THE DISTRIBUTION, RESPIRATION AND GILLS OF A LOW OXYGEN TOLERANT CRAB, *Munida quadrispina* (BENEDICT, 1902) (GALATHEIDAE, DECAPODA) IN AN INTERMITTENTLY ANOXIC FJORD

by

BRENDA JEAN BURD

B.Sc., Queen's University, 1979

ACCEPTED
FACULTY OF GRADUATE STUDIES
[redacted]
DEAN
DATE 1 June 83

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
in the department
of
Biology

We accept this thesis as conforming
to the required standard

[redacted]

[redacted]

[redacted]

[redacted]

UNIVERSITY OF VICTORIA
February 1983

ABSTRACT

Supervisor: Dr. R.O. Brinkhurst

Aspects of the ecology of the galatheid crab Munida quadrispina were examined as part of an overall study of the cliff community in Saanich Inlet, an oxygen depleted fjord. Using submersible and trap sampling, distributions of M. quadrispina were measured in Saanich and two other B.C. fjords. Respiration and gill measurements were made to examine possible low oxygen adaptations, and to compare with field information.

In Saanich, crabs were tolerant of oxygen levels ≥ 0.1 to 0.15 ml/l, where population density was always highest. Density distributions and total population estimates suggest that epibenthic crabs remained within these limits by vertical migration. Carapace length of adults increased significantly ($p = 0.01$) with decreasing oxygen, such that only the largest animals were present at limiting oxygen levels. This size gradient was not significantly different (ANCOVA $p = 0.01$) from that predicted by the relationship of carapace length and critical oxygen level (Pc) from respiration experiments, indicating that the size gradient was based on metabolism (rate of oxygen consumption). In large crabs from oxygen poor areas of Saanich, gill weight increased exponentially with body weight. However, gill weight increased linearly in *M. quadrispina* from other areas, and in *M. gregaria*. *M. quadrispina* from Saanich Inlet had a greater percent gill weight in low oxygen areas than in high oxygen areas, indicating that a cause and effect relationship exists between gill size and habitat oxygen.

[redacted]

R.O. Brinkhurst

[redacted]

J. L. Littlepage

[redacted]

R. Burke

[redacted]

G. Poulton

TABLE OF CONTENTS

Title Page i

Abstract ii

Table of Contents iv

List of Tables vii

List of Figures viii

Acknowledgement x

Introduction 1

  Study Area 3

  Benthic Studies in Anoxic Marine Basins 6

  Biology of Galatheids 9

  Aquatic Invertebrate Respiration 12

FIELD DISTRIBUTIONS OF <u>MUNIDA</u> <u>QUADRISPINA</u> 19

Methods and Materials 20

  Water Samples 20

  Submersible Dives 26

  Live Trapping 29

Results 31

  Water Samples 31

  Adult Depth Distribution 49

Table of Contents (continued)

Adult Population Density 56

Size Distribution with Depth from Trap Data 65

Size Distribution with Oxygen from Trap Data 65

Size Distribution with Depth from Phototransect Data 70

Depth Distribution of Juveniles 72

Behavioural Observations 78

Discussion 80

RESPIRATION OF *MUNIDA QUADRISPINA* 86

Methods and materials 87

Results 91

Discussion 100

GILL MORPHOLOGY OF *MUNIDA QUADRISPINA* 103

Methods and Materials 104

Results 105

Discussion 118

Summary 124

References cited 126

Table of Contents (continued)

Appendices

1. Density Distribution from phototransects in Saanich Inlet 135

2. Phototransect size distributions from Saanich Inlet 138

3. Weight/Size relationships of M. quadrispina 145

4. Trap sample size distributions from Saanich Inlet 147

5. Life History Extrapolations 149

LIST OF TABLES

Table 1. Sample Methods, Locations and Dates 23

Table 2. Estimated Abundance of *M. quadrispina* from each Phototransect 62

Table 3. Regression Equations for Carapace Length vs. Depth in *M. quadrispina* measured from phototransects 71

Table 4. Estimated Respiration Rates at 10°C of Different Species of Decapod Crustaceans 102

Table 5. Types and Numbers of Phyllobranche Gills in *M. quadrispina* and *M. gregaria* 117

Table 6. Estimated Carapace Length of *M. quadrispina* at Depth of Secondary Density Peak 151

LIST OF FIGURES

1. Sample areas 21

2. Example of scale photo from Pisces IV 27

3. Oxygen profile from McCurdy Point 32

4. Oxygen profile from Elbow Point 34

5. Oxygen profile from Finlayson Arm 36

6. Oxygen profile from Tozier Rock 38

7. Oxygen profiles from Howe Sound 40

8. Salinity profiles from McCurdy Point 43

9. Salinity profiles from Elbow Point 45

10. Salinity profiles from Finlayson Arm 47

11. Temperature profiles from McCurdy Point 50

12. Temperature profiles from Elbow Point 52

13. Temperature profiles from Finlayson Arm 54

14. Pisces IV photo of high density of M. quadrispina 57

15. Density distribution of M. quadrispina at McCurdy Point and Elbow Point 59

16. Frequency distribution of M. quadrispina in Howe Sound and Jervis Inlet 63

17. Carapace length vs. oxygen and depth from McCurdy Point trap data 66

LIST OF FIGURES (continued)

18. Carapace length vs. oxygen and depth from Elbow Point trap data 68

19. Juvenile distribution at McCurdy Point 73

20. Juvenile distribution at Elbow Point 75

21. Respiration apparatus 88

22. Examples of weight specific respiration rates in *M. quadrispina* 93

23. Relationships of weight specific respiration rates and Pc vs. wet weight in *M. quadrispina* 95

24. Comparison of carapace length vs. Pc and habitat oxygen relationships 98

25. Relationship of gill weight to organic body weight in *M. quadrispina* from Saanich Inlet 107

26. Relationship of gill weight to organic body weight in *M. quadrispina* from other B.C. areas and in *M. gregaria* 110

27. Mean % gill weight vs. habitat oxygen in *M. quadrispina* from Saanich Inlet 113

28. Phyllobranche gill of *M. quadrispina* 115

29. Setae on gill filament 115

30. Pore canal on gill lamella 115

ACKNOWLEDGEMENTS

This study was made possible by Dr. R.O. Brinkhurst, who provided the opportunity to use _Pisces IV_ and other facilities at the Institute of Ocean Sciences, and who gave of his time and talents in the production of this manuscript. I thank him sincerely for his support. Thanks are also extended to Dr. V. Tunnicliffe, who kept me motivated and taught me a great deal. The crew of _Pisces IV_ made the work fun and productive. I thank them for cheerfully putting up with the problems and work I gave them, and for their excellent performance. I also thank Dobrocky Seatech Ltd. for financial support, and the many others at the Institute of Ocean Sciences and the University of Victoria who helped the study in any way.

I especially thank Bill for patience, moral support, constructive criticism, and for caring.

INTRODUCTION

The fjords of North America, Europe, New Zealand and South America rank among the most productive coastal marine habitats (Brattegard 1979). Commercial and sports fisheries depend upon the combined freshwater, estuarine and marine habitats enclosed in these glacially carved basins. Aquaculture is especially well suited to the sheltered fjord environment, which is accessible and easily monitored. However, isolated fjord basins are often geomorphologically constructed to act as nutrient sinks due to limited bottom water renewal and low mixing resulting in strong vertical stratification of temperature and salinity. The resultant stagnation of bottom water leads to deoxygenation, which can adversely affect the benthic community, thereby limiting recycling of organic material in the fjord. Tolerance of the benthic community to oxygen depletion will greatly affect the productivity of such fjords.

