic and sulfide rich waters.

MATERIALS AND METHODS

Study Area

Saanich Inlet (Fig. 1) is a fjord located on the southeast coast of Vancouver Island, British Columbia. All physical, chemical and biological sampling was done at a single station located at 48°37.80'N and 123°30.00'W. Water depth at this station is about 225 m.

Hydrographic Protocol

Hydrocasts were carried out during the field experimental periods in order to determine the physical and chemical characteristics of the water column in Saanich Inlet.

Hydrographic data of Saanich Inlet were obtained by using Nansen bottles equipped with reversing thermometers aboard the University oceanographic vessel, the John Strickland. The dates, depths and procedures of sampling are summarized in Tables 1 and 2.

Water samples of 50 cc for oxygen determination were drawn from the Nansen bottles by pretreated airtight 60 cc B-D plastipak syringe, fixed immediately and titrated in the laboratory according to the Winkler method (Strickland & Parsons, 1972). Samples for sulfide measurement were drawn in the same way, treated with a mixed solution of N,N-dimethyl-p-phenylenediamine sulfate and ferric

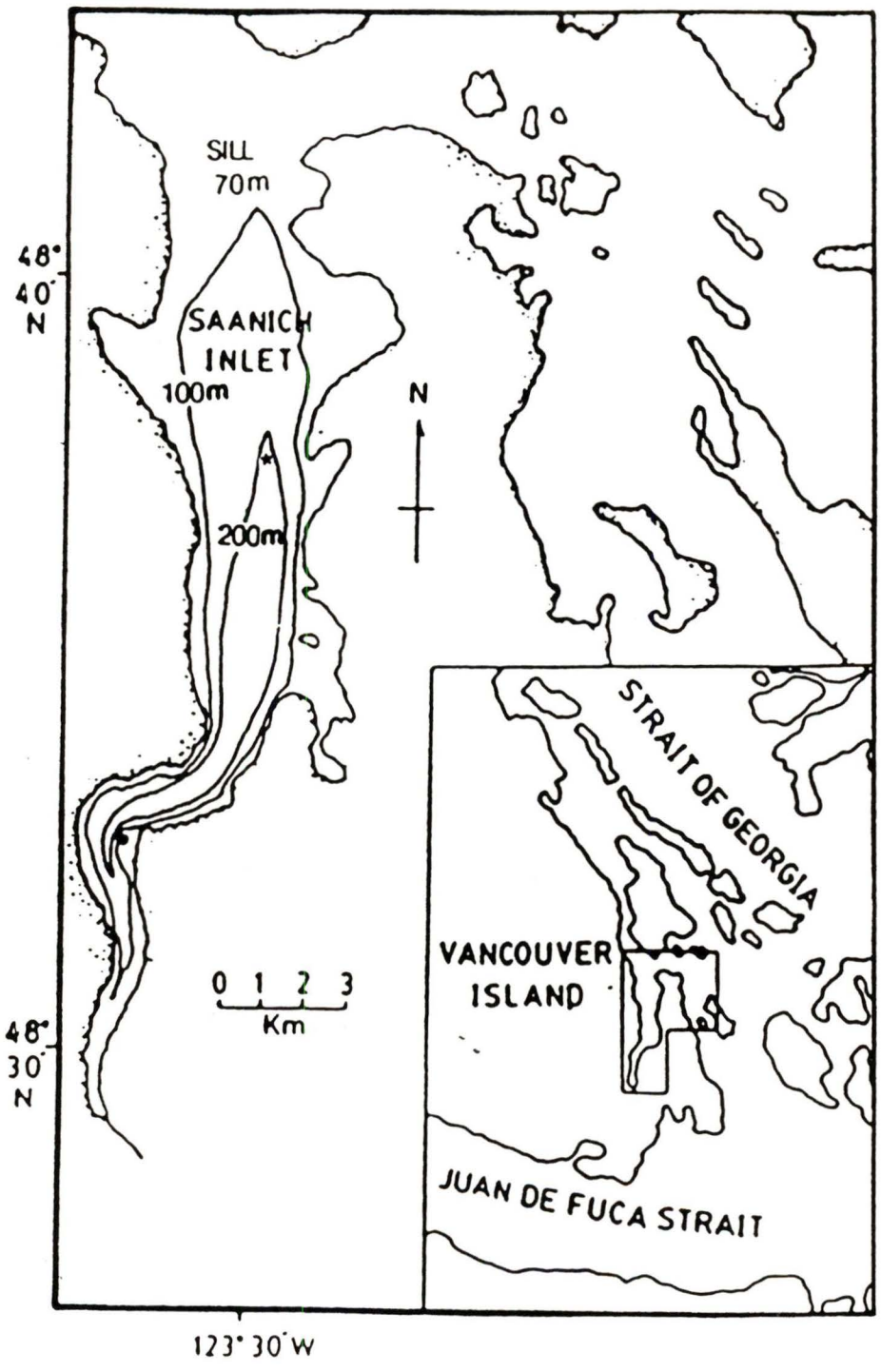

Figure 1. Location of study area. * shows the station for sampling and field experiments.

TABLE 1. HYDROGRAPHIC SAMPLING DATES AND DEPTHS*

DEPTH m DATE	0	10	30	50	75	100	125	150	175	200	225
MAR 15 '86	+	+	+	+	+	+	+	+	+	+	+
MAY 14	+	+	+	+	+	+	+	+	+	+	+
JULY 29	+	+	+	+	+	+	+	+	+	+	+
SEPT 15	+	+	+	+	+	+	+	+	+	+	+
OCT 3	+	+	+	+	+	+		+			
NOV 17	+	+	+	+	+	+	+	+	+	+	+
DEC 12	+	+	+	+	+	+	+	+	+	+	+
JAN 14 '87	+	+	+	+	+	+					
FEB 9	+	+	+	+	+	+	o	+	+	o	o
MAR 3	+	+	+	+	+	+	+				
APRIL 3	+	+	+	+	+	+	+	+	+	+	o
JUNE 22	+	+	+	+	+	+		+			

* +: sample for determinations of temperature, salinity, dissolved oxygen and sulfide.

o: sample for oxygen determination only.

Table 2. SUMMARY OF THE HYDROGRAPHIC SAMPLING PROCEDURES

ITEM	TECHNIQUE	INSTRUMENT
TEMPERATURE	Hydrocast	Reversing thermometer
SALINITY	Induction salinometer	Beckman RS7-C
OXYGEN	Winkler titration	Airtight sampler
SULFIDE	Cline colorometric	Airtight sampler

chloride in acidic medium and measured later in the laboratory with a B & L Spectronic 21 spectrophotometer (Cline, 1969).

Laboratory Protocols

Experimental Animal

Orchomenopsis affinis (Holmes) is a gammaridean amphipod of the Family Lysianassidae. The Family Lysianassidae has 112 genera and more than 400 recorded species. Systematically speaking, this family is still very confused at the genus level. Barnard (1969) pointed out that specialists are not satisfied with current classification of this family because of the lack of clear descriptions of the type-species.

Orchomenopsis affinis is known by several synonyms. They are Orchomenella obtusa (Sars, 1895; Hurley, 1963; Fulton, 1968), Orchomenopsis obtusa (Stebbing, 1906), Orchomenella affinis (Holmes, 1908) and Orchomenopsis

affinis (Bousfield, W., National Museum in Ottawa, pers. comm. 1986). It was difficult to decide which genus and species name should be used in this thesis. Dr. J. L. Barnard (pers. comm.) advised me that Dr. W. Bousfield had worked on the taxonomy of Canadian amphipods and that he would be the best person to consult. Dr. Bousfield confirmed that this species was Orchomenopsis affinis (Holmes). Thus this name has been used in my thesis.

Experimental Animal Collection and Maintenance

Monospecific collections of Orchomenopsis affinis were obtained from the sampling station (225 m) in Saanich Inlet using cat food baited amphipod traps and amphipod bucket traps (Figs 2, 3). Amphipod bucket trap was constructed from a 20 litre plastic bucket fitted with hinged lid which with a bouyant rubber ring. The bucket would remain open when the buckets were stationary in the water. A piece of lead was put in the bottom of the bucket to keep it bottom down. A port near the bottom covered by nitex netting (500 um) allowed water to flow into the bucket facilitating sinking. The sampling time of the amphipod bucket trap was varied as required. When the bucket trap was hauled upwards, the door closed in response to water resistance. The traps (modified Niskin Sampler) used water soluble spheres (jaw-breakers) as an approximately 60 minute timer for door closing.

Captured amphipods were kept in a cooler chest and

returned to the University as soon as possible. They were maintained in aquaria with circulating sea water for a maximum of 10 days. If necessary they were fed with frozen sardines. All food was withheld 24 hours prior to experimentation.

Standard Conditions

For ease of experimentation, only one factor at a time was altered in the trials, with other external factors kept at constant conditions which were similar to its habitat conditions. Those conditions were called standard conditions. The standard conditions for my experiments are 9°C (temperature), 30°/oo (salinity) and total darkness. All laboratory experiments were carried out in the environmental chambers of the oceanography laboratory at the University of Victoria.

Sea Water

Experimental sea water was collected from a depth of 80 m in central Saanich Inlet. Water was filtered through 0.45 u MSI Microsep membrane filters and stored in the dark at 8.5°C. To reduce the activity of bacteria, experimental water was autoclaved at a temperature of 121°C for 30 minutes and returned to storage for at least 24 hours before use. Salinity and pH were checked and adjusted if necessary prior to each experiment.

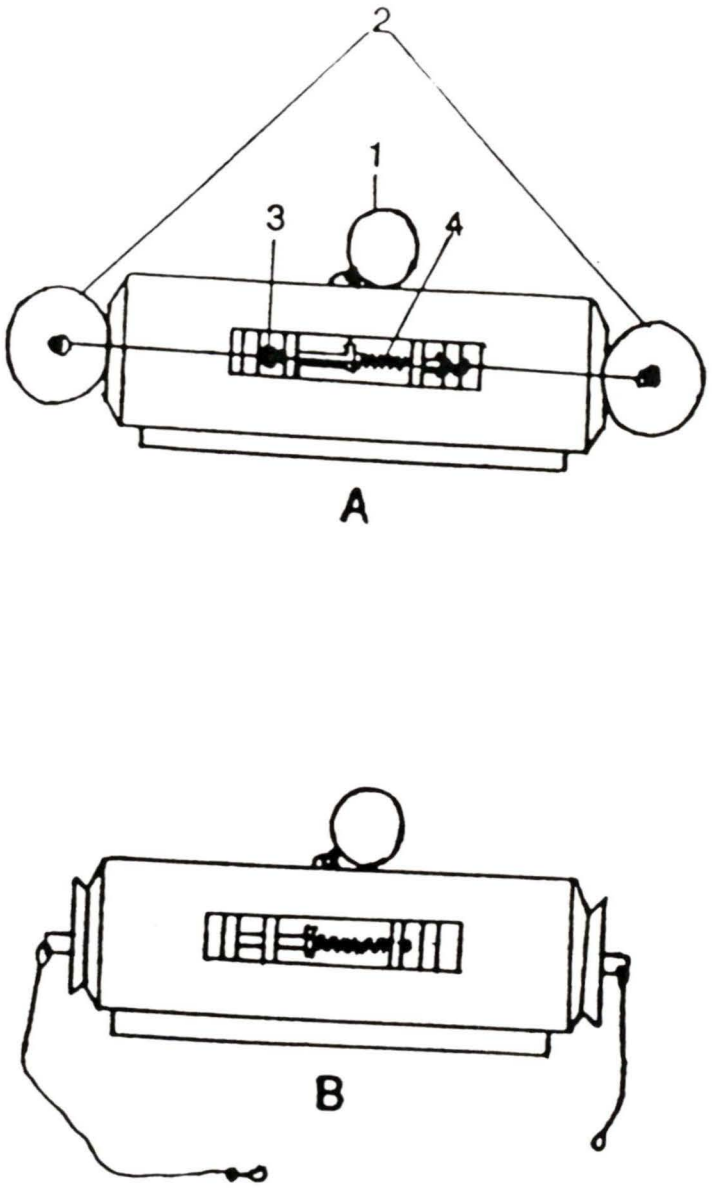

Figure 2. Amphipod traps. A: trap open. B: trap closed. 1, float. 2, stretched lids pulled tight by rubber tubing inside the cylinder. 3, water soluble sphere (jaw-breaker). 4, lid release spring.

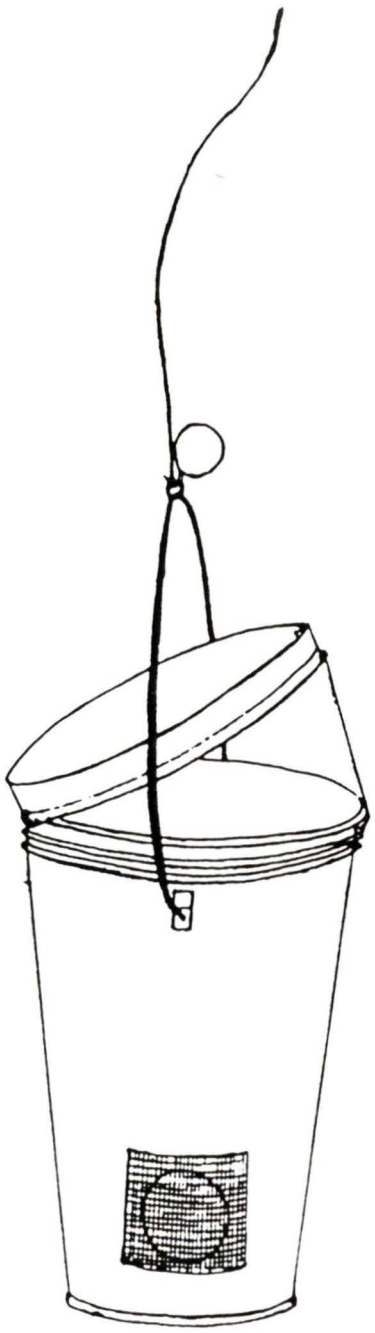

Figure 3. Amphipod bucket trap for amphipod collection and field experiments.

Dry Weight

Following each experiment, animals were removed from the media, rinsed quickly with distilled water, placed in a freezer at -20°C for 20 minutes and then freeze-dried for 24 hours prior to weighing on a Sartorius 2400 analytical balance. All weights unless stated otherwise are expressed as milligram (mg) dry weight.

Temperature

Experimental temperatures were controlled by water baths in the environmental room where room temperature was 1.0°C lower than the set temperature of the water bath. The temperature was recorded at the beginning and the end of each experiment. The variation of temperature was less than 0.2°C during any of the experiments.

Salinity

Salinity was adjusted by dilution with distilled water or by heated evaporation. Experimental salinities from 0 to 65°/oo in 5°/oo increments were produced in this way. Salinity was measured by Beckman RS7-C Induction Salinometer.

Oxygen

Dissolved oxygen gradients and oxygen-free seawater were made by bubbling purified nitrogen gas through the autoclaved sea water for a varying period. Oxygen content was monitored by a YSI Model 54 oxygen meter. The absolute

amount of dissolved oxygen was determined with a Winkler titration.

Since Winkler (1888) published his well-known method for the determination of dissolved oxygen in water, there have been many modifications of the classic Winkler procedure (Fox & Wingfield, 1938; Carpenter, 1965; Duval et al., 1976; Carritt & Carpenter, 1966; Strickland & Parsons, 1972; Bryan, et al., 1976; Chernyakova et al., 1982; Parsons et al., 1984). To get accurate analyses, it is necessary to keep the water sample out of contact with the air (Carpenter, 1965; Carritt & Carpenter, 1966). In order to insure minimum air contact, all sampling and reagent addition was by use of 60 ml B-D Plastipak syringes. These syringes are not airtight when supplied by the vendor. Air can enter into the syringe through the tip hole and/or through the rubber diaphragm of the plunger. Prior to use syringes were prepared as follows: The internal groove of the rubber diaphragm was filled with hypoxic water to serve as an airtight "buffer". Double layers of sheet parafilm sealed with the tip cap completed the preparation. Prior to sampling it was rinsed twice with sample water. Other procedures were the same as described by Parsons et al. (1984). A complete minimum oxygen contact respiration sampling and reagent addition device is shown in Figure 4. Syringes serve as respiration chamber, water sampler, and for reagent addition, all

within an oxygen-free closed system.

Oxygen measurements by oxygen meter are not as accurate as the Winkler method, but this method has the advantage of simple operation and continuous recording of the changing dissolved oxygen content in experimental containers (Omori & Ikeda, 1984).

Oxygen uptake rates were measured by using a battery powered YSI Model 54 oxygen meter (Gnaigen & Forstner, 1983) in conjunction with a specially designed respiration chamber (Fig. 5) consisting of a 268 ml plexiglass cell sealed by a lid fitted with an O-ring. A polarographic oxygen sensor with high sensitivity membrane was mounted into the side wall of the chamber. Water recirculation in the chamber was achieved by a magnetic bar stirrer. Nitex filters prevented blocking of ports and valves by experimental animals. Temperature was controlled with a circulating water jacket connected to a water bath by a peristaltic pump (Cole-Palmer Masterflex Pump Model 7020C).

Before and after each experiment, the meter was first calibrated with oxygen free autoclaved sea water, and then with oxygen saturated autoclaved sea water. To correct for oxygen electrode demand, a blank was run for one hour following the calibration.

A calibration correction value "K" was calculated to insure meter readings and titration were equal. Meter

readings were made while samples were taken for titration analysis. Least-squares regression analysis was performed on the data pairs from meter readings and titration values (Appendix Figure 1).

$$K = O_w/O_m$$

Where O_w is the value of dissolved oxygen from titration and O_m is from meter reading.

For experiments on the oxygen uptake of this species, thirty animals were incubated in the chamber under standard conditions. Samples for determination of oxygen were drawn in sequence using air-tight syringes. Animals were then rinsed quickly and frozen for later dry weight determination.

Calculation of Respiratory Rate

The following equation was used for calculation of respiratory rates:

$$R = 1000K(O_o-O_1)V/WT$$

R is respiratory rate (ug O_2/mg dry weigh/hour). K is as above. O_o and O_1 are the meter readings (mg/l) from control and experimental chamber respectively. V is the volume of the chamber (litre). W is dry weigh of experimental animals (mg) and T is incubation time (hour).

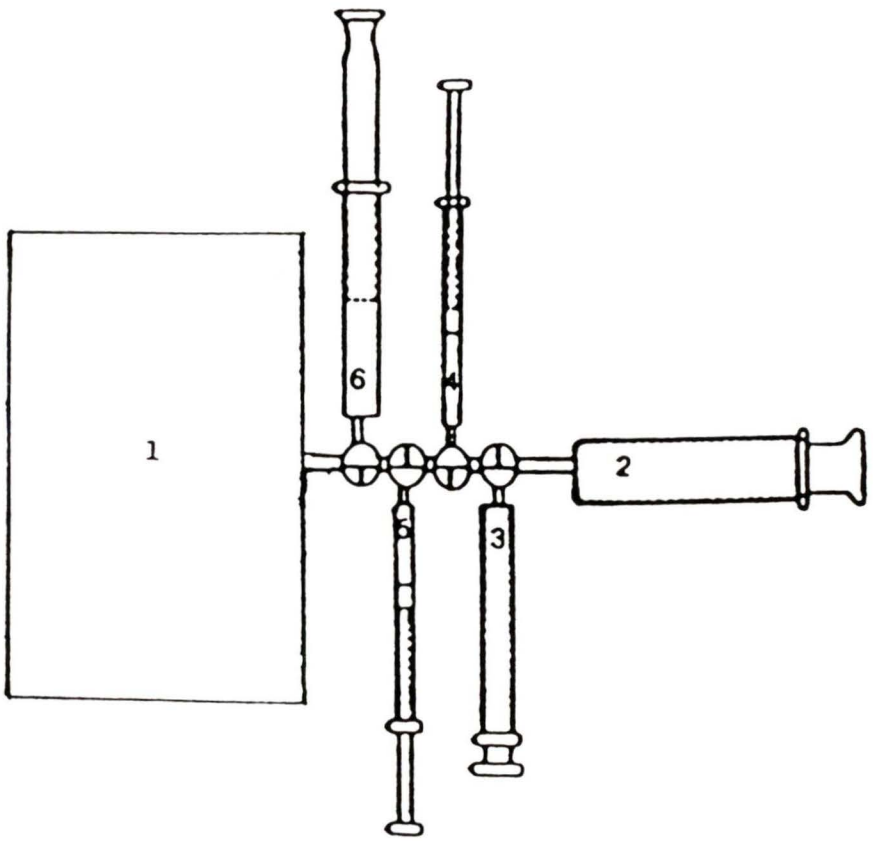

Figure 4. Diagram shows apparatus for sampling with minimum air contact sampling. Unit 1 connected to a respiration chamber or other containers, Syringe 2. for sampling. Syringe 4, 5 and 6 contain reagents. Syringe 3 is for collecting rinsed water from syringe 2.

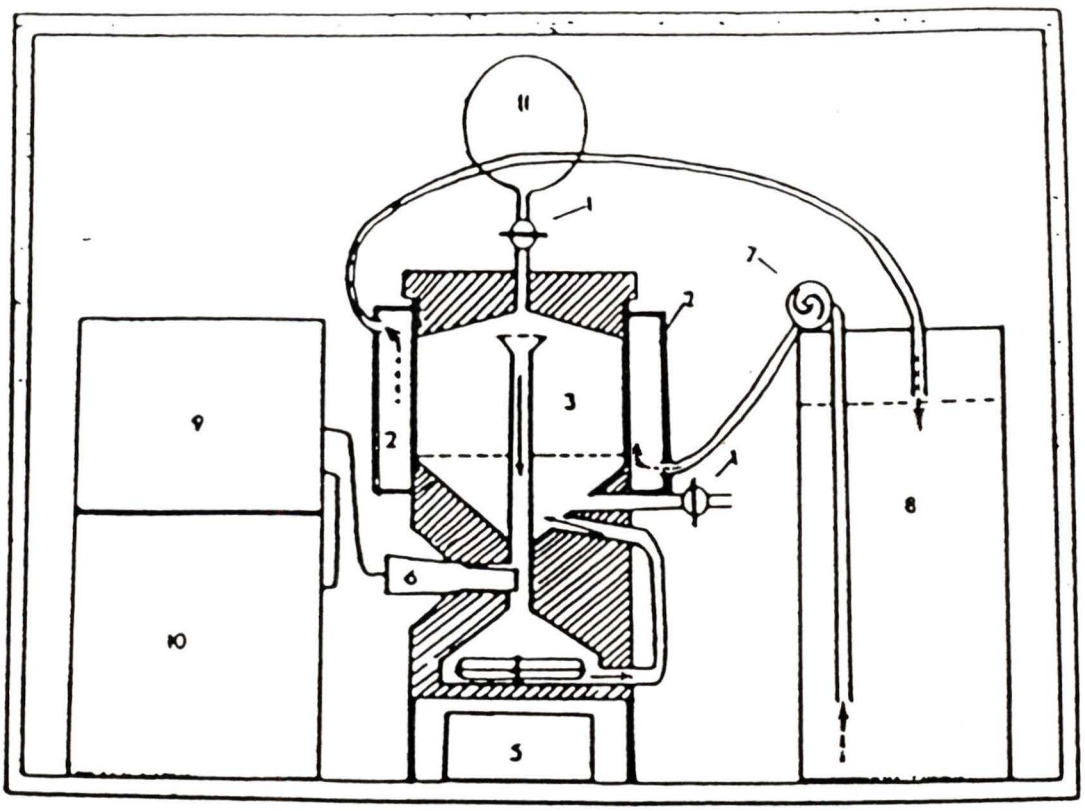

Figure 5. Diagrammatic cross-section of respiration chamber. Solid arrows indicate the direction of water circulation. Dashed arrows show the direction of temperature controlled water circulation. 1, valve. 2, water jacket. 3, respiration chamber. 4, magnetic spin bar. 5, synchronous motor. 6, oxygen probe. 7, pump. 8, temperature controlled water bath. 9, oxygen meter. 10, chart recorder. 11. nitrogen filled expansion chamber (balloon).

Oxygen Uptake after Anoxia

Thirty O. affinis were kept in a 500 ml airtight glass bottle filled with oxygen-free seawater for 10 hours and then transfered into the respiration chamber filled with oxygen satuated seawater and oxygen uptake of animals recorded by an oxygen meter.

Ammonia Determination

Ammonia was determined by the method developped by Riley (1953) and Solorzano (1969) and recommended by Strickland and Parsons (1972) and Parsons et al. (1984). Seawater is treated in an alkaline citrate medium with sodium hypochlorite and phenol in the presence of sodium nitroprusside which acts as a catalyzer. The blue indophenol color formed with ammonia is measured spectrophotometrically.

Sulfide

Sampling procedures were identical to those described for oxygen. Dissolved sulfide (H_2S, HS^-, S^{2-}) concentration was determined by the methylene blue method (Cline, 1969; Parsons, 1984) standardized by analytical grade sodium sulfide dissolved in oxygen-free seawater. Sulfide content of seawater was varied by the addition of analytical grade sodium sulfide to oxygen-free seawater.

Physiological Tolerance

Physiological tolerances of O. affinis to temperature, salinity, sulfide and anoxia were tested. Table 3. outlines the experiments.

Criterion of Death

Physiological tolerances are expressed in terms of the values of the experimental factors at which 50% of the specimens die within a chosen test period (LC_{50}) or mean time to death in a given environment (LT_{50}) (Omori & Ikeda, 1984). LC_{50} and LT_{50} were estimated graphically.

Table 3. PHYSIOLOGICAL TOLERANCE EXPERIMENTS. THREE REPLICATES FOR EACH TRIAL. N=NUMBER OF ANIMALS IN EACH TRIAL

FACTOR	RANGE	INCUBATOR	N
TEMPERATURE ^{o}C	-1-->25	250 ml jar	20
SALINITY $^{o}/oo$	0-->65	250 ml jar	20
SULFIDE mM	0-->4.0	60 ml syringe	10
OXYGEN mg/l	0-->10	268 ml chamber	30

Sprague (1963) used the inability to locomote after a recovery period of 24 hours under normal environmental conditions as the criterion of death for his experimental animal. Sprague's criterion was used in these experiments.

After tolerance testing, the amphipods were transferred to fresh oxygenated seawater, left in the environmental chamber for 24 hours, and percentage mortality determined.

Survival in Natural Anoxic Water

Hydrographic data from Saanich Inlet show that many environmental conditions are relatively constant. However, sulfide and dissolved oxygen levels have pronounced seasonal changes.

In order to compare laboratory experimental results with natural anoxia and sulfide toxicity, a field experiment was undertaken on April 3, 1987.

Ten Orchomenopsis affinis were put into each of 28 zooplankton cages (diameter 78 mm X 110 mm). Four cages were placed at each selected depth from 105 to 205 m. Temperature, salinity, dissolved oxygen and sulfide levels of the selected depths were determined. After 27 hours incubation, all of the cages were retrieved and the number of survivors counted. Animals were returned to a cooler chest filled with 50 m seawater and the number of survivors confirmed after 24 hours.

Respiratory and Excretory Rate Measurements

Five experimental animals were rinsed three times with autoclaved sea water and placed in a 60 cc syringe containing 55 cc autoclaved seawater. Three blanks and 6 to 13 replicates were done for each experiment. Experiments usually started at 9:00 am and continued for 4

hours. Respiratory rate is calculated using the following equation:

$$R = 1000(C_o - C_1)V/WT$$

Where V is the volume of the experimental containers (litre); T is the incubation time (hour); W is dry weight of animals (mg); R is respiratory rate (ug O_2/mg dry weight/hr) and C_o and C_1 are the dissolved oxygen content (mg O_2/l) in the control and in the experimental containers respectively.

Excretory rate is calculated with a similar equation:

$$E = 1000(E_1 - E_o)V/WT$$

Where E is excretory rate (ng-at N/mg dry weight/hr); E_1 and E_o are the ammonia-nitrogen content (ug-at N/l) in the experimental container and in the controls respectively. V, W, and T are the same as above.

Comparison with Other Hypoxia Tolerant Species

Neomysis rayii and Parathemisto pacifica were collected utilizing a Reeve net (Reeve 1981). Munida quadrispina was collected with a munida trap (Burd, 1983). Experiments were carried out with respiration chamber connected to the oxygen meter. The chamber was filled with

seawater with a dissolved oxygen content of 0.5 mg/l. Twenty each of Neomysis rayii and Parathemisto pacifica and 3 of Munida quadrispina were incubated in the same chamber. The activity and survival time noted. This experiment was repeated twice.

Activity Rhythm and Vertical Migration

Field Surveys

Net Observations: A Bogorov closing net (mesh opening 330 um) was used in a vertical haul mode to sample discrete depth intervals. Haul speed was kept constant at about one meter per second. In order to reduce the disturbance of the water column, samples were taken from surface to bottom (210 m) in following orders: 25 to 0, 50 to 25, 75 to 50, 125 to 75, 175 to 125 and deeper depths (210 to 175 m) were sampled on occasion. The net was washed down with sea water after every tow and samples were preserved in buffered 5% formalin.

Submersible Observations: Pisces IV submersible operated by the Institute of Ocean Sciences, Sidney, British Columbia, was used for underwater observations. Photographs were taken through the observation windows by hand held camera. Quantitative estimates were aided by a 50 cm x 50 cm frame fixed to the front of the submersible. Counts and behaviour notes were taken by observers using tape recorders.

Laboratory Protocol

Zooplankton Column: A plexiglass column (diameter 80 mm x 156 mm) filled with filtered, bubble free seawater was used for observation of the diel activity patterns of O. affinis.

Freshly collected adult O. affinis were kept at 9°C under darkness in a walk-in environmental room for 24 hours before experimentation. Fifty animals were then transferred into the column and the number of animals swimming in the water column was counted hourly by direct observations with a flashlight equipped with a deep red lamp. Experiment 1 was implemented from noon of March 29, 1987 to midnight of March 31, 1987 and experiment 2 from 1:00 am April 4, 1987 to midnight of April 5, 1987.

Feeding Behaviour

Laboratory Experiments

Response to Food: Animals starved for two days were placed in 3 identical aquaria. A piece of sardine was gently dropped into a corner when there were no animals nearby and search and feeding responses noted.

Feeding Rate: Maximum feeding rates were estimated from the weight change during feeding. Six hundred similarly sized animals starved for one week were divided into two aliquots. Three hundred animals were frozen for dry weight determination. The other 300 animals which were allowed to

feed for two hours on 10 g wet weight of sardine in a seawater aquarium, removed and frozen for determination of dry weight. This experiment was repeated twice.

Field Methods

Trap Observations: To test my hypothesis that O. affinis feeds at the sediment-water interface under oxygen depleted conditions, baited amphipod bucket traps were set from depths of 225 m or 200 m (bottom) to 25 m in 25 meter intervals for 1 hour, returned to the surface and the number of animals in each bucket counted.

In order to investigate if this species could use mechanoreceptors to receive feeding vibrations from individuals which had been feeding on the food source, in situ tests were carried out. About 5 g of fish remains were put into each of 12 heat sealed plastic sandwich bags filled with filtered sea water. Ten O. affinis each were added to 6 of these bags and all the bags were sealed with a heat sealer. Each bag was placed in an amphipod bucket trap and all lowered to the seafloor for 1.5 hours. Buckets were then retrieved and animal numbers counted.

Predation

Twenty O. affinis starved for two days were put into each of three aquaria under standard conditions. Twenty live Calanus plumchrus and 5 frozen Calanus plumchrus were added to each aquarium. Numbers of copepods were counted once a day for 6 days.

To compare the escape capacity of O. affinis with other amphipods, Ten each of three similar size local amphipod species; Parathemisto pacifica, Cyphocaris challengeri and O. affinis, were placed in the same aquarium and then two university aquatic unit cultured young coho salmon, Oncorhynchus kisutch were introduced to the aqurium. Numbers of amphipods were counted every two hours until all O. affinis disappeared from the aquarium.

RESULTS

Habitat

Annual temperature cycles in the top 150 m of the water column are shown in Figure 6. Temperatures fluctuated less below 100 m, and were almost constant at 9.28°C below 150 m thoughout the year. The annual temperature range at selected depths decreased with increasing depth (Table 4).

Table 4. ANNUAL TEMPERATURE RANGES AT SELECTED DEPTHS

DEPTH m	0	10	30	50	100	150	200
RANGE °C	9.11	4.59	3.14	2.41	0.82	0.02	0.03

The annual salinity range of surface water was much more variable than that of deeper water (Fig. 7). Fluctuating between 19.23°/oo and 30.14°/oo. Lowest salinity in surface water occurred in February. Salinities were relatively homogeneous throughout the water column in November with a difference of 1.19°/oo between surface and bottom waters. Salinities were relatively constant below 50 m during the study period. Salinity of the deep-water is higher than that of surface water.

Dissolved oxygen content decreased with increasing depth (Fig. 8) except between August and November when oxygen increased in bottom waters below a mid depth oxygen minimum zone. Oxygen content had a clear annual cycle at every depth. From March to December, the dissolved oxygen content was less than 2.0 mg/l below 100 m. Anoxic conditions were commonly found below 150 m.

Sulfide concentrations increased and extended upwards with time from February to September (Fig 9). Detectable sulfide was found as shallow as 125 m and values as high as 36 uM sulfide were found in bottom waters in March. Sulfide could be rarely detected in the bottom water from late July to early January. However, a sulfide value of 20 uM was found at depth of 150 m from August to October.

Figures 10 and 11 illustrate the development of sulfide conditions and the corresponding depletion of oxygen.