Sampling of benthic invertebrates can be difficult in steep sided fjords. A considerable portion of the benthic fauna in these basins may occupy the sheer rock walls normally inaccessible to remote sampling devices. Therefore cliff fauna of fjords is largely undescribed below the depth accessible by SCUBA.

Tunnicliffe (1981) used the submersible Pisces IV to study the benthos in Saanich Inlet, an intermittently anoxic fjord. She found a high diversity and abundance in the epibenthic attached fauna in spite of the fluctuating oxygen conditions characteristic of this fjord (Herlinveaux 1962, Anderson & Devol 1973). The present study deals with the effect of oxygen fluctuations on the distribution of a mobile species in this community, the galatheid crab *Munida quadrispina* (Benedict, 1902). Sampling was carried out over a ten month period using the submersible *Pisces IV*, stationed at the Institute of Ocean Sciences at Pat Bay in Saanich Inlet. This vessel allowed close-up photography, water sampling and sediment and rock collection along the cliff, with minimum disturbance of the fauna.

A series of submersible dives made in Saanich Inlet in May of 1980 revealed that *Munida quadrispina* was the dominant mobile invertebrate species on the cliff. These crabs were present in large monospecific concentrations in severely oxygen depleted areas, with only one or two attached invertebrate species present (usually a small encrusting sponge and ocassionally a small anemone). It was hypothesized that the distribution of *M. quadrispina* in the severely oxygen depleted areas of Saanich Inlet was profoundly affected by abiotic factors, and in particular, oxygen.

The second part of the study involved measuring the respiratory capacities of *Munida quadrispina* for comparison with oxygen levels at which this species lives in the field, in order to determine if distributions of this species can be directly related to its ability to withstand low levels of oxygen.

Finally, the morphology and size of the gills of *Munida quadrispina* were examined to determine if they were affected by habitat oxygen conditions, as suggested by Jones (1972). In particular, the weight of the gills relative to organic body weight in *M. quadrispina* from Saanich Inlet was compared with similar measurements for *M. quadrispina* from other coastal areas of B.C. and with a pelagic species found in the western Pacific, *Munida gregaria* (Fabricius).

Study Area

The bulk of the study was carried out in Saanich Inlet, a fjord located on the south-east side of Vancouver Island. The main basin has a maximum depth of 236m. The cliff walls are gneissic substratum, partially covered with fine silt which is often deoxygenated below a water depth of 150m. The physical and chemical oceanography of Saanich Inlet has been studied by researchers for many years. Notable data contributions have been made by Herlinveaux (1962), Pickard (1961,1963), Richards (1965), Anderson & Devol (1973) and Emerson *et al*. (1979).

Saanich Inlet is isolated from outside water mixing below 150m by a shallow sill (70m) at the mouth of the Inlet. Bottom water renewal is thus prevented for about 8 months of the year. Consequently the deep water stagnates throughout the winter and summer, producing deoxygenation and a build-up of hydrogen sulfide to concentrations of 40um/l (Emerson et al. 1979), as well as other metabolic byproducts of anaerobic bacterial respiration. Hydrogen sulfide is only present in Saanich Inlet where oxygen is absent or in minute quantities (less than 0.1 ml/l, loc. cit. 1979). The reducing conditions in deep water often produce a distinct white particulate layer in the water composed of manganese, organic carbon (bacteria) and copper, which extends into oxygenated water to a concentration of about 0.15 ml oxygen/l (Emerson et al. 1979).

In late summer deep water with density greater than the bottom water of Saanich Inlet upwells off the coast of British Columbia and flows into Satellite Channel, then over the sill into Saanich Inlet, forcing deoxygenated water upwards to midwater depths and finally dispersing it (Herlinveaux 1962, Anderson & Devol 1973). By October or November, deoxygenated water has usually been forced up to its shallowest depth or dispersed (Pickard 1963) at the peak of flushing. After flushing, stagnation proceeds again. The flow characteristics of this dense flushing water were measured by Anderson & Devol (1973) using temperature-salinity characteristics and nitrate budget analysis, on the assumption that nitrate was a conservative constituent of the anoxic water.

Saanich Inlet has relatively low freshwater input from the Cowichan River North west of the sill, and a much smaller imput from Goldstream river at the head of the inlet (Pickard 1961). Strong vertical stratification of water density (Anderson & Devol 1972, Herlinveaux 1962) prevents mixing of the water column, hence the possiblity that Saanich Inlet has low productivity due to the effective nutrient sink produced by the anoxic layer. In fact 1°productivity is quite variable (Hobson, pers. comm.).

The hydrographic processes that produce stagnant conditions in fjords were described by Gade and Edwards (1979). Other anoxic fjords in B.C. include Indian Arm (Gilmartin 1962), Howe Sound (Levings 1980a), and Nitinat Lake.

For comparative purposes, the distribution of Munida quadrispina in relation to oxygen concentrations was examined in two other fjords along the B.C. coast. Two locations in Howe Sound were examined, one inside and one outside the inner sill. Howe Sound is about 300m deep. Bottom water is thought to be completely exchanged within the sill every three or four years (Bell 1973). Water characteristics have been examined by Pickard (1961), Bell (1973), and McDaniel et al. 1978). Benthic macrofauna was extensively sampled by Levings et al. (1980b) during a period of anoxia. The other fjord sampled in this study was Jervis Inlet, a deep (700m) fjord with a well flushed basin which does not develop anoxia. The water characteristics of Jervis Inlet have been examined by Pickard (1961) Lazier (1973) and McDaniel et al. (1978).

Benthic Studies in Anoxic Marine Basins

There are a number of common features that occur in the benthic macrofauna of oxygen depleted basins. In his review of this subject, Pearson (1979) stated that recovery from anoxia in marine basins is characterized by a rapid influx of small rapidly breeding opportunistic invertebrates, notably spionid and capitellid polychaetes. Furthermore, in intermittently anoxic areas the benthic community remains in the early successional stages in terms of diversity and abundance of species, with a steady decrease in biomass with increasing depth. Tunnicliffe (1981) disputed this in her study of the benthic epifauna of Saanich Inlet, since the community maintained a high diversity and abundance in very low oxygen concentrations. However, this controversy can perhaps be clarified by examining the differences between basins that are naturally and regularly anoxic, and those that are recently and artificially so.

Rosenberg (1979) was able to conclude from his survey of European fjords that naturally ocurring anoxia destroys more benthic life than oxygen depletion caused by pollution. It therefore seems ironic that polluted marine basins are more commonly studied than naturally anoxic ones. Pearson and Rosenberg (1978) described macrobenthic succession in several polluted marine basins in Europe that experience anoxia. These basins displayed occassional increases in abundance of a few opportunistic invertebrates which reproduce rapidly (i.e. polychaetes), a marked suppression of species in oxygen concentrations less than 0.7 ml/l and total lack of macrofauna below 0.21 ml/l oxygen concentration. The Bornholm Basin in Sweden is a polluted fjord in which oxygen concentration decreases to very low levels below 70m (Leppakoski 1969, Tulkki 1965). The most common animals trapped from the Bornholm basin during progressive oxygen depletion have been nematodes, nemerteans and polychaetes, including Capitella capitata, a cosmopolitan pollution indicator. The only crustaceans found by Leppakoski (1969) were two amphipod species, which were less hypoxia tolerant than the polychaetes.