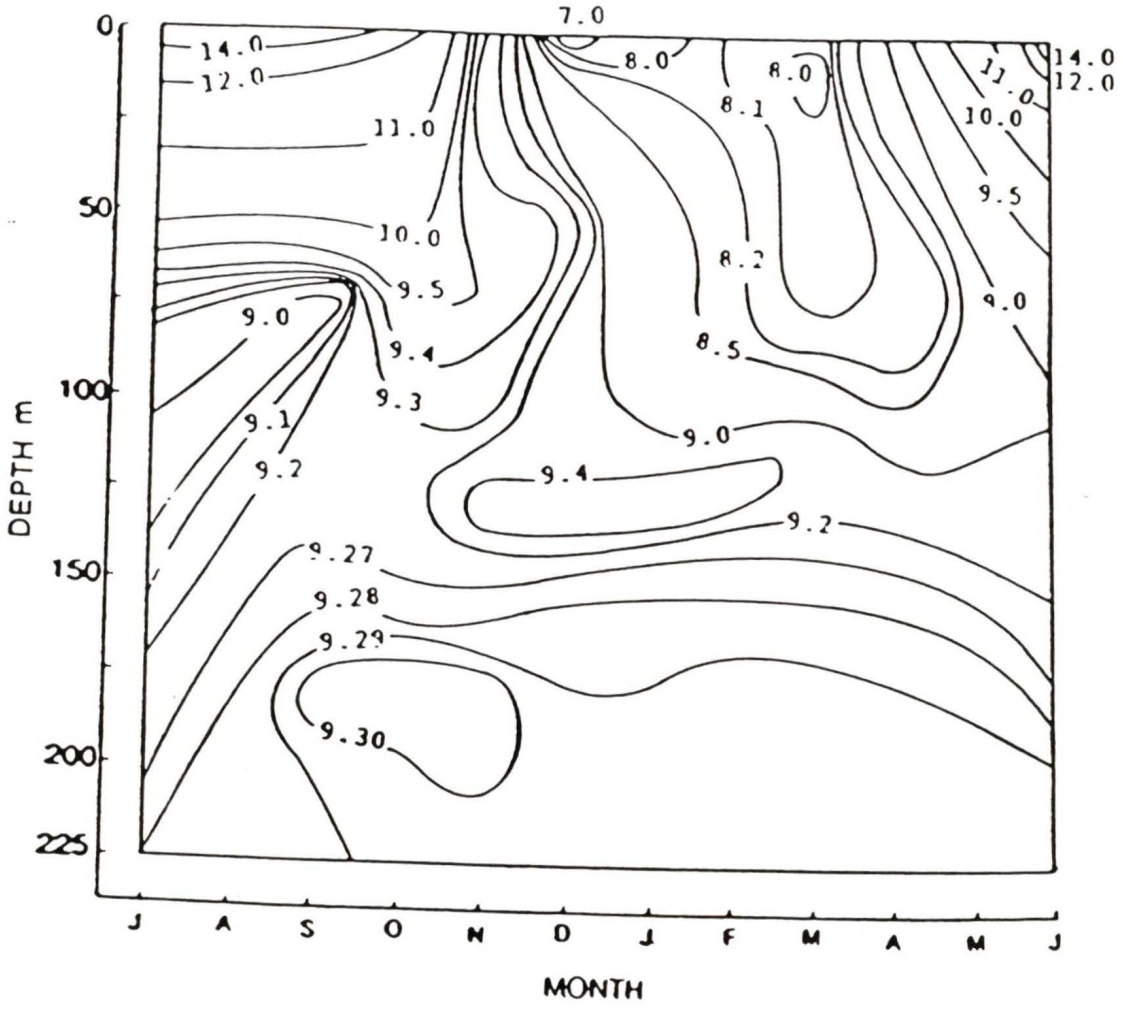

Figure 6. Seasonal cycle of temperature at six depths from July, 1986 to June, 1987. Appendix Table 1 shows sampling dates, data and depths.

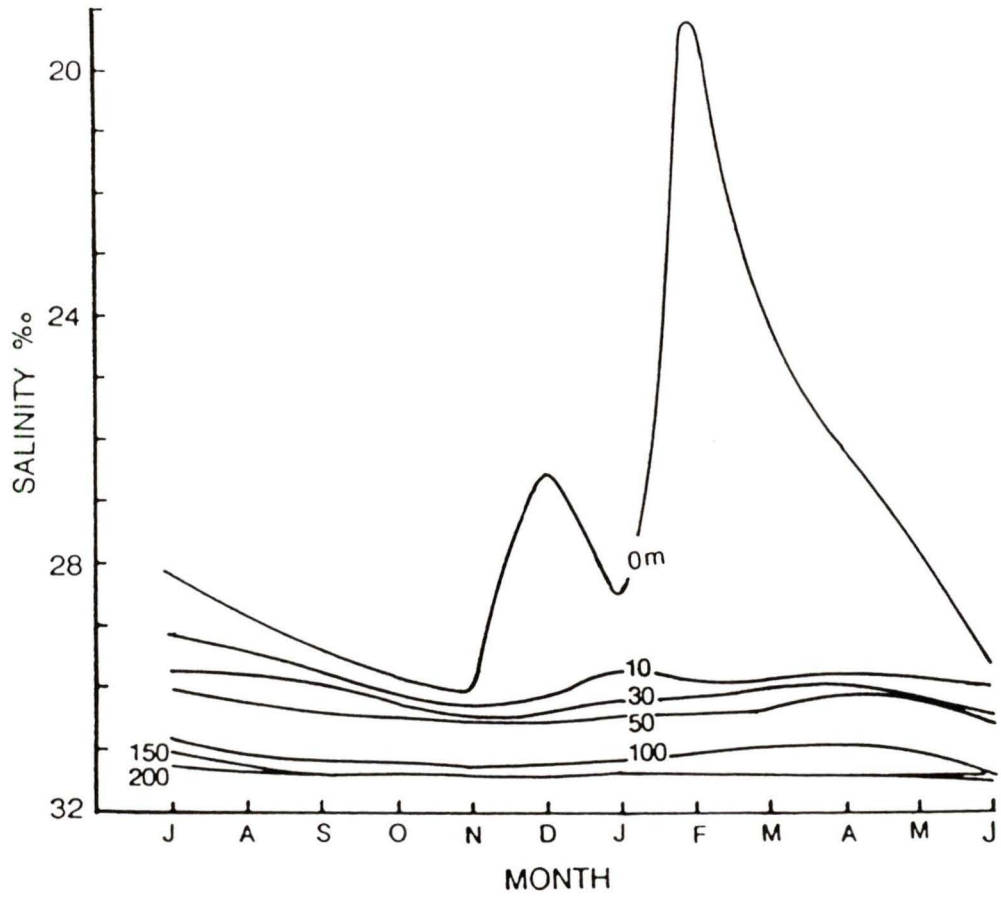

Figure 7. Seasonal cycle of salinity at seven depths from July, 1986 to June, 1987. Appendix Table 2 shows the sampling dates, depths and data.

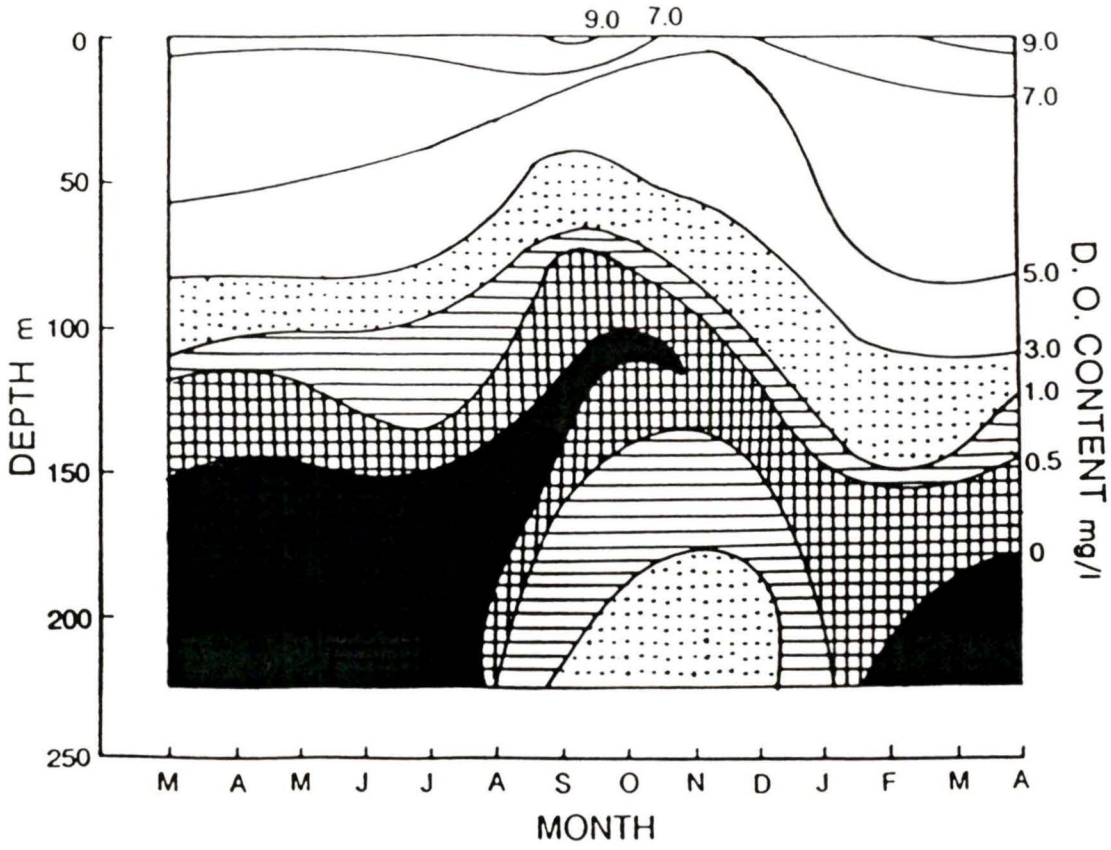

Figure 8. Dissolved oxygen contents in mg O_2/l from March 1986 to April 1987 in Saanich Inlet. Black area indicates anoxic zone. Data are shown in Appendix Table 3.

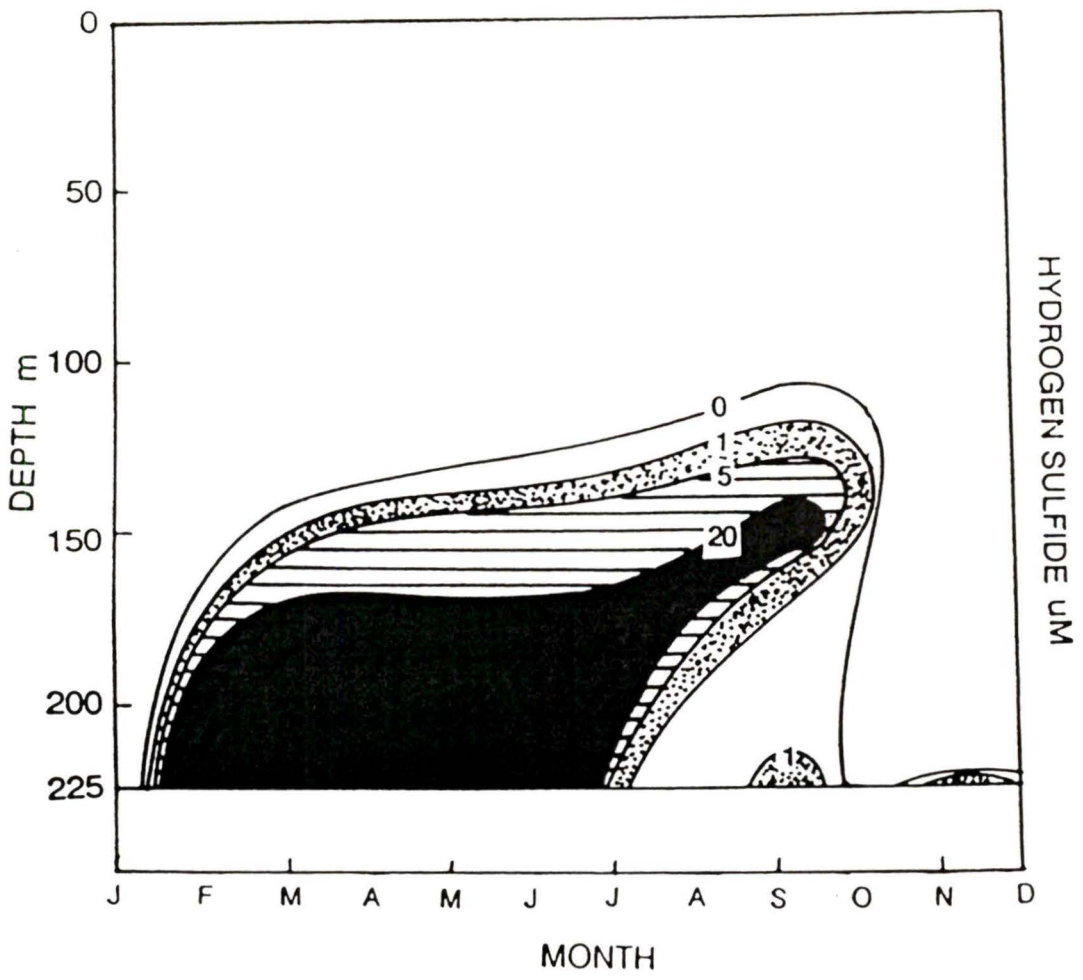

Figure 9. Profiles of hydrogen sulfide in Saanich Inlet in 1986. Black area indicates sulfide concentration greater than 20 uM (Appendix Table 4).

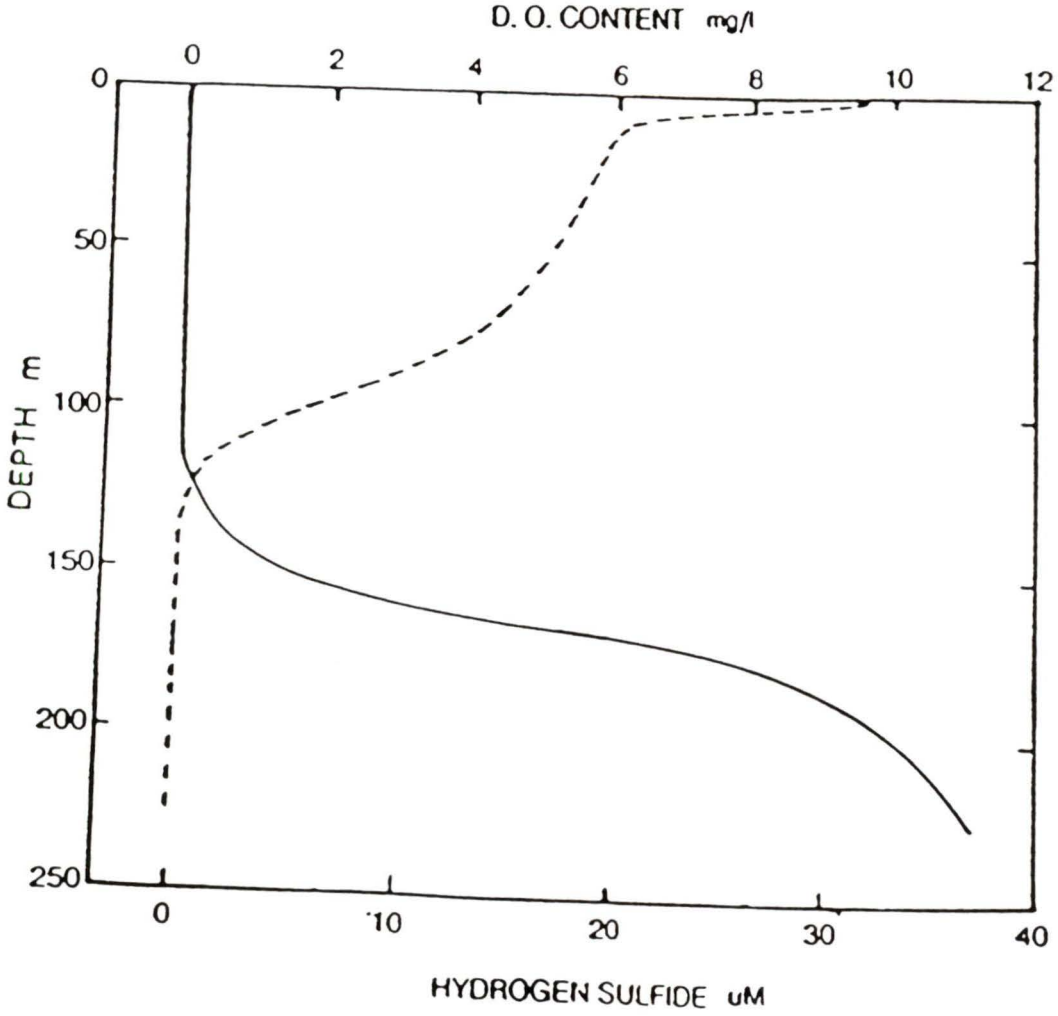

Figure 10. Distribution of sulfide (solid line) and dissolved oxygen (dashed line) in Saanich Inlet on March 15, 1986 (Appendix Table 5).

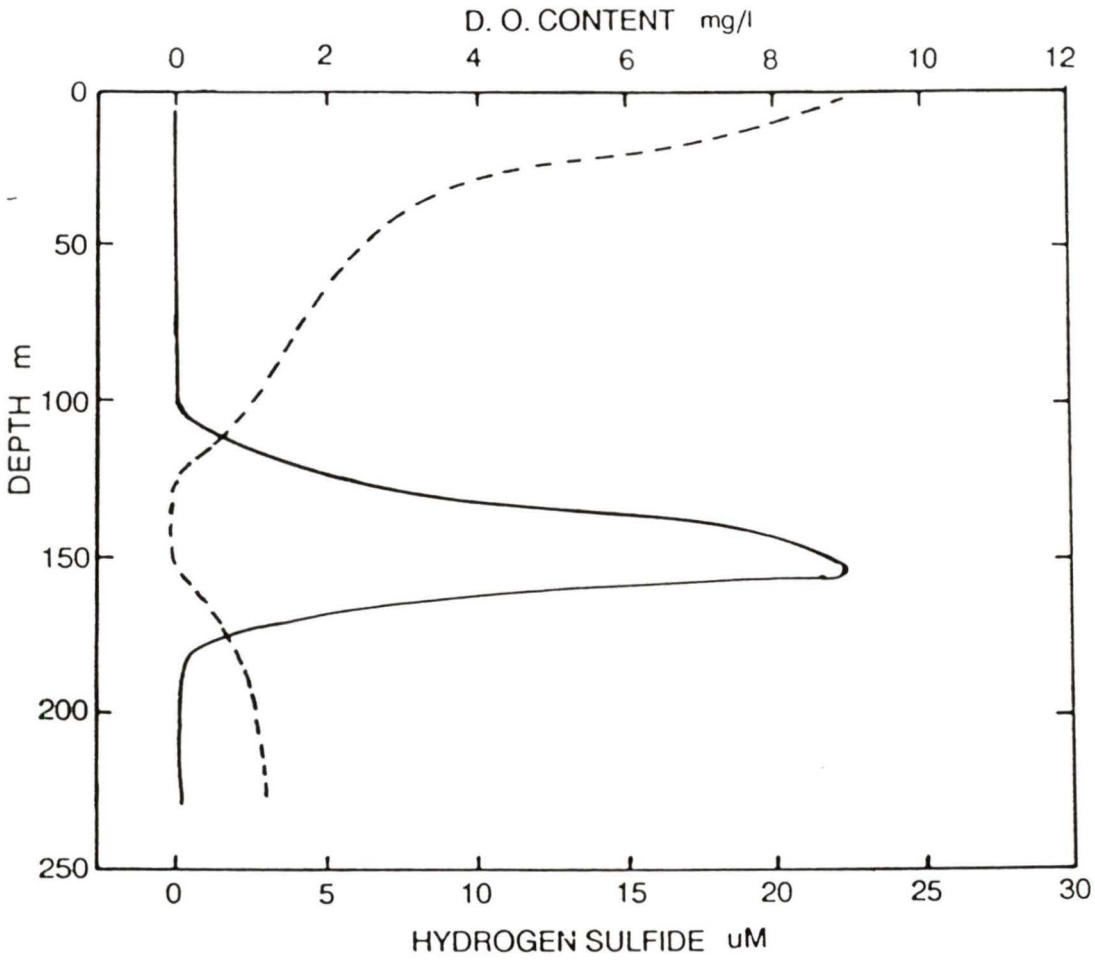

Figure 11. Distribution of sulfide (solid line) and dissolved oxygen (dashed line) in Saanich Inlet on September 15, 1986 (Appendix Table 6).

Physiological Tolerances

Temperature

Orchomenopsis affinis was tested under temperature range from -1 to 25°C. Temperature tolerance range of Orchomenopsis affinis is from 0 to 19°C under a salinity of 30°/oo. When the temperature was lower than 8°C, animals markedly reduced their swimming activity.

O. affinis swam rapidly when temperatures were higher than 13°C and died within 4 hours at 20°C (Table 5).

TABLE 5. SURVIVAL RATES OF O. AFFINIS UNDER DIFFERENT TEMPERATURES FOR 24 HOURS. THREE REPLICATES OF 20 ANIMALS FOR EACH TRIAL

TEMPERATURE °C	SURVIVAL RATES %
-1	0
0	63
1	100
5	100
9	100
13	100
17	100
18	100
19	100
20	23
21	0
25	0

Salinity

O. affinis could survive for at least 10 days in the salinity range from 20°/oo to 50°/oo. Animals died within

four hours when they were transferred into water where salinity was lower than 5°/oo. However, they could survive for 14 hours under the salinity of 10°/oo. When the salinity was lower than 10°/oo, some lipid-like material was ejected from the animal's mouth.

TABLE 6. LT_{50} AND RECOVERY RATES OF O. AFFINIS ON SALINITY TOLERANCE EXPERIMENTS

SALINITY °/oo	LT_{50} (hr)	% RECOVERY
0	0.57±0.03	0.0±0.0
5	4.17±0.67	0.0±0.0
10	13.93±4.62	0.0±0.0
15	36.50±1.50	55.0±5.0
20	DND	100.0±0.0
30	DND	100.0±0.0
40	DND	100.0±0.0
50	DND	100.0±0.0
55	19.47±1.96	74.3±13.5
60	9.73±0.46	80.0±4.4
65	3.33±0.25	56.7±16.1

DND: did not die in an incubation period of 10 days.

In order to investigate the survival capability of the animals incubated in various salinities, surviving animals were transferred into normal seawater (30°/oo) as

soon as half of the animals died. Table 6 shows the results after 24 hours recovery. Higher long-term survival rates were achieved at the higher salinities. No animals survived when they had been incubated in water with salinities lower than 10°/oo.

Sulfide

The effects of sulfide on the survival of O. affinis were measured after exposure to different concentrations of sulfide for 24 hours. Results are given in Table 7. Sulfide levels of 0.5 mM were tolerated with no apparent adverse effects.

TABLE 7. PERCENTAGE SURVIVAL OF ORCHOMENOPSIS AFFINIS IN DIFFERENT CONCENTRATIONS OF SULFIDE FOR 24 HOURS. THREE REPLICATES OF 20 ANIMALS FOR EACH TRIAL

CONCENTRATION mM	PERCENTAGE SURVIVAL
0.05	100.0
0.10	100.0
0.50	100.0
1.00	97.0
2.00	90.0
3.00	83.0
4.00	70.0

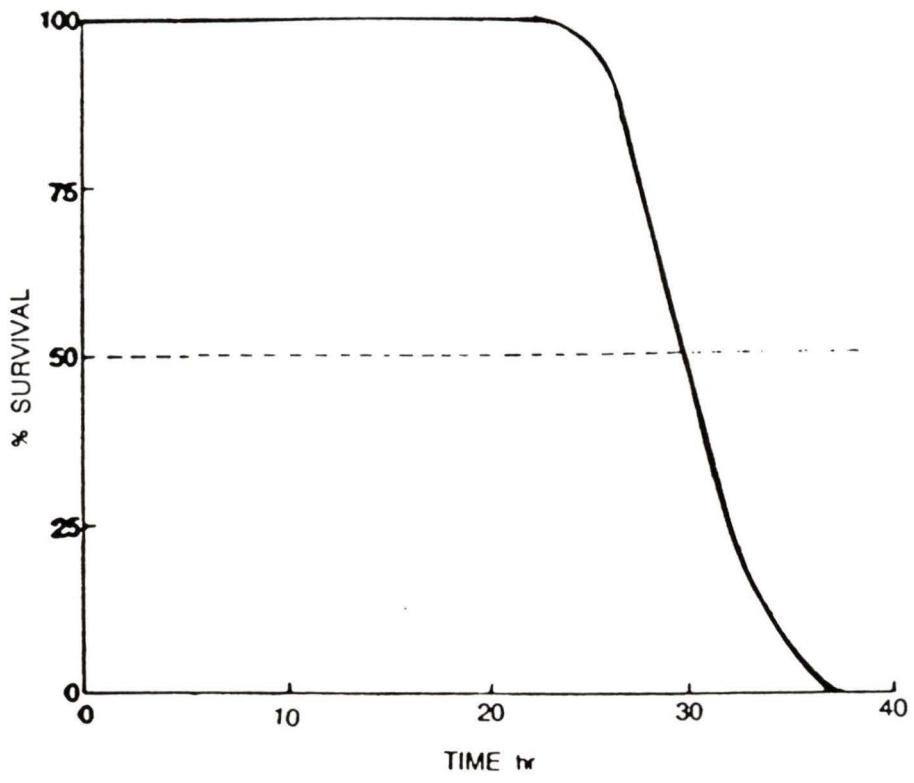

Figure 12. Survival time and survival rate of Orchomenopsis affinis under anoxic condition (Appendix Table 7).

Anoxia

Laboratory experiments indicated that this animal could survive anoxia for at least 25 hours. The LT_{50} was reached after 30 hours of anoxia (Fig. 12).

In order to confirm the results of anoxic tolerance obtained from laboratory experiments, a field test was carried out. Results are shown in Table 8.

TABLE 8. FIELD TEST ON SURVIVAL RATES OF ORCHOMENOPSIS AFFINIS UNDER OXYGEN DEFICIENT CONDITIONS FOR 27 HOURS. FOUR REPLICATES FOR EACH TRIAL

DEPTH m	D. O. mg/l	H_2S uM	% SURVIVAL
105	1.2	0.0	100
125	0.8	0.0	100
145	0.3	0.0	100
165	0.1	0.0	30
185	0.0	6.8	10
195	0.0	10.4	25
205	0.0	36.2	35

In situ test results showed that some O. affinis can tolerate anoxic conditions for more than 25 hours. O. affinis shows 100% survival under oxygen concentration as low as 0.3 mg/l. Percentage survival decreased with decreasing oxygen. However percentage survival gradually

increased with increase in sulfide concentration.

In comparison with some other crustaceans known to frequent anoxic zone in Saanich Inlet, O. affinis could survive anoxia much longer than others tested (Table 9).

TABLE 9. TOTAL SURVIVAL TIME TO INITIAL DEATH OF O. AFFINIS AND THREE OTHER CRUSTACEANS UNDER ANOXIA. THREE REPLICATES FOR EACH TRIAL

SPECIES	TIME hr
Orchomenopsis affinis	25
Munida quadrispina	18
Neomysis rayii	5
Parathemisto pacifica	4

Influences of Environmental Factors on Respiration and Excretion

Temperature

Experimental results show that respiratory rates were very sensitive to temperature changes. Respiratory rates increased with increasing temperature (Fig. 13; Table 10) with a Q_{10} of 1.8 between 5 and 13°C and 3.6 between 13 and 18°C. The average Q_{10} over the entire range tested from 5 to 18°C was 2.4. The ammonia excretory rates closely paralleled respiratory rates (Fig. 13) with a correlation coefficient of 0.876.

TABLE 10. EFFECT OF TEMPERATURE ON THE METABOLIC RATES OF O. AFFINIS (means±SD). SIX REPLICATES OF FIVE ANIMALS FOR EACH TRIAL

TEMPERATURE °C	AMMONIA EXCRETION ng/mg/h	OXYGEN UPTAKE ug/mg/h
5	0.434±0.082	0.478±0.060
9	0.484±0.093	0.630±0.122
13	0.810±0.132	0.767±0.117
15	0.911±0.161	1.070±0.216
18	2.574±0.222	1.460±0.276

Salinity

The respiratory rates of O. affinis were altered by extreme salinity changes in a constant temperature regime. Within the range of 30 to 45°/oo oxygen uptake averaged 0.575 ug/mg/h with little variability (Fig. 14). At a salinity of 20°/oo this nearly doubled to 0.951 ug/mg/h.

TABLE 11. EFFECT OF SALINITY ON THE METABOLIC RATES OF ORCHOMENOPSIS AFFINIS (means±SD). SIX REPLICATES OF FIVE ANIMALS FOR EACH TRIAL

SALINITY °/oo	OXYGEN UPTAKE ug/mg/h	AMMONIA EXCRETION ng/mg/h
15	0.597±0.111	4.128±0.327
20	0.951±0.118	7.516±0.837
25	0.803±0.105	5.299±0.946
30	0.597±0.057	1.964±0.986
35	0.585±0.112	1.847±0.497
40	0.570±0.089	1.250±0.233
45	0.549±0.049	0.618±0.102
50	0.369±0.163	0.416±0.125

Depression of oxygen uptake rates occured at salinities less than 20°/oo and higher than 45°/oo. This change in metabolic rate with salinity was reflected in ammonia excretory rates (Fig. 14; Table 11) with a correlation

coefficient between oxygen uptake and ammonia excretion of 0.966.

Diel Respiration Rhythm

Evidence (Fig. 15) also showed that respiratory rates of this species had a distinctly diel rhythm. Respiratory rates of this species always reached a peak around midnight and the lowest rates were found around noon. The ratio of respiration between midnight and noon is about 3.

Feeding Condition and Ratios of O:N

Results of the ratios of O:N are shown in Table 12. Oxygen uptake ranged from 30.97 to 52.09 ng-at O_2/mg/h; ammonia excretion varied from 1.03 to 3.31 ng-at N/mg/h.

The atomic ratios of oxygen uptake to nitrogen excretion (O:N) were affected by the feeding condition of animals (Table 12). Immediately after feeding, the O:N ratio was lower than that of starved animals.

Dissolved Oxygen

Respiratory rates of O. affinis were constant under dissolved oxygen levels of 0.5 mg/l to 10.0 mg/l. Respiratory rates decreased quickly when dissolved oxygen content was lower than 0.5 mg/l. However, the average respiratory rates of this animal at night were twice as high as those during daylight hours(Figure 16).

TABLE 12. OXYGEN UPTAKE, AMMONIA EXCRETION AND O:N RATIOS OF O. AFFINIS UNDER DIFFERENT FEEDING COMDITIONS (values are means±SD, n=number of replicate, hour=hours after feeding)

NO	HOUR	n	OXYGEN UPTAKE ng-at O_2/mg/h	AMMONIA ng-at N/mg/h	O:N	MEAN
1	4	13	52.09±4.80	3.31±0.77	15.74	
2	4	12	36.84±5.32	2.35±0.44	15.68	15.71
3	12	10	30.97±6.41	1.45±0.20	21.36	
4	12	6	36.77±3.38	1.75±0.32	20.01	20.69
5	72	10	43.24±12.16	1.03±0.43	41.98	
6	72	10	57.51±22.01	1.46±0.15	39.39	
7	72	6	41.89±6.07	1.15±0.48	36.43	39.27

Oxygen Uptake after Anoxia

Table 13 shows the change observed with time in respiratory rates in oxygen saturated sea water after O. affinis is maintained under anoxic conditions for 10 hours. Respiratory rate reached a peak about 10 minutes after recovery in the oxygen saturated sea water.

TABLE 13. OXYGEN UPTAKE OF ORCHOMENOPSIS AFFINIS IN OXYGEN SATURATED SEAWATER AFTER 10 HOURS ANOXIA

TIME (hr)	0	0.2	1.5	3.5	6.5	10.5
RESPIRATION ug/mg/hr	0.0	6.23	1.18	0.91	0.38	0.32

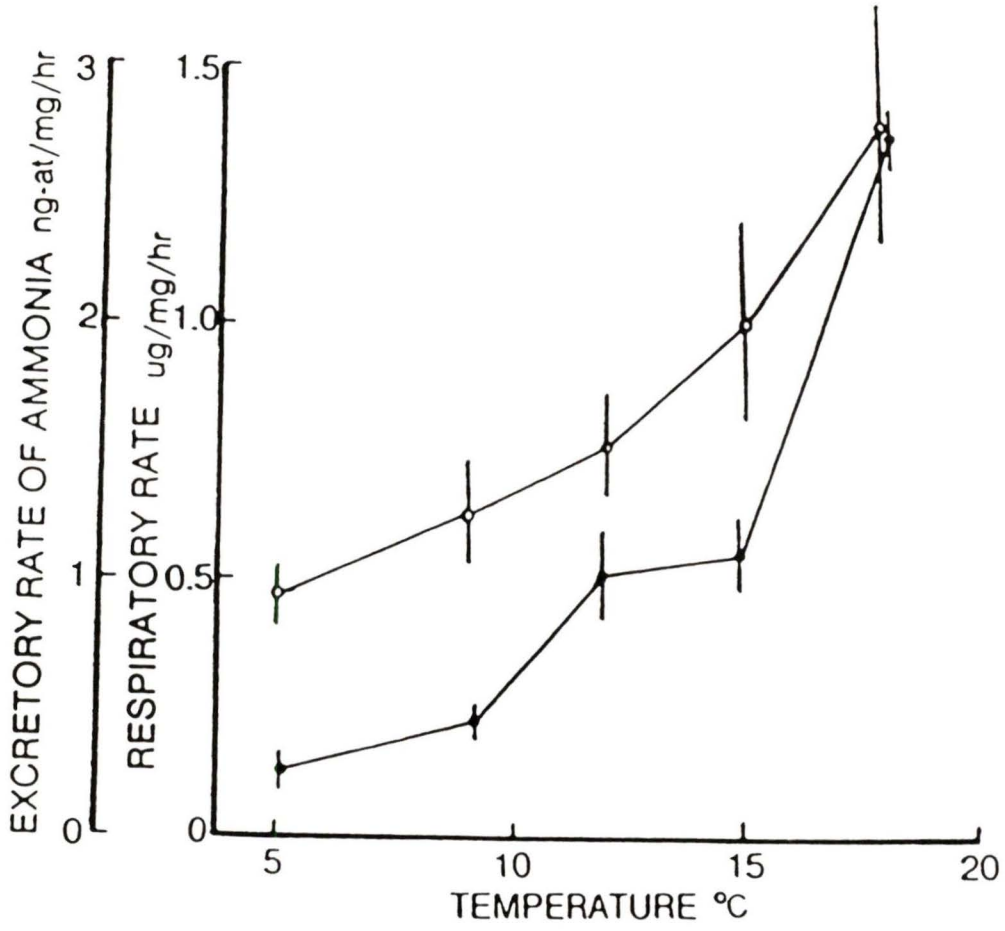

Figure 13. Effects of temperature on the respiratory rates (means ± SD, n=6) of Orchomenopsis affinis. Circles indicate respiratory rates, Solid circles are excretory rates of ammonia.