Jorgensen (1980) described the typical community of Limfjorden in Denmark, which suffers from progressive pollution. The actual ennumeration of species present, and analysis of their distribution and behaviour during oxygen depletion were done by SCUBA. However, only a qualitative description was given of the species present. Mytilus edulis (mussel) were living in dense beds where water processing by the community was rapid and oxygen depletion accelerated, making these populations the most vulnerable to deoxygenation. The next populations to die during progressive oxygen decline included the shore crabs and shrimp, followed by polychaetes and lamellibranchs, and finally anemones.Jorgensen (1980) stated that most of the invertebrates present were limited by oxygen levels of 0.7 ml/l, as Pearson and Rosenberg (1978) had concluded. In Jorgensen's study anoxia was marked by a turbid, milky zone, much like that noted in Saanich Inlet during anoxic periods (Emerson *et al*. 1979).

In areas that experience natural anoxia due to geomorphological configuration, such as parts of the Baltic Sea, and certain European fjords (Rosenberg 1979), the devastation of benthic fauna due to anoxia can be extensive. In 1975, Rosenberg estimated that benthic biomass loss in the Baltic Sea due to anoxia was 1.7 million tonnes over an area of 84,000 square kilometres. In all areas of the Baltic examined during this period crustaceans were never among the hypoxia tolerant species found. However, such vast devastation is an uncommon event. In the Baltic, and in polluted basins, anoxia represènts an infrequent or recent event for which there is no evolutionary adaptation possible, producing what Pearson and Rosenberg (1978) refer to as community instability. The general consensus of such studies is that polychaetes, lamellibranchs, anemones and starfish are the most hypoxia tolerant groups found in oxygen depleted areas, and are often capable of anaerobiosis for extended periods (Hochachka 1980), followed by rapid reproduction upon recovery.

The species diversity and stability of the benthic macrofauna might be expected to be fairly stable in areas where the community has adapted over long periods of regular oxygen depletion. Tunnicliffe (1981) noted this phenomenon in Saanich Inlet.

Howe Sound in British Columbia experiences episodic anoxia for much the same reasons as Saanich Inlet (Levings 1980a). These two basins might be expected to have similar benthic communities. Levings listed the decapod crustaceans *Munida quadrispina* and *Spirontocaris sica* (Rathbun), as two of the species most consistently found (70% of samples) in the low oxygen areas of Howe Sound.

Biology of Galatheids

In recent years, a number of new galatheid species have been described by several authors (Pequenat & Pequenat 1970, Mayo 1972, Ambler 1980). It has become evident, through the recent revision of two *Munida* species, *subrugosa* (White) and *gregaria* (Fabricius) that the use of certain allometically affected characteristics for taxonomy are questionable in this family due to wide variation in form caused by environmental factors. Williams (1971, 1980) described progressive and substantial changes in the morphology of specimens identifed as pelagic *M. subrugosa* such that they were transformed into the benthic *M. gregaria* over a series of moults. This occurred when pelagic crabs were brought into the laboratory and allowed to settle to the bottom of tanks. The two species were therefore revised to Munida gregaria by Williams (1980). The plasticity of form exhibited by this species under different environmental conditions indicates that care is needed in identification of galatheid crabs.

Galatheids are found in a diversity of pelagic and benthic habitats including the Galapagos rift vents (Ballard 1979), northeast Pacific sea-mounts (Tunnicliffe pers. comm.) as well as many subtidal and abyssal habitats (Ambler 1980), wood fibre beds in British Columbia (McDaniel et al. 1977) and oxygen depleted habitats (Boyd 1967, Levings 1980b). The galatheid Pleuroncodes planipes (Stimpson) has been found in the plankton of the oxygen minimum layer off the coast of California and Mexico at oxygen levels of 0.1ml/l or less (Quetin & Childress 1976) and on the coastal shelf slope at oxygen levels of less than 0.5ml/l (Boyd 1967). Other galatheids inhabit the anoxic fjords of New Zealand (Zeldis pers. comm.).

Nicol (1932) reviewed the feeding habits of galatheids, indicating that most species are omnivorous, and that Pleuroncodes planipes sifts the substrate with its appendages to find food. In its pelagic form, this species is an obligate herbivore which concentrates in upwelling areas with dense plankton blooms (Blackburn 1977). Aside from this, there is very little known of the general habits of galatheids.

The two semi-pelagic species Pleuroncodes planipes and Munida gregaria have probably been studied more carefully than any other galatheid crabs. These species can spend the first several years of life in the plankton, but eventually settle to the bottom (Boyd 1967, Williams 1971). In both species, the largest animals reach a length of about 70mm and have a life span of three to four years (Boyd 1967, Williams 1980). They swim in swarms which provide important food for fish, porpoises and whales whereas the benthic stages are most commonly preyed on by bottom fish such as rockfish and lingcod (Blackburn 1977, Boyd 1967, Wilkie 1971). P.planipes has been found in the benthos on the continental shelf-slope off Baja California from 75m to 300m in an area affected by the oxygen minimum layer (Childress 1975), with the deepest crabs having a significantly greater carapace length than shallow ones (Boyd 1967). Therefore only the largest crabs live at oxygen levels < 0.5ml/l. This species was measured by Boyd (1967) at densities as high as $100/m^2$ in the plankton, though densities of $9-10/m^2$ commonly occur in the benthos. Biomass has been measured at $100g/m^3$ (Blackburn 1977) in the plankton. The benthic distribution of Munida gregaria is not known, although this species does swarm in the plankton of the Antarctic Ocean, where its distribution may be affected by temperature fluctuations (McWhinnie & Marceniak 1964).

There is no literature on the life history, habits or habitat of Munida quadrispina, though it is widespread in waters bordering Pacific Canada and the Northwestern United States.

Aquatic Invertebrate Respiration

The oceans contain numerous habitats that are constantly or occasionally anoxic. Partially as a result of this fact, there have been many investigations on respiratory physiology of aquatic invertebrates. Only relevant studies will be discussed here since this literature is so vast.

The literature is almost devoid of studies relating natural oxygen habitats to laboratory oxygen tolerances. Some general comparisons of this nature have been made on intertidal animals which must periodically close to prevent dessication or retreat into burrows and crevices which retain small amounts of slowly stagnating water. Such animals are readily studied in situ, or in the laboratory, since they are easily accessible. Teal and Carey (1967) actually measured the oxygen concentration in marsh burrows of the decapods *Uca pugnax* and *U.pugilator* prior to measuring their respiration. Thompson and Pritchard (1969) studied the oxygen tolerance of burrowing shrimp that would frequently encounter hypoxia in reduced sediments. Quetin and Childress (1976) and Childress (1975) measured the respiratory tolerance of a pelagic galatheid crab and other crustaceans for which the habitat oxygen range had been determined previously (Judkins 1979). The respiration of infaunal invertebrates such as oligochaetes has been measured since they are often found in anoxic sediments (Gnaiger 1980, Chapman *et al.* 1982). Some studies have attempted to compare respiration in animals from different habitats. Bridges and Brand (1980a) examined the difference in tolerance between burrowing and epibenthic crab species, discovering that the burrowing crab was more hypoxia tolerant than the epibenthic one. This general trend is not very surprising.

In designing experimental procedures for respiration experiments, several apparatus problems can arise. Continuous flow chambers require simultaneous calibration of inflow and outflow oxygen probes, with the difference being necessarily high enough to measure, making low respiratory rates difficult to measure (Famme 1982). However, it has long been suggested that the buildup of metabolites and bacteria may affect the respiration of animals in closed chambers. Teal & Carey (1967) indicated that bacterial respiration was negligible in the closed chambers used to examine <u>Uca pugnax</u> respiration. Bacterial accumulation can also be effectively prevented by the addition of antibiotics such as streptomycin (Quetin & Childress 1976). Excretion product buildup over 2 to 3 days is also a potential problem, expecially if the animals are fed just prior to, or during experiments. However, any effect of metabolites should be evident by a constantly increasing change in respiration rates during the experiment. Mangum & Van Winkle (1973) and Jones (1972) in fact concluded that carbon dioxide accumulation does not affect hypoxia survival in marine invertebrates. In the crustaceans tested this may have been due to internal buffering of the haemolymph with calcium carbonate from the exoskeleton (Defur *et al.* 1980, McMahon *et al.* 1978). It has even been suggested that carbon dioxide may enhance the uptake of oxygen by the respiratory pigments (i.e. reverse Bohr effect), allowing animals to regulate respiration to very low oxygen levels (Jones 1972, Butler *et al.* 1978, Hochachka 1980). Certainly crab respiratory pigments exhibit a Bohr shift caused by increased unloading of hemocyanin during hypoxia (Taylor *et al.* 1977).

Low oxygen tolerance is difficult to measure since depleted levels of oxygen must be maintained over long periods of time to test survival, and other complications (such as fouling) can occur during experiments. What is usually measured instead is the critical oxygen tension (Pc) at which animals can no longer regulate respiration independently of the ambient oxygen concentration. At oxygen levels less than Pc, respiration is dependent on ambient oxygen (i.e. oxygen conformity). There is no clear distinction between oxygen regulators and oxygen conformers. Measures have been developed to describe the degree of respiratory regulation of a given animal, by relating Pc/VO_2 (VO_2 = weight specific oxygen consumption) to Pc, giving a line with slope K1 and y intercept K2 (Tang 1933). A low K1/K2 indicates a substantial regulatory ability under given experimental conditions. However, there are no studies testing the ecological significance of Pc to invertebrate survival in the natural habitat.

Perhaps one of the most important factors affecting low oxygen tolerance is the amount of time the animal has to acclimate to the change, or the rate of change in ambient oxygen concentration (Jones 1972, Davis 1975, Bayne & Livingstone 1977, Schottler 1979). This is certainly a factor that could be important to the survival of benthic Munida quadrispina in Saanich Inlet, since anoxic water can develop and move quickly. In the laboratory the rate of change in oxygen concentration is affected by the volume of water in the chamber in relation to the size of animal. Rapid changes in oxygen concentration due to low volume of water during experiments on decapod crustaceans can temporarily change oxygen regulators into oxygen conformers (Thompson & Pritchard 1969).

Acclimation to the experimental conditions and time that animals are kept in the laboratory are also thought to affect oxygen consumption in invertebrates (Bayne 1971, Taylor 1976, Bayne & Livingstone 1977, Butler et al. 1978). For example, animals kept in the laboratory for long periods may have increased oxygen consumptions compared to fresh specimens, indicating that changes occur in physiological condition over a long period within the lab.

Physical factors that can affect metabolism and cause stress reactions have been studied in invertebrates. Temperature increases of about 10°C can decrease hypoxia tolerance and double oxygen consumption, since metabolism is increased at higher temperatures (Johanssen 1965, Theede et al. 1969, Winget

1969, Belman & Childress 1973, Davis 1975, Taylor et al. 1975, Laird et al. 1976, Quetin & Childress 1976, Taylor et al. 1977, Butler et al. 1978).

Normal and stress related increase in activity of animals may also increase respiration, since more oxygen is needed at the increased metabolic rate necessary to maintain activity (Ayers 1938, Vernberg 1956, Bayne 1971, Davis 1975, Bayne & Livingstone 1977, Butler et al. 1978). However, increased activity in the lab can be considerably reduced by acclimation to the experimental chamber (Bayne 1971, Taylor 1976, Bayne & Livingstone 1977, Butler et al. 1978). Changes in respiration caused by bursts of activity should be readily detectable as sudden increases in oxygen consumption by the animal if oxygen levels are constantly monitored.

Reduction of activity to a minimum level is thought to be an adaptation to the effects of hypoxia in invertebrates and fish (Davis 1975) but some lactate accumulation will still occur in mobile species which must maintain some activity under hypoxic or anoxic conditions (Teal & Carey 1967, Taylor et al. 1977, Pritchard & Eddy 1979, Bridges & Brand 1980b). Some sedentary burrowing crustaceans such as Callianassa genus can withstand anoxia for several days by accumulating a measurable lactate concentration or oxygen debt (Felder 1979), though large mobile crustaceans are not normally considered to have any long term tolerance of anoxia

(Hochachka 1980). Other invertebrates such as attached or tube dwelling forms can survive exposure to anoxia for extended periods by switching completely to anaerobic respiration (loc.cit. 1980).

Respiration demands increase substantially during moulting in crustaceans (Laird et al. 1976, Thompson & Pritchard 1969), due to a burst of activity and increase of permeability of the exoskeleton which necessitates metabolic imput into internal regulation. A 2.5 fold increase in respiration has been recorded during ecdysis in Crangon vulgaris (Hagerman 1976). This makes moulting animals more sensitive to changes in environmental oxygen conditions (Hagerman 1976). This suggests that newly settled juvenile crustaceans may be more vulnerable to changes in habitat conditions than adults.

Other physiological stress conditions that have been shown to affect hypoxia tolerance include poor nutrition (Bayne et al. 1977, Leffler 1973), change in pH (Mangum 1972, Theede et al. 1969), and the presence of hydrogen sulfide (Theede et al. 1969), though Theede et al. (1969) showed no conclusive difference in survival of decapods in anoxic and in anoxic+H_2S conditions (no statistical test was done). Hydrogen sulfide is often present in the sediments in Saanich Inlet (F. Whitney, pers. comm.) and in anoxic water (Anderson & Devol 1973), and its effects on benthos are largely unknown.

Typical physiological responses of decapod crustaceans to reduced oxygen tension include:

1. Decrease in heart rate (Thompson & Pritchard 1969, Taylor et al. 1977) and decrease in heart output (Taylor 1976).
2. Increase in scaphognathite beat and ventilation volume (Butler et al. 1978, McMahon et al. 1974, Larimer 1961, Taylor 1976, Taylor et al. 1977) which increases the oxygen uptake by the gills.
3. Decrease in oxygen saturation of haemocyanin or increase in oxygen contribution to tissues by the respiratory pigments (Jones 1972, McMahon et al. 1974, Taylor 1976).
4. Increase in haemocyanin production (Fox 1949, Jones 1972).
5. Accumulation of oxygen debt (McMahon et al. 1974, Pritchard & Thompson 1979, Taylor et al. 1977, Teal & Carey 1967).
6. Possible reverse Bohr effect at high carbon dioxide and low oxygen (Jones 1972) and increase in oxygen affinity of haemocyanin (Butler et al. 1978). It has also been suggested that a buildup of CO_2 in the haemolymph is buffered by dissolution of calcium carbonate from the exoskeleton (McMahon et al. 1978, Defur et al. 1980) allowing the animal to withstand large oxygen debts.

FIELD DISTRIBUTIONS OF *Munida quadrispina*

METHODS AND MATERIALS

Three locations at the head of Saanich Inlet were sampled extensively from May of 1980 to March of 1981. These locations were chosen because they are far from the sill, or flushing source of the inlet. For this reason, oxygen depletion is extensive and prolonged. The three areas are McCurdy Point (48°33.6'N,123°31.5'W) Elbow Point (48°32.8'W,123°31.9'W) and Finlayson Arm (48°31.5'N,123°32.3'W) (Figure 1). Tozier Rock and Bamberton (48°34.6'N,123°31.1'W) in Saanich Inlet were sampled once.