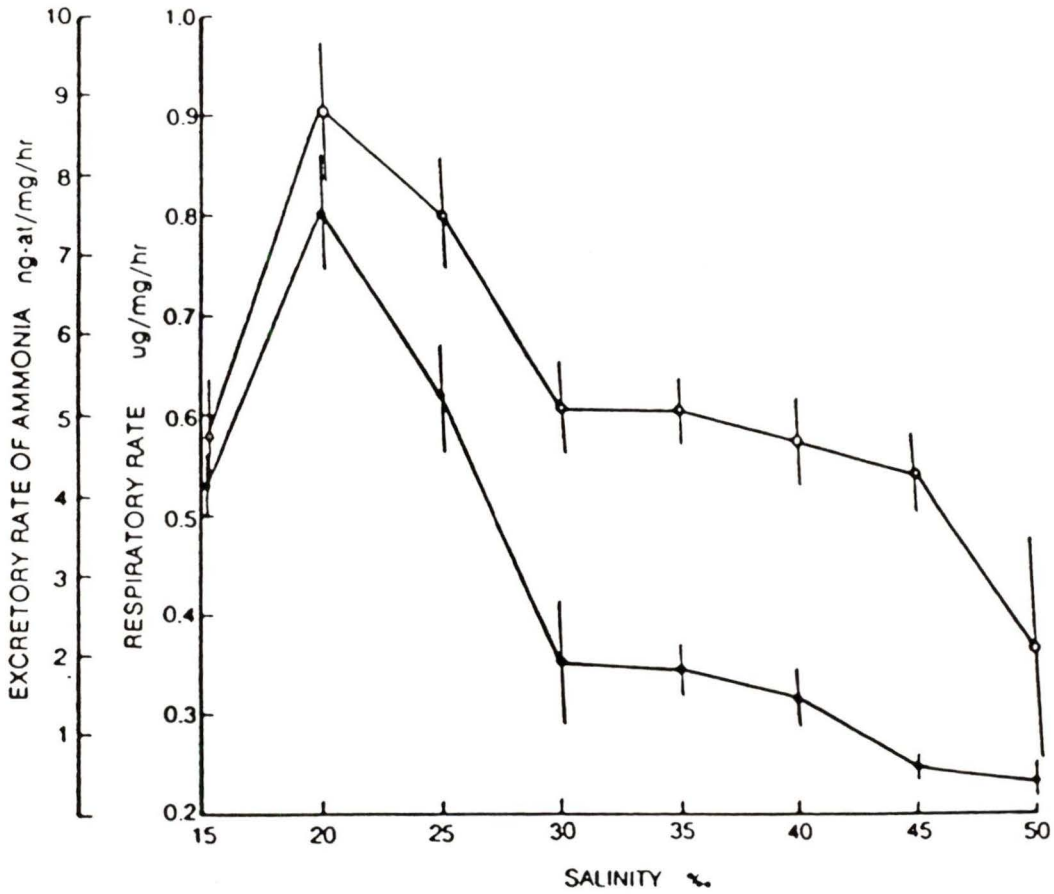

Figure 14. Effect of salinity on the respiratory rates (n=6, means±SD) of Orchomenopsis affinis. Open circles: respiratory rates; solid circles: excretory rates of ammonia.

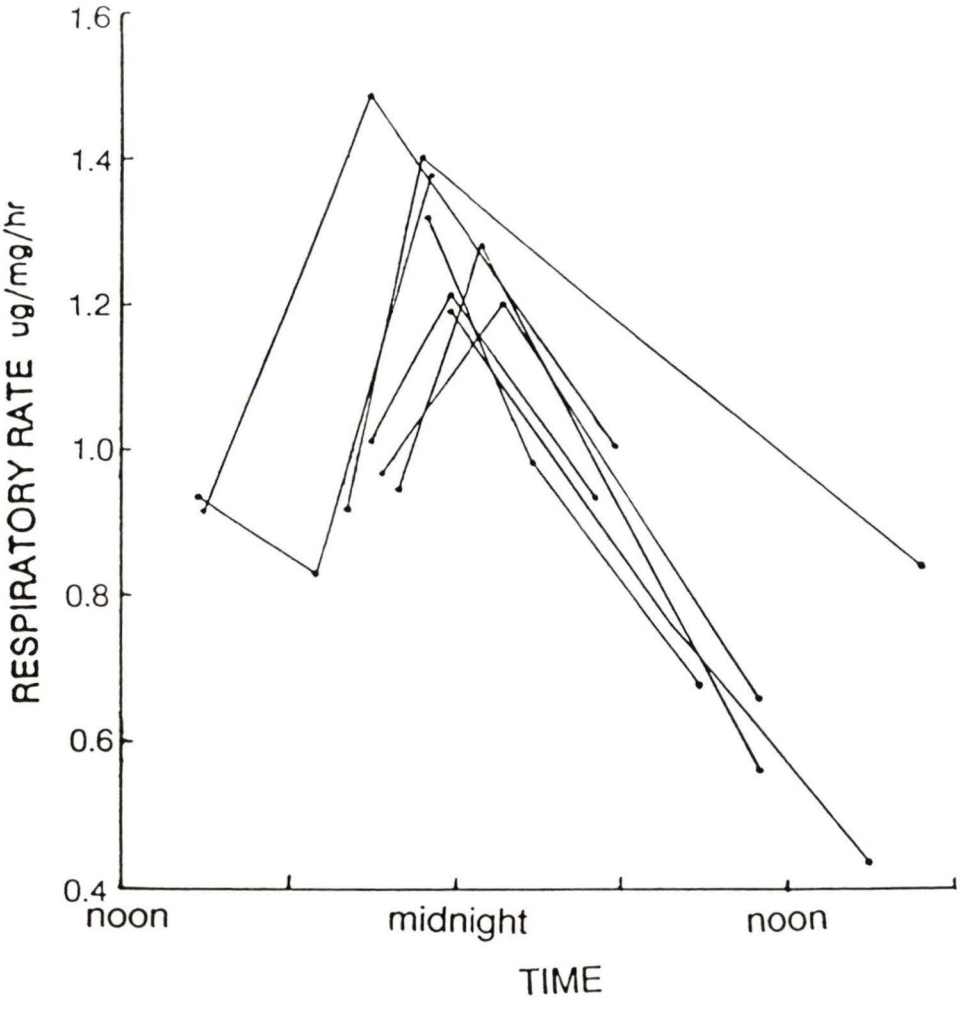

Figure 15. Diurnal changes of respiratory rates and activities (Appendix Table 8).

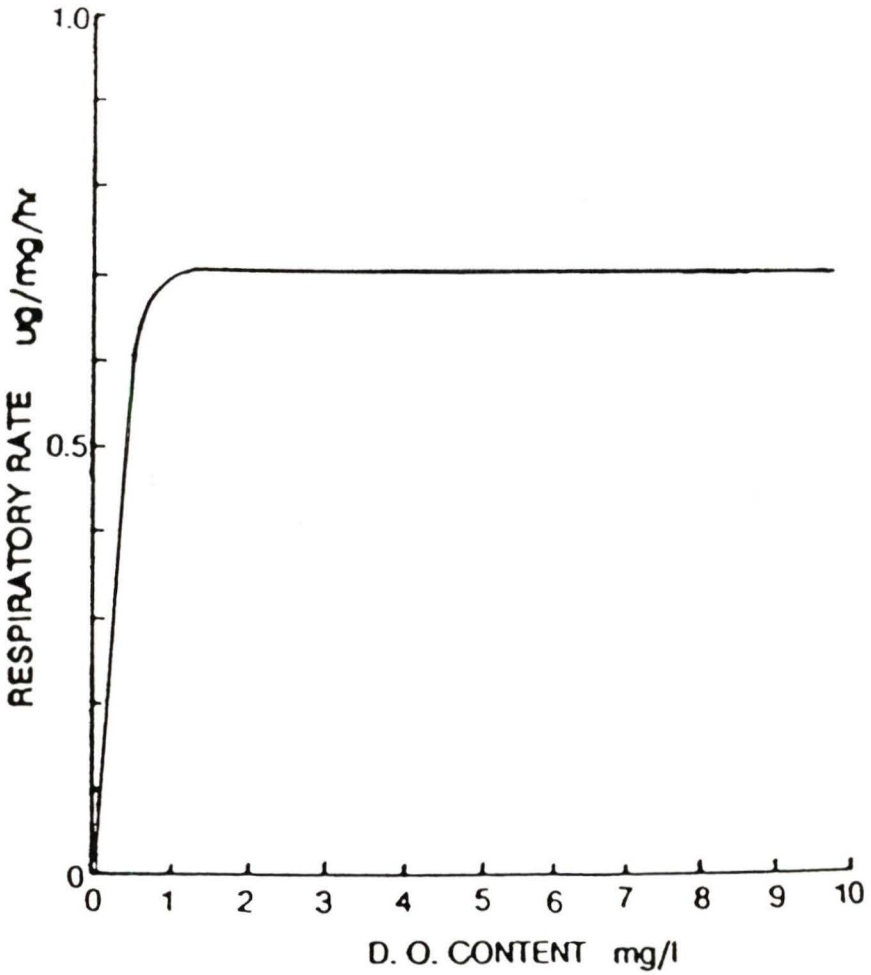

Figure 16. Respiratory rates of O. affinis under different oxygen levels (Appendix Table 9).

Activity Patterns and Vertical Migration

Diel Vertical Distribution

Bogorov net amphipod capture data are shown in Table 14 and Figure 17. At dawn, the distribution centre of the "swimming population" was close to the seafloor. Subsequently, the distribution centre moved upwards to a depth of 75-125 m and remained there from noon to midnight.

Results from submersible observations indicate that the highest population density of O. affinis is on or near the seafloor. On average, there were about 16 individuals per square meter on the seafloor and 3 individuals per cubic meter in the water column within 15 m from the bottom. Based on net and submersible data, it is estimated that the total biomass of O. affinis for the whole water column is 510 mg/m^2.

The combination of data from submersible observations and sampling with zooplankton nets resulted in a modification of the vertical distribution as shown in Figure 18 and Table 15. Maximum uniformity in vertical distribution was found at midnight, in contrast at dawn nearly the entire population was found in bottom water. However two distribution centres were found at noon and dusk; one was on or near the seafloor, the other was in the oxygenated layer.

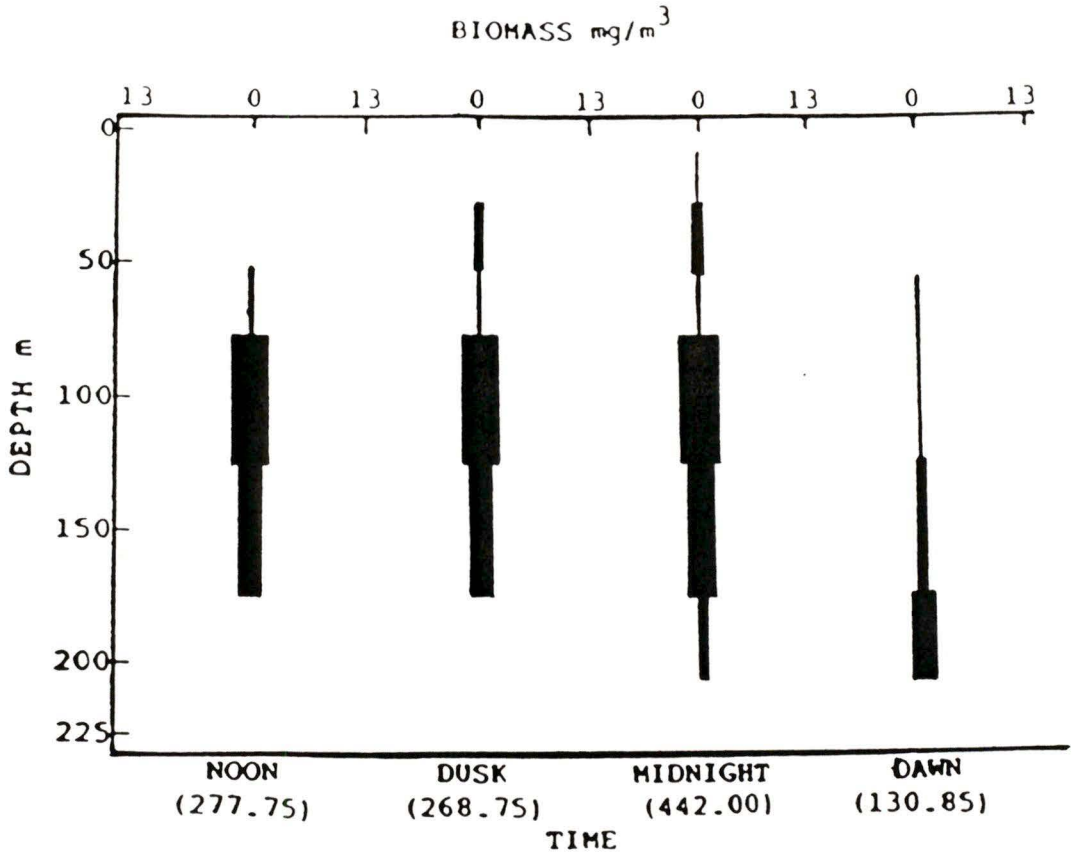

Figure 17. Vertical distrution of O. affinis in Saanich Inlet based on the data from zooplankton net sampling.

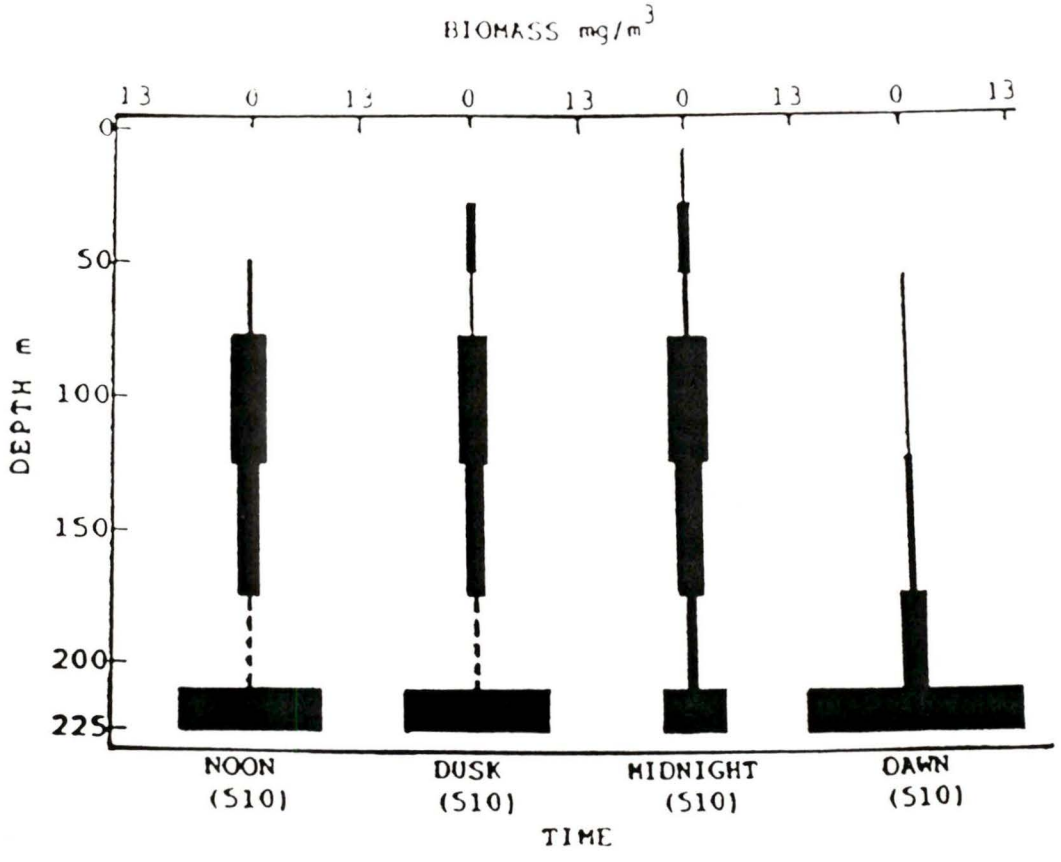

Figure 18. Vertical distribution of Orchomenopsis affinis in Saanich Inlet based on the results from both submersible observation and net sampling.

TABLE 14. VERTICAL DISTRIBUTION OF O. AFFINIS IN SAANICH INLET ACCORDING TO ZOOPLANKTON NET DATA

DEPTH RANGE m	BIOMASS mg/m^3 NOON	DUSK	MIDNIGHT	DAWN
0-25	0.00	0.00	0.40	0.00
25-50	0.00	0.49	0.91	0.00
50-75	0.61	0.14	0.72	0.27
75-125	3.40	2.81	3.70	0.40
125-175	1.84	2.25	3.53	0.78
175-210	0.00	0.00	0.85	1.86
TOTAL mg/m^2	277.75	268.75	442.00	130.85

TABLE 15. A MODIFICATION ON THE VERTICAL DISTRIBUTION OF O. AFFINIS IN SAANICH INLET BASED ON THE RESULTS OF SUBMERSIBLE OBSERVATION AND ZOOPLANKTON NET SAMPLING

DEPTH RANGE m	BIOMASS mg/m^3 NOON	DUSK	MIDNIGHT	DAWN
0-25	0.00	0.00	0.40	0.00
25-50	0.00	0.49	0.91	0.00
50-75	0.61	0.14	0.72	0.27
75-125	3.40	2.81	3.70	0.40
125-175	1.84	2.25	3.53	0.78
175-210	0.00	0.00	0.85	1.86
210-225	15.52	16.08	4.53	25.28
TOTAL mg/m^2	510.00	510.00	510.00	510.00

Activity Pattern

Observations of 50 O. affinis in a laboratory zooplankton column and data from respiration measurements

TABLE 16. DIEL ACTIVITY OF O. AFFINIS

LOCAL TIME	%POPULATION SWIMMING EXPERIMENT 1 MAR29	MAR30	MAR31	EXPERIMENT 2 APR4	APR5	MEAN	SD
0100		68	72	60	56	64.00	7.30
0200		64	60	64	52	60.00	5.66
0300		68	56	62	48	58.50	8.54
0400		50	40	52	50	48.00	5.42
0500		34	32	22	26	28.50	5.51
0600		26	20	10	14	17.50	7.00
0700		16	12	6	8	10.50	4.43
0800		4	6	0	4	3.50	2.52
0900		0	0	0	0	0.00	0.00
1000		0	0	0	0	0.00	0.00
1100		0	0	0	0	0.00	0.00
1200	0	0	0	0	0	0.00	0.00
1300	0	0	0	0	0	0.00	0.00
1400	0	0	0	0	0	0.00	0.00
1500	0	0	0	0	0	0.00	0.00
1600	0	0	0	0	0	0.00	0.00
1700	4	0	0	10	8	4.40	4.56
1800	10	6	8	16	24	12.80	7.29
1900	28	30	24	34	48	32.80	9.23
2000	56	52	38	44	50	48.00	7.07
2100	70	64	60	56	60	62.00	5.29
2200	68	66	72	60	48	62.80	9.34
2300	72	74	70	60	60	67.20	6.72
2400	70	76	72	70	56	68.80	7.56

with an oxygen meter have shown that O. affinis is a nocturnally active animal (Table 16 and Fig. 19). During daylight hours, animals seldom move in the laboratory column. Higher activity occurred at night. However, not all of the population swam at the same time.