Locations outside of Saanich Inlet that were sampled one or more times included Port Mellon (49°31.3'N,123°27.9'N) and Brittania Beach (49°37.3'N,123°13.25'W) in Howe Sound and Dark Cove (49°48.5'N,123°57.0'W) in Jervis Inlet. Sample methods, locations and dates are summarized in Table 1.

Water Samples

Niskin bottle casts were done from the IOS launchs "Squamish" and "Sea-truck" to sample water from 20m to 200m at the three main sample locations in Saanich Inlet. Dissolved oxygen analysis was done using a modified Winkler titration method (Strickland & Parsons 1972). Oxygen sampling was also done in situ by obtaining external water samples through a port during submersible dives. These samples were usually obtained within 2m of the cliff, fixed immediately and later analysed aboard ship by Winkler titration.

Figure 1. Sample areas 1 = McCurdy Point, 2 = Elbow Point, 3 = Finlayson Arm, 4 = Bamberton, and 5 = Tozier Rock in Saanich Inlet on Vancouver Island, British Columbia.

Enclosed section shows sampling areas 6 = Port Mellon and 7 = Brittania Beach in Howe Sound, and sample area 8 = Dark Cove in Jervis Inlet, British Columbia.

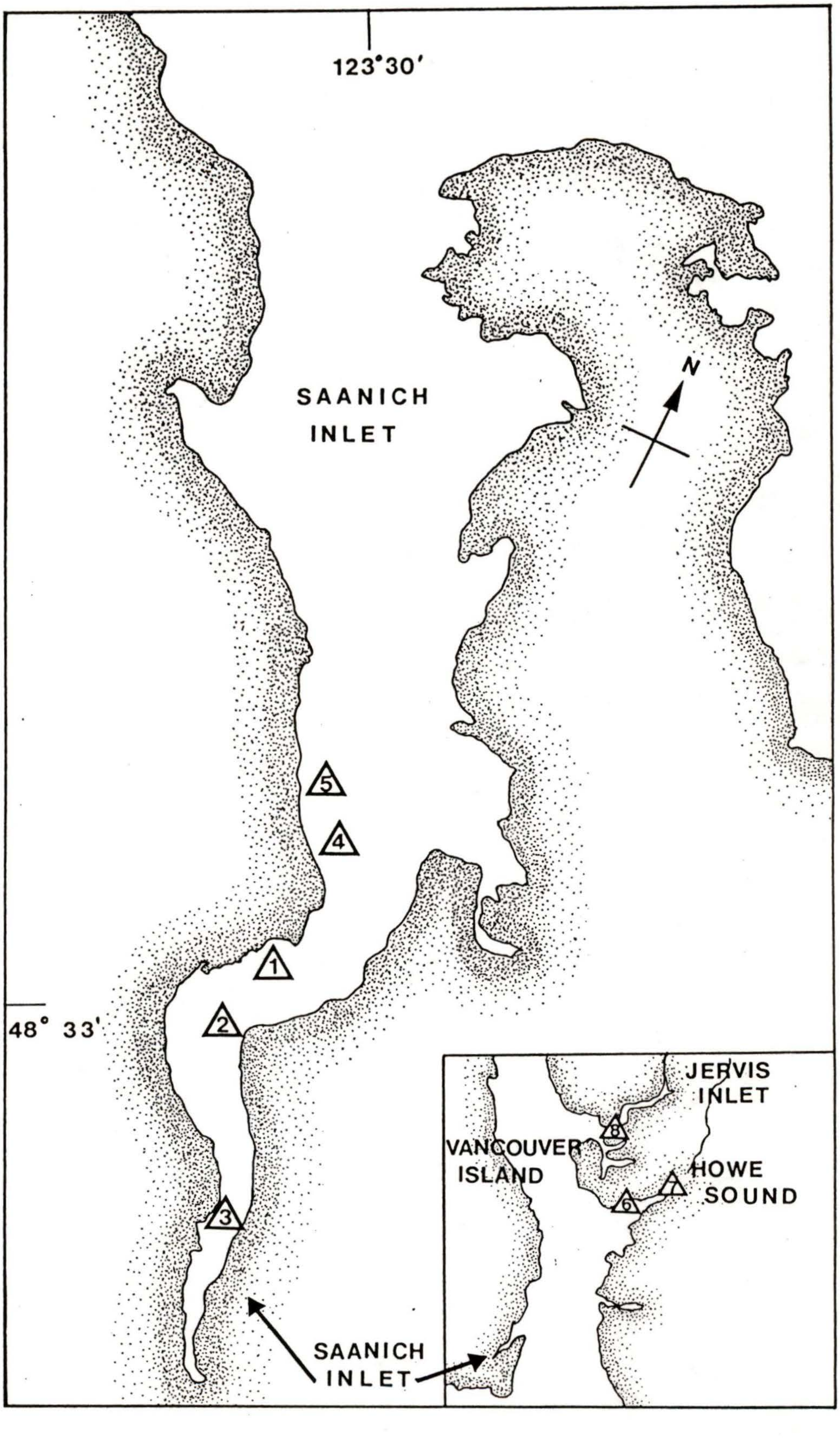

123°30'
SAANICH
INLET
N
5
4
1
2
48° 33'
3
SAANICH
INLET
JERVIS
INLET
8
VANCOUVER
ISLAND
HOWE
SOUND
6
7

Table I. Sample methods, locations and dates

Date	Location	Dives		Oxygen	Traps
1980		Phototransect	Observation		
May 15*	McCurdy Pt	-	+	*	-
May 15*	Elbow Pt	-	+	*	-
June 15	Dark Cove	-	+	-	-
July 16*	McCurdy Pt	-	-	*	-
July 16*	Elbow Pt	-	-	*	-
July 16*	Finlayson	-	-	*	-
Aug 19*	McCurdy Pt	-	-	*	+
Aug 19*	Elbow Pt	-	-	*	+
Aug 19*	Finlayson	-	-	*	-
Sept 3	McCurdy Pt	+	+	+	+
Sept 2,4	Elbow Pt	+	+	+	+
Sept 5	Bamberton	-	+	-	-
Sept 5	Tozier Rock	+	+	-	-
**Sept 29,30	Dark Cove	+	+	+	-
Oct 16*,23	McCurdy Pt	+	-	*+	+
Oct 16*,23	Elbow Pt	+	-	*+	+
Oct 16*	Finlayson	-	-	*	-
Nov 13*20,25,27	McCurdy Pt	+	+	*+	+
Nov 13*18,19,27	Elbow Pt	+	+	*+	+
Nov 13*18,19	Finlayson	+	+	*+	-
Dec 4*	McCurdy Pt	-	-	*	-

Table 1 continued

Date	Location	Dives		Oxygen	Traps
1980		Phototransect	Observation		
Dec 4 *	Elbow Pt	-	-	*	-
Dec 4 *	Finlayson	-	-	*	-
1981					
Jan 15 *	McCurdy Pt	-	-	*	-
Jan 15 *	Elbow Pt	-	-	*	-
Jan 15 *	Finlayson	-	-	*	-
Feb 3,4,18*	McCurdy Pt	+	+	*+	+
Feb 3,5,18*	Elbow Pt	+	+	*+	+
Feb 2,18*	Finlayson	+	+	*+	-
**Feb 23	Dark Cove	+	+	+	-
Mar 23*,24,26	McCurdy Pt	+	+	*+	+
Mar 24,25	Elbow Pt	+	+	+	+
Mar 19	Port Melon	+	-	+	-
Mar 17	Brittania	-	-	+	-
May 26 *	McCurdy Pt	-	-	*	+
May 26 *	Elbow Pt	-	-	*	-
May 26 *	Finlayson	-	-	*	-
July 30 *	McCurdy Pt	-	-	*	-
July 30 *	Elbow Pt	-	-	*	-
July 30 *	Finlayson	-	-	*	-

Table I continued

Date	Location	Dives		Oxygen	Traps
1981		Phototransect	Observation		
Aug 7 *	McCurdy Pt	-	-	*	-
Sept 30*	McCurdy Pt	-	-	*	-
Sept 30*	Elbow Pt	-	-	*	-
Sept 30*	Finlayson	-	-	*	-
Nov 17*	McCurdy Pt	-	-	*	-
Nov 17*	Elbow Pt	-	-	*	-
Nov 17*	Finlayson	-	-	*	-

* Bottle cast sampling

** Data supplied by V. Tunnicliffe

Data was combined from multiple sample sets i.e. Sept 29,30

Oxygen data for February 1980 was supplied by Ocean Chemistry at the Institute of Ocean Sciences. Several reagent sets and sample methods for oxygen analysis were compared. Data from bottle casts was combined with submersible data (all oxygen values were ± 0.05ml/l). Values <0.1ml/l were not considered accurate due to possible contamination by H_2S (Whitney, Anderson, pers.comm.).

Temperatures were measured by duplicate reversing thermometers on the Niskin bottles and temperature probe in Pisces IV. Salinity was calculated by measuring conductivity of water samples.

Submersible Dives

Sampling from the submersible consisted of taking several photographs every 5 or 10m in depth up the cliff face, using two 35mm cameras. The slides were taken using 160 ASA Ektachrome film specially designed for use with tungsten lights, such as those mounted outside the viewports of the Pisces IV. In phototransect dives a rubber bumper arm extended out from the front of the submersible below the viewport, supporting a 30x30cm square frame on the distal end. This frame was placed gently against the cliff and photographed (Figure 2). M.quadrispina did not move away from the frame unless touched, never moving more than a few centimetres. The area of the photograph, carapace length of visible animals and number per unit area could be calculated by projection of the colour slides onto a screen, using the scale as a measurement reference. All usable photographs were as nearly vertical in plane

Figure 2. Example of scale photograph taken through the viewport of *Pisces IV* at Finlayson Arm on November 18, 1980 at 88m depth. Area of reference square = $0.09m^2$.

as possible, though some distortion due to the angle of the photograph was unavoidable. Patchiness error in population density calculations was reduced somewhat by determination of mean number of crabs per square metre from several photographs at each depth, plus or minus standard error. However, population density was only used as a comparison of relative abundances of animals. The relationship between carapace length and depth was examined using regression analysis. In the observational dives photographs were taken without the reference scale. From these dives the depth limits and approximate abundances of the *Munida quadrispina* populations could be determined.

All *Munida quadrispina* except for newly settled juveniles were large enough to identify. Animals to a minimum of about 0.5cm folded length were therefore measured from the photographs. These measureable animals will be referred to as adults, although they may represent immature specimens as well. Depth of occurrence of benthic and pelagic juveniles was recorded during each dive although density could not be calculated from the phototransects.

In February of 1981, one hour was spent at 83m, Elbow Point to observe aggression and feeding behaviour of the *M. quadrispina*.

Live Trapping

Adult *Munida quadrispina* were obtained by trapping at McCurdy Point and Elbow Point. Traps made of 40cm lengths of 15cm diameter PVC pipe with two conical mesh ends were weighted and the traps baited with fresh salmon. Nine traps were attached at 20m intervals to a 554m terelyne line. The deep end was weighted, with a 1/4 Volt 27 cycles per second pinger attached to the weight. The line was lowered along the cliff and tied to shore. The pinger was then located from the submersible Pisces IV so that the line could be followed from bottom to top. Each trap along the line was thereby located and photographed. Depth, substrate and orientation of the traps were recorded. Oxygen samples were taken at most trap depths.

In both May and June of 1981, four traps had to be lowered to specific depths predetermined by depth sounding and checked by line length as the traps touched bottom. This was necessary since the submersible was unavailable and precise depth was not known.

All traps were left for three days before recovery. The animals collected by trap were sexed, measured for carapace length and width, total length, and were then preserved in 70% alcohol for later examination. Size distribution of Munida quadrispina with depth and oxygen were calculated using regression analysis, combining all trap data collected from McCurdy Point and from Elbow Point respectively. In this way it was possible to see if the size distributions obtained from trap animals was similar to that measured from phototransects. On four occasions large trap catches were brought to the lab and kept in a large tank to qualitatively observe aggression and feeding behaviour.

RESULTS

Water Samples

The cyclic change in oxygen concentration measured at the three main sample areas in Saanich Inlet is illustrated in Figures 3,4 and 5. The complete cycle of oxygen depletion and replenishment which is an annual event in Saanich Inlet (Anderson & Devol 1973, Herlinveaux 1962) can be clearly observed. Oxygen concentrations at the three main sample areas of Saanich Inlet varied from 0 to 5.5 ml/1 from the bottom up to 30m (the upper limit of benthic Munida quadrispina).

At McCurdy Point (Figure 3) and Elbow Point (Figure 4), anoxia developed in April 1980 and dissipated before October 23. An influx over the sill of dense oxygenated bottom water began in late August of 1980, forcing the anoxic layer upwards to a midwater depth in September of 1980 and finally dissipating anoxia in October. Flushing ended before January of 1981, and progressive stagnation of the water column resulted in the development of a second anoxic layer by May 1981, which disappeared by late August. A second anoxic period did not develop at Finlayson Arm (Figure 5), possibly because the anoxic layer observed at McCurdy Point and Elbow Point did not penetrate as shallow as the bottom depth at Finlayson Arm.

Figure 3. Oxygen profile with depth from February 1980 to November 1981 at McCurdy Point in Saanich Inlet, with emphasis on the 0.1 to 0.15 ml/l oxygen zone (lightly shaded), and showing that maximum depth of penetration by *Munida quadrispina* adults (open circles) is within this zone. Oxygen levels from 0.1 to 0 ml/l are darkly shaded, with anoxia black.