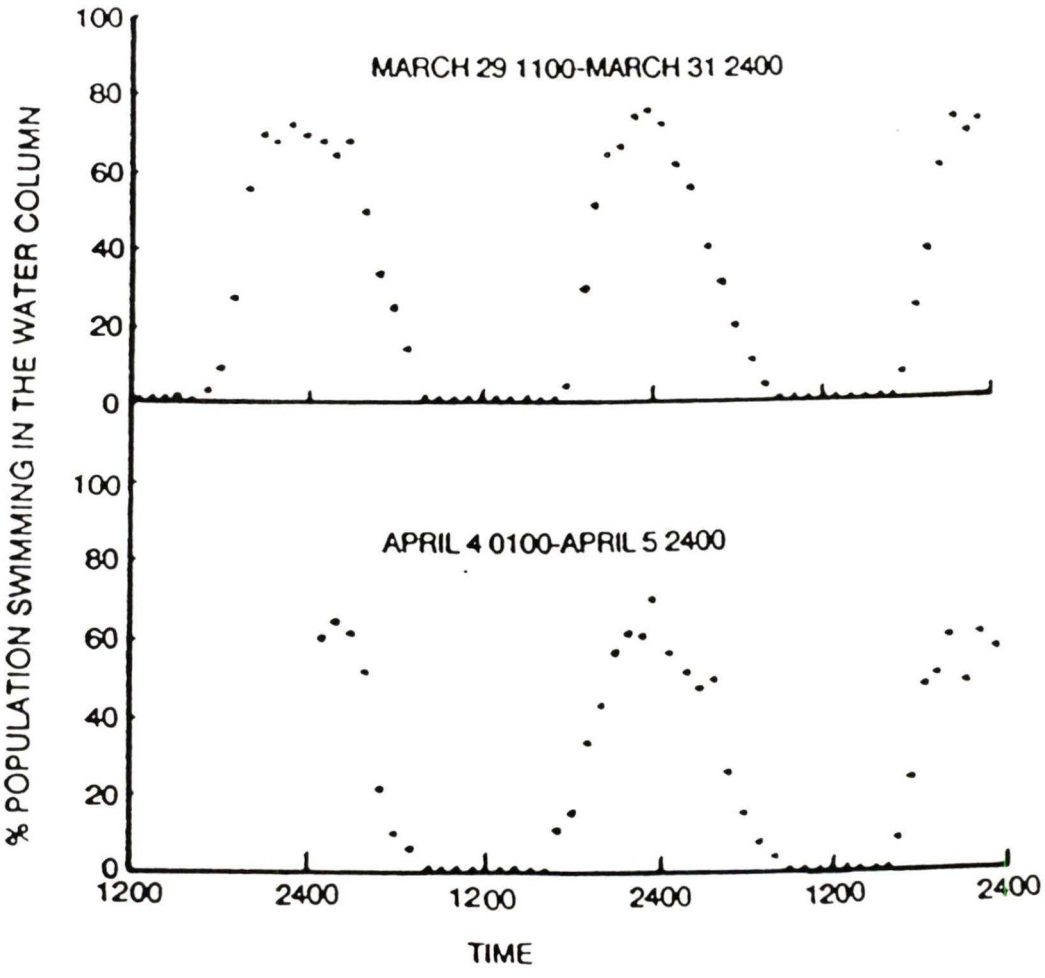

Figure 19. Laboratory activity patterns under dark conditions in the environmental chambers. Data in Table 16.

Feeding Behaviour

Response to Food

Feeding behaviour of this animal has been observed both in the laboratory and in submersible observation. When a food source was sensed, some O. affinis responded immediately. They swam towards the bait, but they were not able to reach the bait directly. However they swam rapidly and directly to the bait as soon as one or more O. affinis reached the bait and started to feed on it. Hundreds of O. affinis clung to the bait and ate voraciously. Highly turbulent water around the bait caused by animal activity moved and rolled the bait on the seafloor or on the bottom of the container. After feeding, O. affinis always carried a piece of food with them and swam vertically to the upper layer.

Feeding Rates

Feeding experiments in laboratory conditions show that O. affinis can consume food up to one tenth of its body weight. (Table 17).

Trap Observations

Amphipod bucket traps used to collect O. affinis at selected depths yielded only a few animals in the water column. The largest number of O. affinis were collected by those buckets which were placed on the surface of the sediment (Table 18).

TABLE 17. FEEDING RATES OF O. AFFINIS

EXPERIMENT	DRY WEIGHT mg		% BODY WEIGHT
	UNFED	FED	
1	162.70	182.47	12.15
2	156.83	173.28	10.49
3	154.56	171.11	10.71
MEAN	158.03	175.62	11.12

TABLE 18. NUMBERS OF ORCHOMENOPSIS AFFINIS COLLECTED BY AMPHIPOD BUCKET FROM SELECTED DEPTHS

BOTTOM DEPTH m	DEPTH m								
	25	50	75	100	125	150	175	200	225
200	0	0	0	0	1	10	6	2533	
200	0	0	0	0	2	0	5	22851	
225	0	0	0	9	1	1	0	6	887
225	0	0	0	0	0	1	12	23	13809
225	0	0	0	0	0	0	0	15	408

Results of the in situ food detection experiments showed that buckets containing punctured bait bags caught more than 5800 O. affinis, while those containing sealed bags only caught a few animals (Appendix Table 10). Field

experiments provided no evidence to support the hypothesis that sounds of Orchomenopsis affinis may guide others to the bait (Appendix Table 11)

Predation

When known numbers of both live and dead small zooplankton were given to O. affinis in the aquaria, O. affinis ate all of the dead zooplankton on the first day. However, no live zooplankton were caught in the following five days.

The observations on predator avoidance by three amphipods were shown in Table 19. Of the three amphipod species tested, O. affinis were the most succeptable to predation by young coho salmon.

TABLE 19. RECORD OF PREDATOR AVOIDANCE. OA = O. AFFINIS, PP = PARATHEMISTO PACIFICA, CC = CYPHOCARIS CHALLENGERI. EXPERIMENT DATE: MAY 20, 1986

TIME	NUMBER OF ANIMALS REMAINING OA	PP	CC
EXPERIMENT 1			
8:00	10	10	10
10:00	2	9	10
12:00	0	7	8
EXPERIMENT 2			
18:00	10	10	10
20:00	3	10	10
22:00	0	8	8

DISCUSSION

Habitat

Saanich Inlet has a weak estuarine circulation and a sill separating the inlet from Satellite Channel. There is no consistent replacement of water below the sill depth (70 m). Consequently, deep-water is usually deficient in oxygen and often contains hydrogen sulfide (Gilmartin, 1962; Herlinveaux, 1962; Pickard, 1963; Richards, 1965; Hoos, 1970; Anderson & Devol, 1973; Pickard, 1975; Emerson, 1979; Thomson, 1981; LeBlond, 1983). Results of my hydrocasts show no major difference with those of previous workers.

Because of isolation by the sill, water below sill depth was stagnant through most of the year. Salinity of bottom water was much higher than surface water throughout the year (Fig. 7). Convective overturn and eddy diffusion are not the major factors in changing the properties of the deep water (Herlinveaux, 1962; Emerson, 1979). Large changes in temperature and salinity occurred only in the upper layers of surface water. The water below 100 m in Saanich Inlet where Orchomenopsis affinis has been frequently found is relatively consistent in salinity and temperature (Fig. 6, 7). However, dissolved oxygen and hydrogen sulfide showed striking annual cycles (Table 20, Fig. 8 to Fig. 11).

TABLE 20. ANNUAL VARIATION OF THE ENVIRONMENTAL FACTORS BETWEEN 100 AND 225 m IN SAANICH INLET

FACTOR	ANNUAL VARIATION	RANGE
TEMPERATURE ^{o}C	0.86	8.50 - 9.36
SALINITY $^{o}/oo$	0.83	30.70 - 31.53
OXYGEN mg/l	3.57	0.00 - 3.57
SULFIDE ug/l	35.90	0.00 - 35.90

Based upon the dissolved oxygen and sulfide data (Fig. 8; 9; Appendix Table 4; 5), two biological seasons can be seen in the deep-water of Saanich Inlet: The season of anoxia with sulfide emergence from February to August and the season of low dissolved oxygen content without sulfide from August to January.

It is clear that these seasonal changes are driven by the dense oxygenated oceanic water which flows over the sill and flushes into the basin of the Inlet in August. The deep oxygen deficient water is displaced by exotic high oxygen content water (Waldichuk, 1957; Anderson & Devol, 1973; Emerson, 1979). A midwater oxygen minimum and sulfide maximum were found at the beginning of the flushing period (Fig. 8; 9). This flush should account for the drastic seasonal change of the water properties in the deep-water.

Physiological Tolerances and Metabolic Rates

Non-acclimated experimental results show that O. affinis could tolerate wide ranges of environmental factors. The physiological tolerance ranges of O. affinis were much broader than the ranges of the natural conditions in Saanich Inlet.

Temperature

The upper limit of thermal tolerance of O. affinis is 19°C which is similar to that of other temperate species. Anraku (1964b) reported that temperatures exceeding 20°C were harmful to Pseudocalanus minutus. Gilfillan (1976) reported that Euphausia pacifica could tolerate temperatures up to 15°C. Many workers have suggested that thermal tolerance might be correlated with habitat conditions (Halcrow, 1963; Lockwood, 1967; Mullin & Brooks, 1970; Gilfillan, 1976; Laybourn-Parry & Tinson, 1985). The upper limits of thermal tolerance for two neritic species of copepods from Chesapeake Bay were measured by Heinle (1969). It was found that the upper limits were the normal temperature of the habitat during the summer.

However, the thermal tolerance range of O. affinis is from 0 to 19°C which goes far beyond the normal habitat temperature (6-16 °C). Possibly this broad thermal tolerance range of O. affinis may result from its diel vertical migration which might on occasion expose it to

large changes in temperature.

Temperature effects on the metabolism of crustaceans have been widely investigated. Generally speaking, the metabolic rate of poikilothermic organisms increases with increasing of temperature under acclimated conditions (Armitage, 1962). Though the respiratory rate of O. affinis increases with increasing temperature, the relationships are not constant (Fig. 13). On average, increase in respiratory rate is 0.036 ug O_2 mg dry wt/h/^oC from 5 to 13^oC and 0.139 ug O_2/ mg dry wt/h/^oC from 13 to 18^oC. These results suggest that this species is well adapted to a temperature range which is close to its habitat temperature range. The steep rise in metabolism that occurs when temperatures were higher than 13^oC may reflect that it can not fully adapt to higher temperatures.

The temperature coefficient of biological processes is expressed in terms of Q_{10}. Q_{10} has been used to describe the effects of a temperature rise of 10^oC on the velocity of physiological rates (Heilbrunn, 1955).

The biological Q_{10} values are between 2 and 3 and thses are similar to that reported for chemical processes. In particular, many enzymatic reactions are accelerated at this rate by increased temperatures. Since the enzymes are catalysts of organic origin, some authors attempted to interpret biological temperature coefficients in terms

of specific chemical reaction (Heilbrunn, 1955; Schmidt-Nielsen, 1964).

Some Q_{10} values for some crustacean plankton from temperatures of 0 to 25°C are shown in Table 21.

TABLE 21. Q_{10} FOR SOME CRUSTACEAN PLANKTON

TAXON	Q_{10}	T°C	SOURCE*
Anomalocera patersoni	2.07	10.0-14.5	1
Anomalocera patersoni	5.61	14.5-18.0	1
Pleuroncodes planipes	2.20	10.0-25.0	2
Euphausia superba	1.20	0.0-18.0	3
Euphausia pacifica	2.00	5.0-12.0	4
Euphausia pacifica	2.21	5.0-10.0	5
Euphausia pacifica	2.55	10.0-15.0	5
Orchomenopsis affinis	1.97	5.0-13.0	6
Orchomenopsis affinis	2.92	13.0-18.0	6

* 1--Champalber & Gaudy, 1972; 2--Quetin & Childress, 1976; 3--McWhinnie & Marciniak, 1964; 4--Lasker, 1966; 5--Paranjape, 1967; 6--This paper.

Q_{10} values of O. affinis are between 2 and 3 which are similar to most of the other species listed in Table 21. However, Q_{10} value of O. affinis under temperature range from 13 to 18°C is 1.5 times higher than that from 5 to 13°C. This result may indicates that this animal is a low temperature accommodation form.

Salinity

Though O. affinis can survive a range of salinity from 20°/oo to 50°/oo, survival rates were greater in higher salinity than those in lower salinity. Respiratory rates of this species increased 59% when the animals were transferred from 30°/oo to 20°/oo sea water. However, the respiratory rate of this animal decreased by 8% when transferred from 30°/oo to 45°/oo seawater.

It appears no single hypothesis can account for the salinity effects shown on metabolic rates reported in literature (Kinne, 1971). Some of the literature indicated that metabolic rates of zooplankton declined with a reduction in salinity (positive correlation) (Anraku, 1964a; Jawed, 1973; Marshall, 1973; Gilfillan, 1976). Others showed the reverse, i.e. an increase in metabolism with decreasing salinity (negative correlation). Schlieper (1931) recorded an 18% decrease in respiratory rate by Gammarus locusta transferred from 16°/oo to 32°/oo. Lowenstein (1935) obtained a 20% decrease in respiratory rates when Gammarus chevreuxi was moved from 25% seawater to 100% seawater. It was suggested that for animals having a negative correlation, osmoregulatory processes may account for a relatively large proportion of the total metabolic demand (Potts & Parry, 1964). Lance (1962) observed that low salinity initially caused violent swimming movement in zooplankton which accounted for

increased metabolic rates.

Gilfillan (1972) suggested that positive correlation between salinity and metabolic rates may be true for the open sea species. Because most of open sea species are stenohaline, lowering of salinity will depress metabolic rate. Negative correlation is common in euryhaline estuarine species, such as Carcinus maenas, Gammarus chevreuxi, Ocypode albicans, Hemigrapsus oregonensis and H. nudus. All of these species show an increase in oxygen consumption when transferred to a more diluted medium (Lockwood, 1967). Orchomenopsis affinis has a negative correlation of respiration to salinity. It shows the euryhaline response.

Dissolved Oxygen

Two categories of invertebrates have been found in oxygen deficient layers (Longhurst, 1967; Thompson & Pritchard, 1969; Mill, 1972; Childress, 1975; 1977; McMahon & Wilkens, 1974; Belman, 1978; Judkins, 1980). The first category includes aerobic animals which are able to survive under extremely low oxygen conditions. However, they have very limited tolerance to anaerobic conditions. Childress (1977) found that some of those animals died within minutes under anaerobic conditions. They are generally found in stagnant, low oxygen content water and show no diel migratory behaviour. The second category includes those animals which can survive in both normally

oxygenated water and periodically anoxic water. A number of species in this category are involved in diel vertical migration. O. affinis belongs to the latter category (Fish, 1968; Hoos, 1970; Mackie & Mills, 1983). Both Fish (1968) and Hoos (1970) showed that O. affinis could survive at oxygen levels of 0.39 ml/l (0.56 mg/l) for at least 24 hours in the laboratory. Fish (1968) further noted that O. pinguis (probably misidentification of O. affinis) could tolerate at least 36 hours in 0.4 ml/l (0.57 mg/l) in the field. There is no published data previous to this report which shows how long the animal could tolerate anoxia.

The Winkler titration method is an accurate and reliable method for dissolved oxygen measurement. However, special care must be taken during sampling when working with anoxic or hypoxic waters. Errors may be introduced into samples through contact with the atmosphere (Carpenter, 1965; Carritt & Carpenter, 1966). Using my specially designed respiration chamber and oxygen-free sampling techniques, it was shown that O. affinis could survive for at least 25 hours under completely anoxic conditions (0.00 mg O_2/l). Of four local zooplankton examined, O. affinis is the most anoxic tolerant species (Table 9). In situ anoxic tolerant test results agree well with the results of laboratory experiments (Table 8).

Because of problems with oxygen sampling technique,

Fish (1968) and Hoos (1970) failed to note the anoxic tolerance of O. affinis and classed it as a low oxygen tolerant species. This problem may have occurred in other reported hypoxia tolerant species.

Hydrogen Sulfide

Sulfide content in the bottom water of Saanich Inlet was higher than 30 uM during the stagnant period. Most animals are killed by sulfide which limits their distribution in sulfide-rich environments. However, O. affinis was uniquely abundant in the bottom waters of Saanich Inlet. Sulfide tolerance experiments in anoxic water showed that O. affinis could tolerate sulfide levels up to concentrations of 3 mM (Table 7).

Sulfide below 500 uM is not lethal to this species over a 24 hour period. Moreover, results from field experiments show that survival rates of this species increase with an increase in sulfide concentration under anoxic conditons. It is suggested that sulfide, or a product associated with sulfide, may have some beneficial effects on the survival of this species under anoxic conditions.

Natural sulfide-rich environments exist in both vent ecosystems and fjord basins. But we should aware of their differences. Fjords are rich in particulate organic matter, while vent systems are poor in particulate organic matter. Saanich Inlet has two biological seasons in deep

water. Anoxia with high concentrations of sulfide predominating in deep water from February to August, and low oxygen conditions prevailing from late August to January. Vent systems do not have such obvious seasonal change. Deep water of a fjord is often stagnant and covered with hypoxic water while vent systems are surrounded by and mixed with highly oxygenated oceanic water.

Recent discoveries have shown that specialized communities of invertebrates which live around sulfide-rich hot vents and in non-vent, sulfide-rich sediments (Felbeck, et al. 1981; Reid, 1980) have evolved mechanisms for prevention of poisoning by sulfide (Vetter, et al., 1987).

Felbeck et al. (1981) claimed that enzymes associated with sulfide metabolism and nitrate reductase, are present in a wide variety of animals inhabiting sulfide rich environments, such as sewage outfalls and deep basins, as well as vents.

Little is known about the biochemical adaptation of O. affinis. It will be necessary to carry out biochemical experiments to clarify the metabolic adaptation of O. affinis to anoxic and sulfide-rich habitats.

Strategies of Adaptation

Respiratory Adaptation

Although O. affinis is able to survive in anoxic conditions for more than 25 hours, it still needs oxygen to meet physiological requirements.

Other hypoxia adaptated invertebrates reported in the literature (Thompson & Pritchard, 1969; McMahon & Wilkens, 1974; Taylor, 1976; Babula, 1978) show excelllent respiratory regulation. In contrast, oxygen independent respiration occurred in O. affinis when oxygen levels ranged from 0.5 to 10.0 mg/l, and oxygen dependent respiration occurred when oxygen levels dropped below 0.5 mg/l. Compared with other species, the oxygen dependant respiration of O. affinis was lower than that of Euphausia pacifica, an animal known to require high levels of oxygen, and higher than those of other low oxygen tolerant species (Table 22).

TABLE 22. CRITICAL LEVEL OF OXYGEN CONTENT (P_c) FOR SOME MARINE CRUSTACEANS

SPECIES	ml O_2/l	mg O_2/l	SOURCE
Orchomenopsis affinis	0.35	0.50	This study
Euphausia pacifica	0.70	1.00	Lasker 1966
Gaussia princeps	0.20	0.29	Childress 1971
Pleuroncodes planipes	0.10	0.14	Quetin 1976
Munida quadrispina	0.14	0.20	Burd 1983

O. affinis is a vertical migrant. Its daytime distribution places the animal in the layers where the dissolved oxygen content is from 0.5 mg/l to zero. It daily encounters anoxic and low oxygen conditions in the anoxic season. During this period it migrates regularly to highly oxygenated waters. Oxygen independent respiration would not be an advantage in this situation and may, in fact, be a liability since frequently respiratory regulation requires more energy (Kinne, 1971).

Oxygen debt accumulated in the bodies of O. affinis when the oxygen pressure fell below the critical point (Table 13). Bulnheim (1979) reported the accumulation of oxygen debt of euryhaline Gammarus in low PO_2. Felder (1979) reported that post anoxia respiratory rates of Callianasa jamaicense in oxygenated water is initially four times that of the pre-anoxia respiratory rates which indicates an oxygen debt was incurred during anoxia. Results of my experiments (Table 13) are similar to Felder's finding.

Since the deep water of Saanich Inlet is often stagnant and anoxic, O. affinis must periodically move into the upper water layers where the oxygen content can meet its physiological requirements. The upward vertical migratory behaviour of O. affinis may be stimulated by its oxygen debt. Longhurst (1967) suggested that most animals which live in oxygen restricted environments (less than

0.2 ml/l (0.29 mg/l)) were either diurnal vertical migrants or resting stages of animals which underwent ontogenetic migrations. Belman (1978) reported that the squid Histioteuthis heteropsis could eliminate oxygen debt accumulated in the oxygen minimum layer by migrating into shallow, more oxygen-rich water at night. Such a strategy has been suggested for other migratory species (Barham, 1971; Gordon et al., 1976; Childress, 1977; Devol, 1981).

McLaren (1963) suggested that vertically migrating zooplankton could utilize their energy reserves more efficiently by growing and developing in the cooler, deep water during the day and feeding in the warmer, upper layer in the evening. The feeding pattern of O. affinis does not agree with McLaren's 1963 hypothesis. Results of my experiments have clearly indicated that O. affinis feeds on or in the sediment which is covered by anoxic or oxygen deficient water. In this case, vertical migration can be explained by the need to eliminate the oxygen debt which accumulates under anoxic conditions.

Feeding Behaviour

Most species of the Lysianassidae are considered scavengers (Dahl, 1979. Thurston, 1979. Meador, 1981. Stockton, 1982). They consume animal corpses and other organic particles. Smith & Present (1983) suggested that scavenging deep-sea amphipods are energetically adapted to a sporadic food source in a food-limited environment by

the following strategies:

1. Two states of metabolism: a resting rate much like a state of torpor or dormancy and an active rate for optimal utilization of a food fall.

2. Quick response to food falls, a rapid rate of food consumption with maximum quantity ingested.

3. Energy storage capabilities for long-term sustenance.

Most of these adaptations can be found in the feeding strategies of O. affinis. However, there are significant differences between O. affinis and deep-sea scavenging amphipods. There is rare chance of finding food in the deep ocean. Based on the fact that no adult amphipods were attracted to the bait in deep open ocean waters, Shulenberger and Hessler (1974) suggested that one large meal might be sufficient to carry a juvenile into reproductive maturity. Childress and Nygaard (1973) hypothesized that a single meal might suffice for as much as several weeks or months for the deeper living animals.

Deep sea lysianassid amphipods are capable of storing large quantities of food in their guts. It is reported that fed and engorged Paralicella sp. were 3 to 5 times the volume of unfed specimens of equal length (Shulenberger & Hessler, 1974). Food is stored in the midgut which can expand to fill the entire body cavity (Dahl, 1979). O. affinis can not ingest as large a

quantity of food at a single feeding as other deep-living amphipods. About one tenth of its body weight in food can be consumed at each meal (Table 17). The distensible food storage portion of the alimentary tract of Orchomenopsis is a relatively small foregut which is restricted by a thicker and more rigid exoskeleton (Thurston, 1979). I suggest that those differences are a result of different food availabilities.

The ways deep-sea animals are able to detect their food sources are critically important for their survival. Chemoreception and mechanoreception were reported to be vital ways to gain information about the location of a distant food source (Hessler, 1974; Mauchline & Ballantyne, 1975; Meador, 1981; Smith & Baldwin, 1982; Bush & Laverack, 1982; Ingram & Hessler,1983; Smith, 1984). Some species of crustaceans exhibit a highly developed chemoreceptive ability and can detect amino acid concentration as low as 0.1 nM to 1.0 pM (Dahl, 1979; Hamner & Hamner, 1977). Shallow-water crustaceans can detect frequency stimuli as low as 8-15 db (Maniwa, 1977).

Observations on the activity of O. affinis towards a food source showed that they were not directly swimming towards the food source until the first animal fed on the bait. Then hundreds of animals swam towards and descended upon the bait from all directions. This phenomenon suggests that chemoreceptors and mechanoreceptors may

operate together. Mechanoreceptors may play an important role in leading other animals towards the bait. For example, vibrations originating from feeding of animals may guide others to the food. Ingram and Hessler (1983) reported that all of the species of amphipods displayed gregarious behavior in their choice of traps. Thay tend to choose bait with other amphipods on it, neglecting similar bait nearby. They prefer to enter traps containing individuals of similar age and sex. Based upon this information, Ingram and Hessler (1983) suggested that at close range, locating a food item is probably based more on information received from other amphipods rather than food odor. To date, it is still not known how this communication works. I have done several experiments to test for mechanoreception (Appendix Table 10). Unfortunately large variations in the experimental results prevented a definite answer to the question. Perhaps animals did not feed in the sealed plastic experimental bags or the vibrations were absorbed by the plastic bag. Further experiments are needed.

Distribution and Activity Pattern

Earlier studies on the distribution of O. afinis utilized traditional zooplankton research methods (Fish, 1968; Hoos, 1970; Devol 1981). Hoos (1970) reported that this animal was abundant about 100 m. Devol (1981) worked

on the vertical distribution of zooplankton respiration in relation to the intense oxygen minimum zone in Saanich Inlet. His conclusion was that the conspicuous lack of oxygen utilization in the water column of the oxygen minimum zone resulted from the virtual absence of zooplankton within this zone. These traditional sampling methods do not give us a real distribution patterns of animals within the oxygen minimum zone, because plankton nets and water samplers fail to collect animals very close to the seafloor or on the sediment. Benthic grabs do not work well in such soft sediments. Epibenthic sleds work well on relatively firm sediments only collecting the animals on or very close to the sea floor. Animals swiming in the layers between 1 to 5 meters above the seafloor would be missed. Using the method of direct submersible observation (Mackie and Mills, 1983), and combining the results from amphipod buckets and open-closing nets, I have come to a more compelete distribution picture of this animal in Saanich Inlet: O. affinis is a diel vertical migratory demersal zooplankter which inhabits soft bottom substrates and periodically swims freely in the water column. Based upon laboratory observations, some of the population swims in the water column while most stay on or in the sediment during daytime. At night, more than half of the population swims in the water column. This species spends most of the time in the anoxic (or oxygen minimum),

sulfide-rich layer. It has some activities in common with other demersal zooplankton. Alldredge and King (1977) and Porter (1977) have suggested that some demersal zooplankton might migrate several times each night and other demersal species may not migrate every night.

Diel vertical migration is a very complicated biological phenomenon. Since diel vertical migration was first recorded in planktonic crustaceans in 1817 (Cuvier, 1834), many hypotheses explaining the phenomenon have been proposed including endogeneous rhythm (Esterly, 1914; Harris, 1963; Enright, 1967); Escape from predation (Longhurst, 1967); optimum light intensity (Clark, 1934; Alldredge & King 1980); food requirement (Huntley, 1982); energy conservation (McLaren, 1963) and so on. But there has not been any single hypothesis which can successfully explain the causes of vertical migration of zooplankton.

O. affinis has a different strategy from those of most of the vertical migrants. It gets its food on or in the sediment under anoxic conditions. Vertical migration may be used to recover from the oxygen debt which accumulated during residence in the anoxic layer. Thus, to Orchomenopsis affinis, the primary stimulus for upward vertical migration appears to be oxygen debt. Nocturnal swimming activity may result from selective predative pressure as has been suggested by several investigators (Hobson & Chess, 1976; Robertson & Howard, 1978). Straight

upward movement of O. affinis after feeding in anoxic conditions has been observed by Littlepage using Pisces IV (pers. comm.). This is in agreement with my laboratory observations. Since the torpid or inactive animal may maintain a very low metabolic rate, the oxygen debt will be accumulated slowly. The presence of food may stimulate the food deprived animal to activity, boosting the metabolic rate sharply. Consequently, the oxygen debt accumulates to its maximum limit in a relatively short time, and the organism has to move upward to repay the oxygen debt.

Considering bioenergetics, the energy required for vertical migration may be a significant term in energy budget of O. affinis. Vertical migration may result in a large net energy loss. Shortening the time required to pass through the anoxic layer by directed vertical upward movement conserves energy. However the animals move almost horizontally in the oxygenated layer where oxygen content is above 0.5 mg/l until the oxygen debt is eliminated. They then return to the seafloor by gravity sinking or occasionally by swimming downwards. Reducing the energy spent in swimming would seem to be an important adaptation for this animal enabling survival in this special environment. My observations agree with the suggestion by several workers that vertical migration occupies a relatively small portion of each day (Kampa & Boden, 1954;

Boden & Kampa, 1965; Torres & Childress, 1983; Torres, 1984).

Ratios of O:N

For marine invertebrates, three types of catabolism have been found: 1. lipid-orientated; 2. carbohydrate-orientated; and 3. protein-orientated (Giese, 1966; Stickle & Duerr, 1970; Butle et al., 1969; 1970; Mayzaud, 1976). Generally speaking, O:N ratios of lipid and carbohydrate orientated metabolisms are higher than those of protein-orientated metabolism. O:N ratios for protein-orientated metabolism are around 8.0 (Conover & Corner, 1968; Ikeda, 1974). Ratios which are higher than 8 suggest lipid-orientated and carbohydrate-orientated metabolism.

In the present experiments, ratios of O:N ranged from 16 to 42 (Table 12). The O:N ratio for equivalent weights of protein and lipid catabolism would be about 27 (Ikeda, 1974; Hiller-Adams & Childress, 1983). El-Sayed et al. (1978) reported that O:N ratios for gammarid amphipods were 12±2. O:N ratios for antarctic and subantarctic zooplankton averaged 26 (Biggs, 1982), 17 to 36 for oceanic salps (Cetta et al. 1986) and 21 to 49 for tropical and subtropical gelatinous zooplankton (Biggs, 1977). O:N ratios of O. affinis are similar to the results of Biggs (1977). But much higher than others (Table 23).

TABLE 23. COMPARISION OF O:N RATIOS FROM PRESENT EXPERIMENTS WITH THOSE FROM PREVIOUS WORKERS. RATIOS ARE BY ATOMS

SPECIES	O:N	SOURCE*
Parathemisto gaudichaudii	15.3±6.2	1
Vibilia antarctica	18.4±3.8	1
Hyperia gaudichaudii	14.4±7.6	1
Acartia clausi	17-21	4
A. clausi	4-8	3
A. australis	11-18	1
Calanus minor	12-14	1
C. finmarchicus	22-30	5
C. hyperboreus	22-35	6
C. gracilis	16-22	1
C. robustior	16	2
C. plumchrus	6.8	8
C. helgolandicus	9.8-15.6	6
C. cristatus	5-7	8
Centropages typicus	18-19	5
C. typicus	8	6
Orchomenopsis affinis	16-42	7

* Source of references: 1. Ikeda (1974), 2. Ikeda (1972), 3. Ikeda and Skjoldel (1980), 4. LeBorgne (1973), 5. Harris (1959), 6. Conover and Corner (1965), 7. this study, 8. Taguchi and Ishii (1972)

High ratios of O:N suggest that lipid is a major metabolite for O. affinis, supporting lipid as the major storage and energy reserve material (Hiller-Adams & Childress, 1983). Results of biochemical analysis show that lipid in O. affinis is about 40% of the body dry weight (Parkyn, pers. comm.).

Evidence shows that O:N ratios may be affected by feeding (Table 12). O:N ratios were lower than 16 during

and shortly after feeding and gradually increased as starvation progressed (20-42). Animals appear to use protein-orientated catabolism while feeding, and switch to lipid-orientated catabolism when starved (Hiller-Adams, 1983). Mayzaud (1976) has also suggested that zooplanktons (Calanus finmarchicus, Sagitta elegans and Acartia clausi) may switch from one type of catabolism to the other. When the animals were maintained in aquaria without food O:N ratios rose gradually. My experimental results agree with the report by Ikeda (1977); starved carnivores showed a higher O:N ratios than fed ones (Table 12), implying a switch from protein to carbohydrate or lipid as the primary substrate for catabolism.

Biological Advantages

Most aquatic animals are excluded by anoxia and hydrogen sulfide (Theede, et al., 1969). O. affinis has successfully adapted to this habitat. Some possible selective advantages of this adaptation are:

1. Availability of food. Deep water of Saanich Inlet is often stagnant. Organic particles from the upper layer must sink to and accumulate on the seafloor. Because of the barrier of anoxia and hydrogen sulfide, not many animals except O. affinis can utilize this food source.

2. Refuge. The swimming patterns of O. affinis are much simpler than those of other crustacean zooplankton in

Saanich Inlet. It appears very slow to respond to its predators. Moreover, its size and visible colour would make it easy prey for planktivorous fish. Laboratory observations showed O. affinis was consumed first when small salmon were introduced to an aquarium contained three amphipod species, Parathemisto pacifica, Cyphocaris challengeri and O. affinis (Table 19). The anoxic and sulfide-rich conditions near the seafloor exclude most, if not all, predator species. O. affinis can only be abundant in this kind of special habitat.

3. Energy conservation. Experimental results show that the minimum respiratory rates of O. affinis occurred in oxygen deficient water. Respiratory rates correlate positively to temperature, but correlate negatively to salinity (Fig. 13; 14). The bottom water in Sannich Inlet with high salinity and constant low temperature provides ideal conditions for this species to reduce its energy consumption.

For many animals, the lack of oxygen or presence of hydrogen sulfide is fatal. Marine regions poor in oxygen are characterized by the presence of strikingly few species (Segerstrale, 1957; Caspers, 1957; Theede, 1969). But O. affinis has benefited from this condition. The animal lowers in respiratory rate at a relatively high level of dissolved oxygen thereby reducing its oxygen requirement and consequently, a large amount of energy is

saved under anoxic condition.

Ecological Significance

Besides the biological advantages of the physiological adaptations of this animal, the author has tried to clarify its ecological status. It has been suggested that downward transportation of organic matter from upper zones to lower zones by migrating animals is very important to the deep midwater and benthic communities (Vinogradov, 1962; Petipa, et al., 1970; Corner & Davies, 1971; Sokolova, 1972; Takahashi & Ikeda, 1975; Fellows, 1981; Angel, 1984). In contrast to these suggestions, this study of the physiology and behavior of O. affinis presents the first example of upward energy transportation from an anoxic layer to a normal oxygenated layer. O. affinis transports food energy captured at depth upward, where it may release nutrients in the form of excreta or provide direct energy transfer by been preyed upon. I propose to name this newly discribed phenomenon Biological Upwelling (Fig. 20).