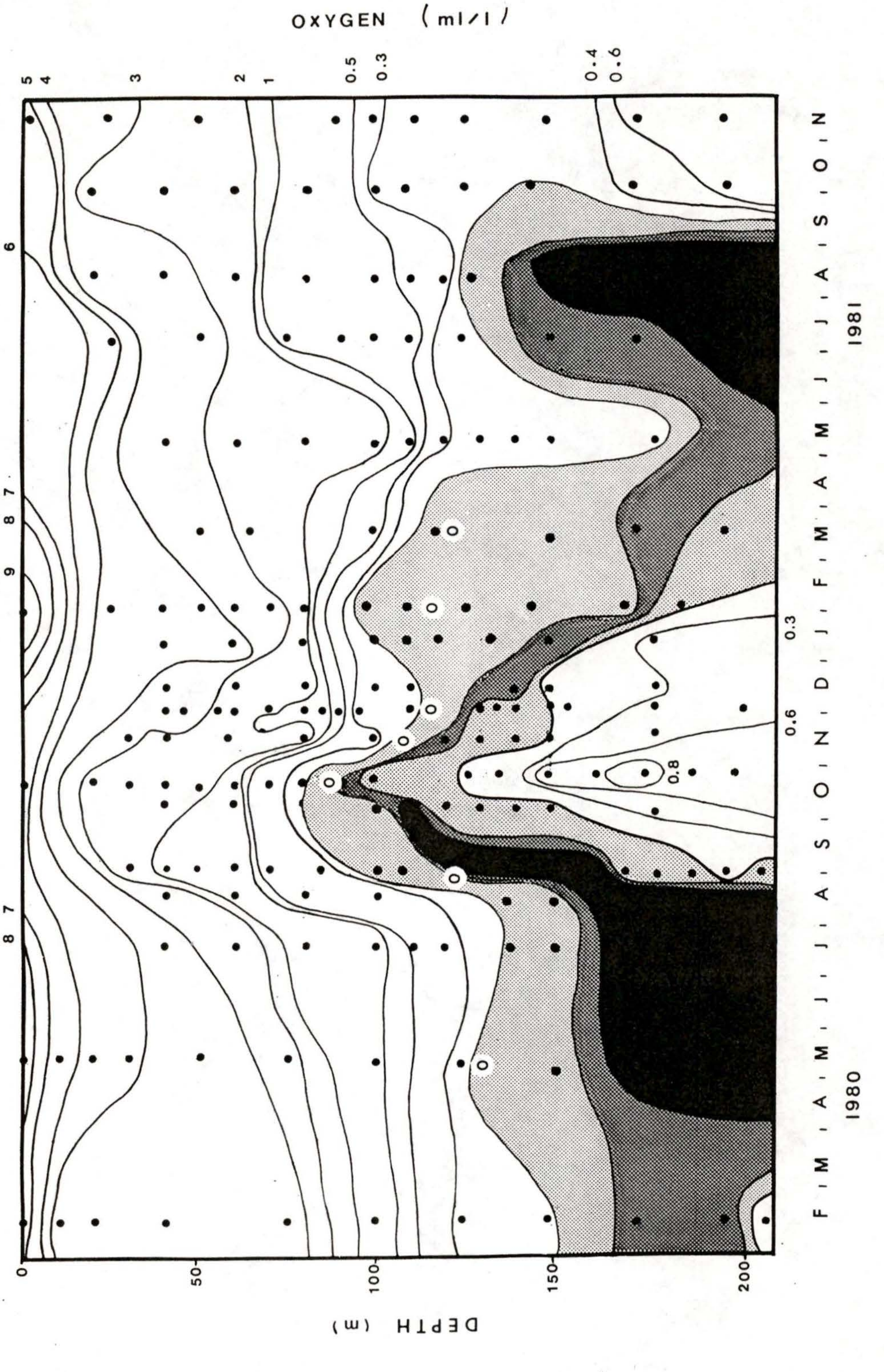

OXYGEN (ml/l)
5
4
3
2
1
0.5
0.3
0.4
0.6
6
8
7
9
8
7
8
7
0.3
0.6
0.8
DEPTH (m)
0
50
100
150
200
F M A M J J A S O N D J F M A M J J A S O N
1980
1981

Figure 4. Oxygen profile with depth from February 1980 to November 1981 at Elbow Point in Saanich Inlet, with emphasis on the 0.1 to 0.15 ml/l oxygen zone (lightly shaded), and showing that maximum depth of penetration by *Munida quadrispina* adults (open circles) is within this zone. Oxygen levels from 0.1 to 0 ml/l are darkly shaded, with anoxia black.

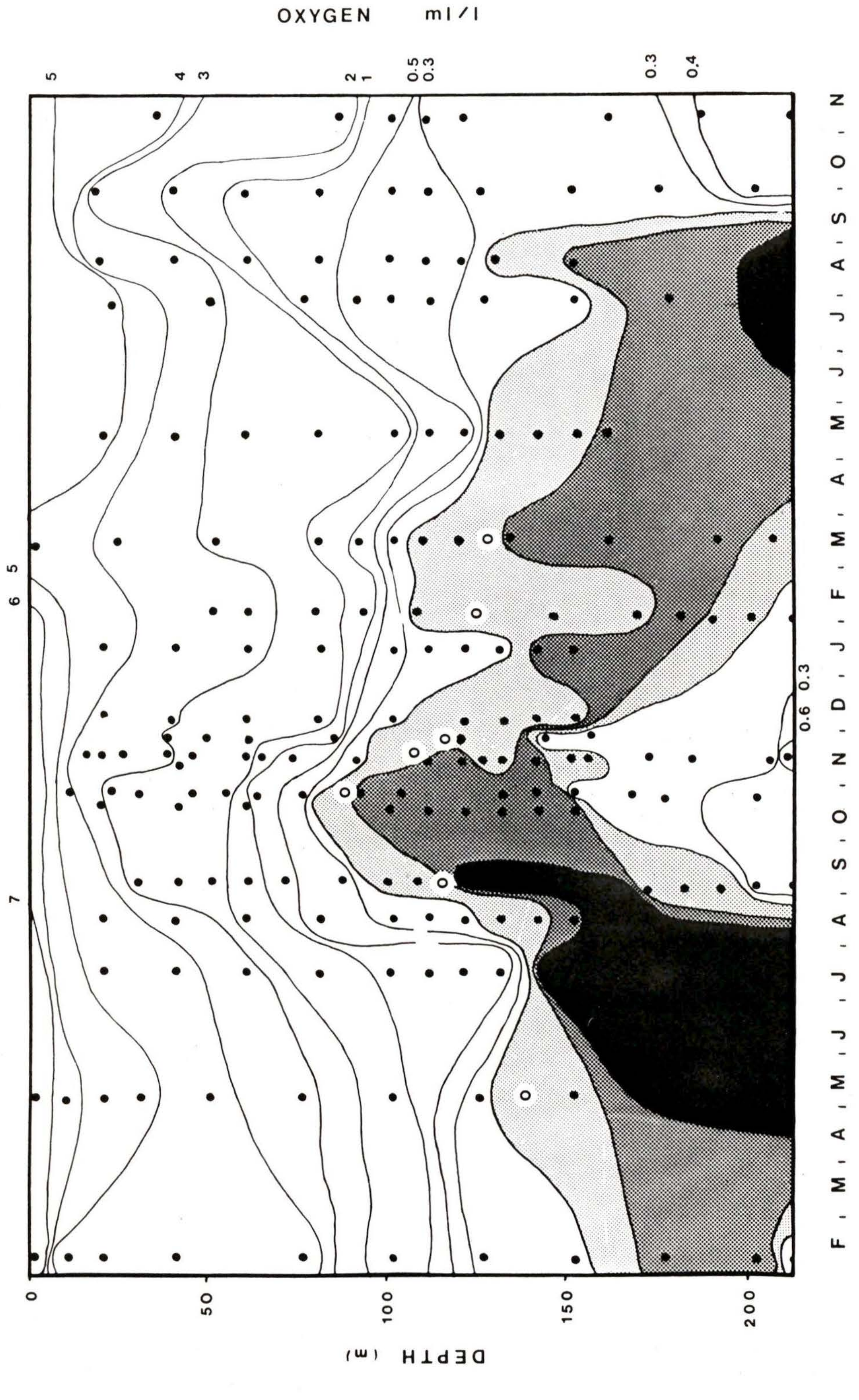

OXYGEN ml/l
5
4
3
2
1
0.5
0.3
0.3
0.4
6
5
7
0.6
0.3
F M A M J J A S O N D J F M A M J J A S O N
DEPTH (m)
0
50
100
150
200

Figure 5 . Oxygen profile with depth from July 1980 to November 1981 at Finlayson Arm in Saanich Inlet, with emphasis on the 0.1 to 0.15 ml/l oxygen zone (lightly shaded), and showing that maximum depth of penetration by Munida quadrispina adults (open circles) is within this zone. Oxygen levels from 0.1 to 0 ml/l are darkly shaded, with anoxia black.