Physical features of isolated basin fjords are unique in that anoxia is common with a large supply of organic particles to the benthos. Holobenthic animals are absent from the sediments covered with anoxic water. If there were no animals able to exploit the organic matter on the seafloor, accumulated organic particulate matter would be consumed only by anaerobic bacteria and result in

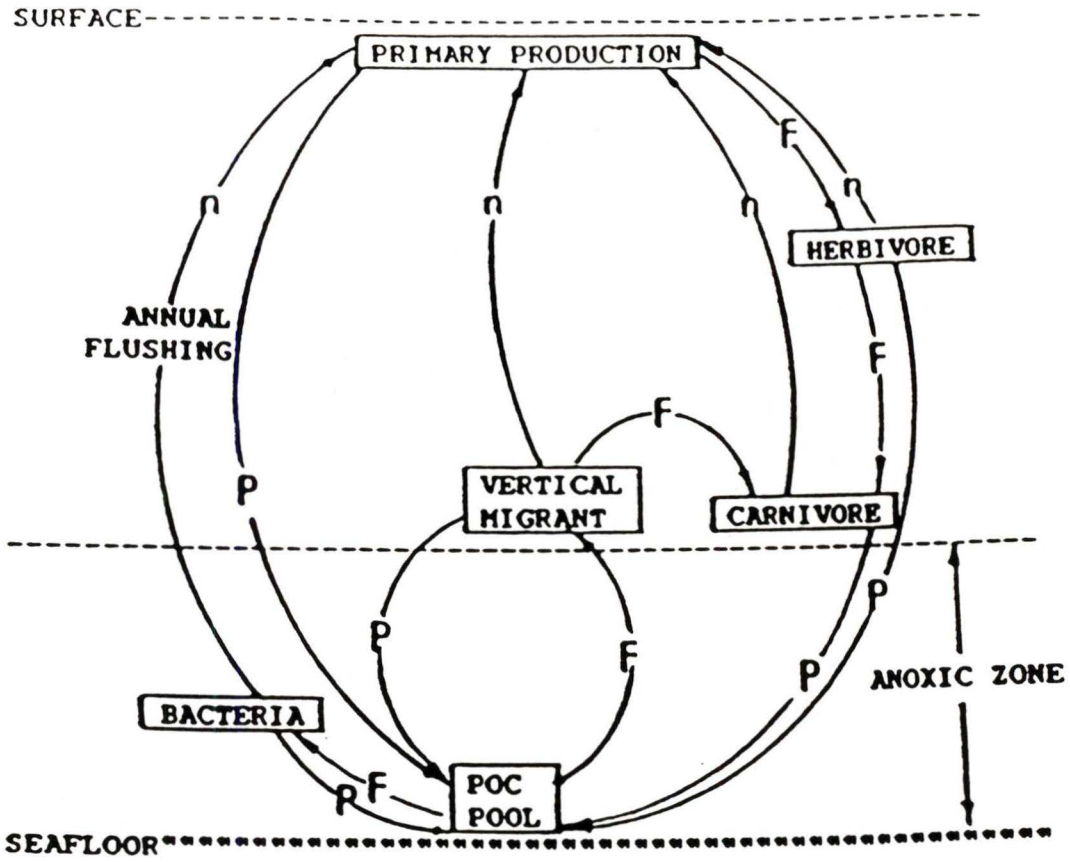

Figure 20. New food chains in the fjord ecosystem. Vertical migrants (e.g. O. affinis) are able to feed under anoxic and sulfide-rich conditios and transport the energy to the upper oxygenated layer; excretion may provide nutrients to phytoplankton while some are preyed upon by carnivores. F: direct feeding processes. P: living and/or dead organisms move towards the seafloor. n: nutrients released to phytoplankton.

increasing sulfide levels and expansion of the anoxic area. Orchomenopsis affinis, an effective scavenger and an excellent energy transporter, removes particulate organic matter from the deep water of Saanich Inlet and transports to mid-depths, increasing the productivity of Saanich Inlet. It must play an important role in ecosystem of Saanich Inlet.

SUMMARY

1. In the deep water of Saanich Inlet, temperatures and salinities are stable, but dissolved oxygen and hydrogen sulfide have clear annual cycles. Anoxic and sulfide-rich conditions are usually found from January to August. Low oxygen conditions are found during the remaining months.
2. O. affinis can survive under anoxic condition for at least 25 hours. It can tolerate sulfide concentration as high as 3 mM.
3. Respiratory rates of O. affinis are low under low temperature and high salinity.
4. Field and laboratory experiments have confirmed that this species is a diel vertical migrant. The majority stay on or in the sediment during the day and migrate vertically to the oxygenated water at night to eliminate the oxygen debt which has accumulated under anoxic conditions.
5. Feeding behaviour in this species showed that this species is a scavenger. Animals can eat under anoxic and normal oxygen condition consuming about 10% of their body weight at each feeding.
6. The ecological advantages to this species in an anoxic, sulfide-rich habitat are: 1. high food availability, 2. anoxic and sulfide-rich conditions serve as barriers to

reduce predation and allow metabolic energy conservation.

7. The ecological importance of this species is: 1. it utilizes particulate organic carbon (POC) in the anoxic layers, 2. it returns nutrients to the oxygenated layer, and 3. it enhances the energy turnover rates in Saanich Inlet.
8. Biological Upwelling is proposed as the name for these newly described links in fjord food chains.

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APPENDIX TABLE 1

FIELD TEMPERATURE DATA

DEPTH m	TEMPERTURE °C July29	Sept15	Oct3	Nov17	Dec12	87-Jan14	Feb9	Mar11	Apr2	Jun22
0	14.86	15.35	12.62	9.40	6.24	7.48	8.10	8.32	8.76	15.02
10	12.76	12.57	11.27	9.46	8.70	8.32	8.09	7.98	8.34	11.55
30	11.09	11.24	11.03	9.35	8.94	8.42	8.31	8.07	8.74	10.52
50	10.05	10.55	10.50	9.46	9.40	8.74	8.43	8.09	8.17	9.63
75	9.18	8.84	9.46	9.47	9.19	8.62	8.28	8.11	8.24	9.12
100	9.09	9.27	9.32	9.36	9.19	9.03	8.92	9.27	8.50	9.00
125	9.00	9.27	/	9.23	9.23	/	/	9.25	9.15	/
150	9.15	9.28	9.27	9.27	9.28	/	9.29	/	9.28	9.27
175	9.25	9.30	/	9.30	9.27	/	9.28	/	9.29	/
200	9.27	9.29	/	9.32	9.29	/	/	/	9.28	/
225	9.28	9.27	/	9.29	9.29	/	/	/	/	/

APPENDIX TABLE 2

FIELD SALINITY DATA

DEPTH m	SALINITY °/oo Jul29	Sept15	Oct3	Nov17	Dec12	87-Jan14	Feb9	Mar3	Apr3	Jun22
0	28.10	29.27	29.79	30.14	26.68	28.17	19.23	24.58	26.06	29.67
10	29.16	29.60	30.05	30.16	30.18	29.48	29.96	29.70	/	29.82
30	29.77	29.86	30.21	30.53	30.31	30.20	30.15	29.89	29.60	30.34
50	30.03	30.44	30.48	/	30.56	30.45	30.41	30.23	29.75	30.54
75	30.65	31.06	31.07	31.13	30.96	30.72	30.63	30.54	30.15	31.26
100	30.82	31.29	31.12	31.33	31.25	30.70	31.04	30.97	30.79	31.53
150	31.07	31.34	31.26	/	31.44	/	31.41	31.44	31.42	/
200	31.16	31.21	31.32	/	31.47	/	/	31.47	31.48	/

APPENDIX TABLE 3

FIELD DISSOLVED OXYGEN DATA

DEPTH m	OXYGEN mg/l 86-Mar15	May14	Jul29	Sept15	Nov17	87-Feb9	Apr2
0	7.49	8.79	8.95	9.13	5.14	9.43	10.85
10	6.13	6.14	6.54	7.98	4.95	7.29	8.01
30	5.65	5.52	5.55	3.76	4.55	6.53	6.19
50	5.17	4.87	4.41	2.43	4.15	6.82	6.25
75	4.25	4.34	3.48	0.47	1.26	6.56	5.60
100	1.67	1.07	1.03	0.23	0.09	3.51	3.57
125	0.33	0.13	1.02	0.00	0.35	2.38	0.95
150	0.00	0.00	0.17	0.00	0.76	1.34	0.49
175	0.00	0.00	0.00	0.72	0.86	0.21	0.00
200	0.00	0.00	0.00	1.01	1.54	0.00	0.00
225	0.00	0.00	0.00	1.08	1.49	0.00	0.00

APPENDIX TABLE 4

FIELD HYDROGEN SULFIDE DATA (1986)

DEPTH m	HYDROGEN SULFIDE uM March 15	May 14	Sept 15	Nov 17
0	0	0	0	0
50	0	0	0	0
100	0	0	0	0
125	0	0	5.84	0
150	4.89	7.23	22.87	0
175	27.25	20.94	1.76	0
200	34.56	25.18	0.88	0.05
225	35.90	26.78	0.47	4.80

APPENDIX TABLE 5

HYDROGEN SULFIDE AND DISSOLVED OXYGEN DATA
(March 15, 1986)

DEPTH m	HYDROGEN SULFIDE uM	OXYGEN mg/l
0	0	7.49
50	0	5.17
100	0	1.67
125	0	0.33
150	4.89	0.00
175	27.25	0.00
200	34.56	0.00
225	35.90	0.00

APPENDIX TABLE 6

HYDROGEN SULFIDE AND DISSOLVED OXYGEN DATA
(Sept. 15, 1986)

DEPTH m	HYDROGEN SULFIDE uM	OXYGEN mg/l
0	0.00	9.13
50	0.00	2.43
100	0.00	0.23
125	5.84	0.00
150	22.87	0.00
175	1.76	0.72
200	0.88	1.01
225	0.47	1.08

APPENDIX TABLE 7

SURVIVAL TIME AND SURVIVAL RATE OF *O. AFFINIS* UNDER ANOXIC CONDITION. 20 ANIMALS FOR EACH TRIAL

TIME hr	Experiment			MEAN	%SURVIVAL
	1	2	3		
0	20	20	20	20.00	100.00
5	20	20	20	20.00	100.00
10	20	20	20	20.00	100.00
15	20	20	20	20.00	100.00
20	20	20	20	20.00	100.00
22	20	20	20	20.00	100.00
24	20	20	20	20.00	100.00
26	18	19	20	19.00	95.00
28	14	16	16	15.33	76.67
30	11	9	9	9.67	48.33
32	5	4	5	4.67	23.33
34	2	1	2	1.67	8.33
36	1	0	0	0.33	1.65
38	0	0	0	0.00	0.00

APPENDIX TABLE 8

DAILY CHANGES OF METABOLIC RATES AND ACTIVITY RHYTHM.

DATA CALCULATED FROM RECORDED CHART OF OXYGEN METER

NO	TIME	OXYGEN UPTAKE ug/mg.l
1	1800-2200	0.920
	2200-2400	1.400
	1241-2100	0.837
2	1300-1700	0.930
	1700-2100	0.832
	2100-2400	1.382
3	2000-2200	1.051
	2200-0100	1.246
	0100-0800	0.931
4	2000-2300	0.954
	2300-0200	1.280
	0500-1700	0.564
5	2000-2300	0.964
	2300-0400	1.203
	0400-1700	0.658
6	1130-1730	0.926
	1900-0100	1.485
	0100-0930	1.020
7	2100-0200	1.216
	0600-1000	0.760
	1300-1700	0.436
8	2100-0100	1.337
	0100-0500	0.985
	0500-1300	0.687

APPENDIX TABLE 9

RESPIRATORY RATES OF O. AFFINIS UNDER DIFFERENT OXYGEN LEVELS

O_2 LEVEL mg/l	RESPIRATORY RATE ug/mg/hr
10	0.70
8	0.70
6	0.70
4	0.70
2	0.70
1	0.65
0.5	0.40
0.2	0.15
0.0	0.00

APPENDIX TABLE 10

RESULTS OF FIELD EXPERIMENTS ON FOOD DETECTION BY *ORCHOMENOPSIS AFFINIS*

EXPERIMENT DESIGN	MEAN OF ANIMAL CAUGHT mean±SD(n)
BAIT IN SEALED PLASTIC BAGS	4±6(6)
BAIT IN PUNCTURED PLASTIC BAGS	5870±556(6)

APPENDIX TABLE 11

RESULTS OF FIELD EXPERIMENT ON FEEDING SOUND OF *ORCHOMENOPSIS AFFINIS* AS A SIGNAL TO GUIDE OTHERS TO THE FOOD SOURCE

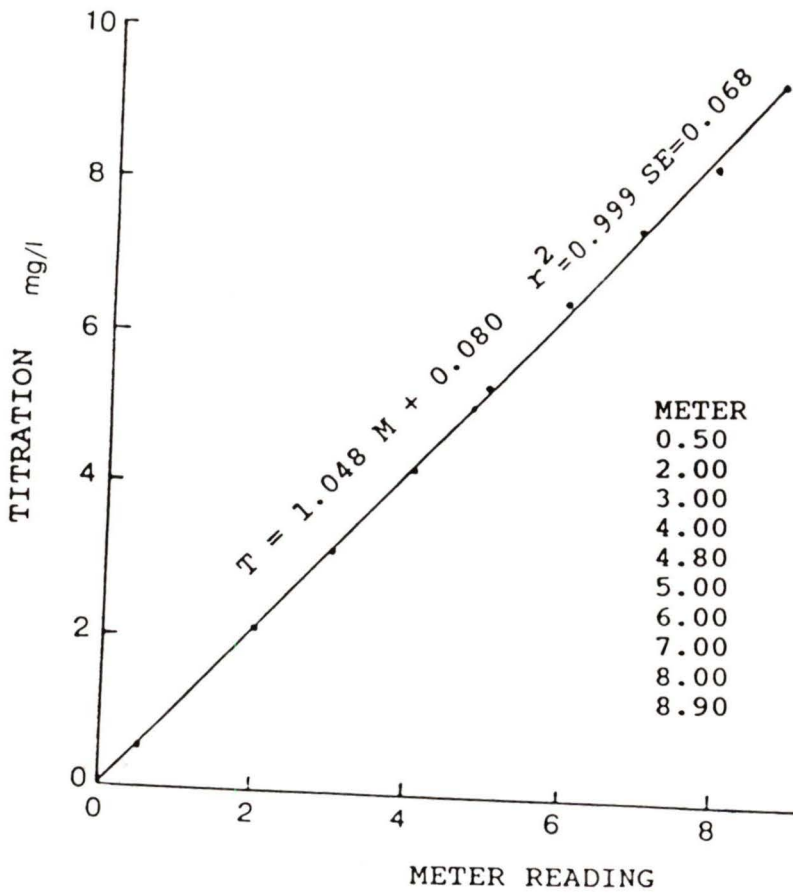
EXPERIMENT DESIGN	MEAN OF ANIMAL CAUGHT mean±SD(n)
SEALED BAITED BAGS WITH ANIMAL	8±12(6)
SEALED BAITED BAGS WITHOUT ANIMAL	6±5(6)

APPENDIX TABLE 12

VERTICAL TOW DATA USING A BOGOROV CLOSING NET
(April 3-4, 1987)

RANGE m	TOW	NOON #	NOON dw mg	DUSK #	DUSK dw mg	MIDNIGHT #	MIDNIGHT dw mg	DAWN #	DAWN dw mg
0-25	1	0	0	0	0	3	2.00	0	0
	2	0	0	0	0	1	0.45	0	0
	3	0	0	0	0	4	9.55	0	0
MEAN		0	0	0	0	2.67	4.00	0	0
BIOMASS/m^3		0	0	0	0	0.27	0.40	0	0
25-50	1	0	0	4	8.37	4	12.05	0	0
	2	0	0	1	2.83	4	6.06	0	0
	3	0	0	2	3.50	5	9.20	0	0
MEAN		0	0	2.33	4.90	4.33	9.10	0	0
BIOMASS/m^3		0	0	0.23	0.49	0.43	0.91	0	0
50-75	1	2	3.24	0	0	10	17.85	2	3.24
	2	1	1.40	4	4.20	2	3.75	2	3.68
	3	8	13.66	0	0	0	0	1	1.19
MEAN		3.67	6.10	1.33	1.40	4.00	7.20	1.67	2.70
BIOMASS/m^3		0.37	0.61	0.13	0.14	0.40	0.72	0.17	0.27
75-125	1	47	58.71	39	45.32	53	64.75	13	11.11
	2	59	99.09	30	52.08	35	70.66	2	7.44
	3	39	46.21	32	71.20	69	86.60	2	5.46
MEAN		48.33	68.00	37.00	56.20	52.33	74.00	5.67	8.00
BIOMASS/m^3		2.42	3.40	1.85	2.81	2.62	3.70	0.28	0.40
125-175	1	73	56.13	85	66.43	77	67.80	19	17.24
	2	12	12.63	23	26.61	92	92.33	9	4.21
	3	32	41.64	32	41.96	50	51.67	17	25.35
MEAN		39	36.80	46.67	45.00	73.00	70.60	15.00	15.60
BIOMASS/m^3		1.95	1.84	2.33	2.25	3.65	3.53	0.75	0.78
175-210	1	0	0	0	0	4	12.05	19	25.00
	2	0	0	0	0	12	13.24	34	34.05
	3	0	0	0	0	9	10.32	12	19.07
MEAN		0	0	0	0	8.33	11.87	21.67	26.04
BIOMASS/m^2		0	0	0	0	0.60	0.85	1.55	1.86
TOTAL BIOMASS/m^2		227.75	277.25	218.00	268.75	362.00	442.00	110.00	137.60

APPENDIX FIGURE 1
CALIBRATION OF OXYGEN METER



METER	TITRATION
0.50	0.58
2.00	2.19
3.00	3.18
4.00	4.25
4.80	5.10
5.00	5.37
6.00	6.50
7.00	7.45
8.00	8.35
8.90	9.40

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