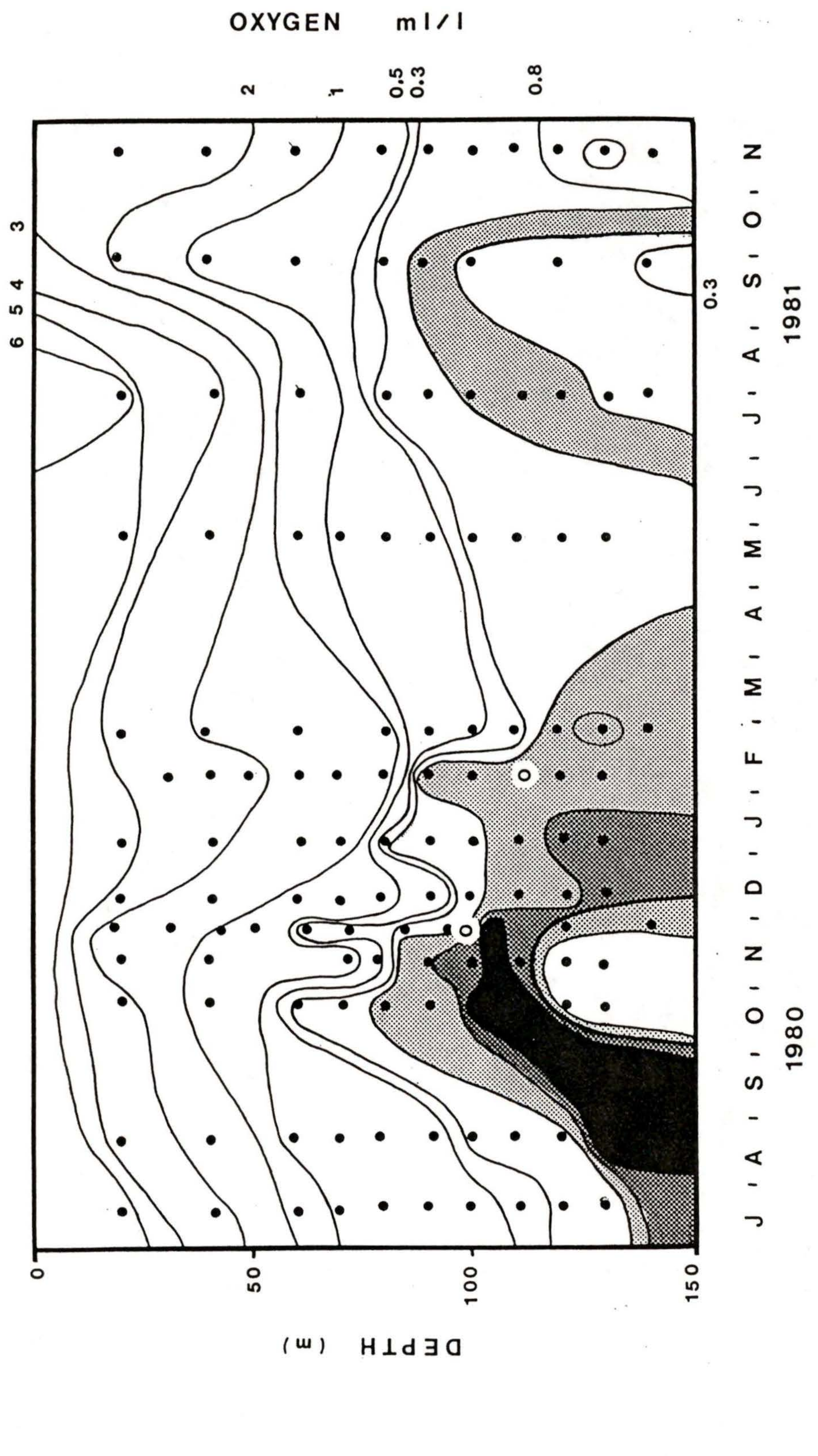

OXYGEN ml/l
2
1
0.5
0.3
0.8
6 5 4
3
0.3
J A S O N D J F M A M J J A S O N
1980
1981
DEPTH (m)
0
50
100
150

Figure 6. Oxygen profile with depth for September 4 1980 at Tozier Rock in Saanich Inlet.

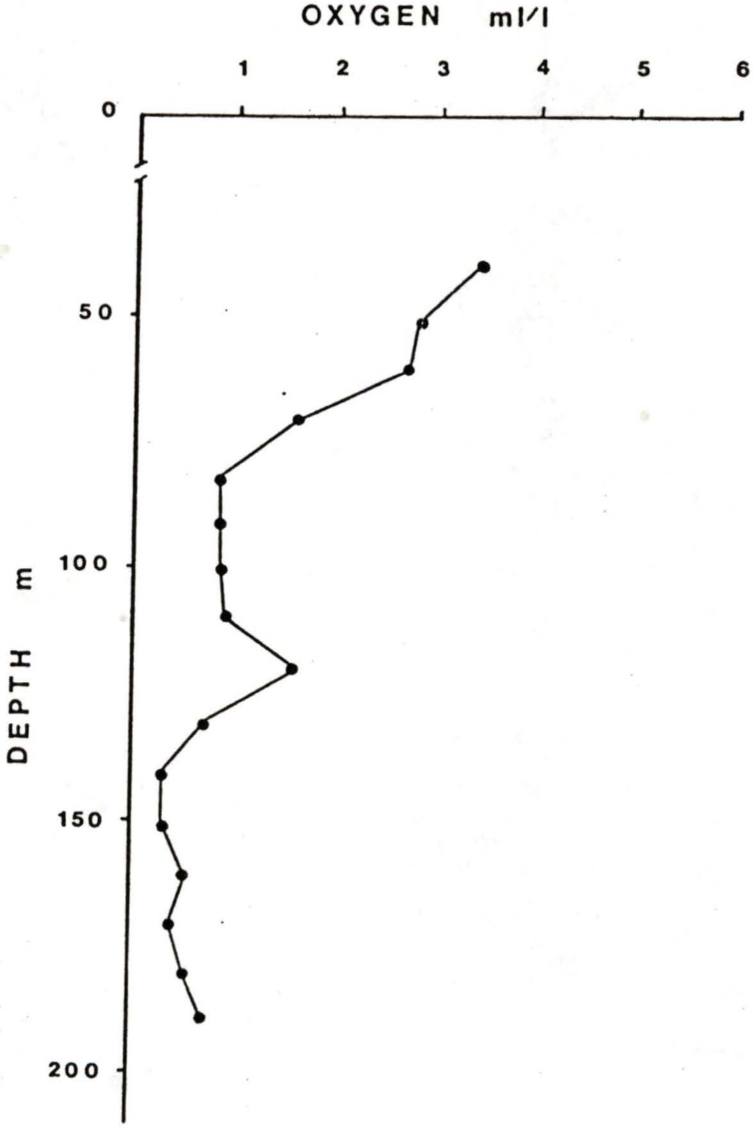
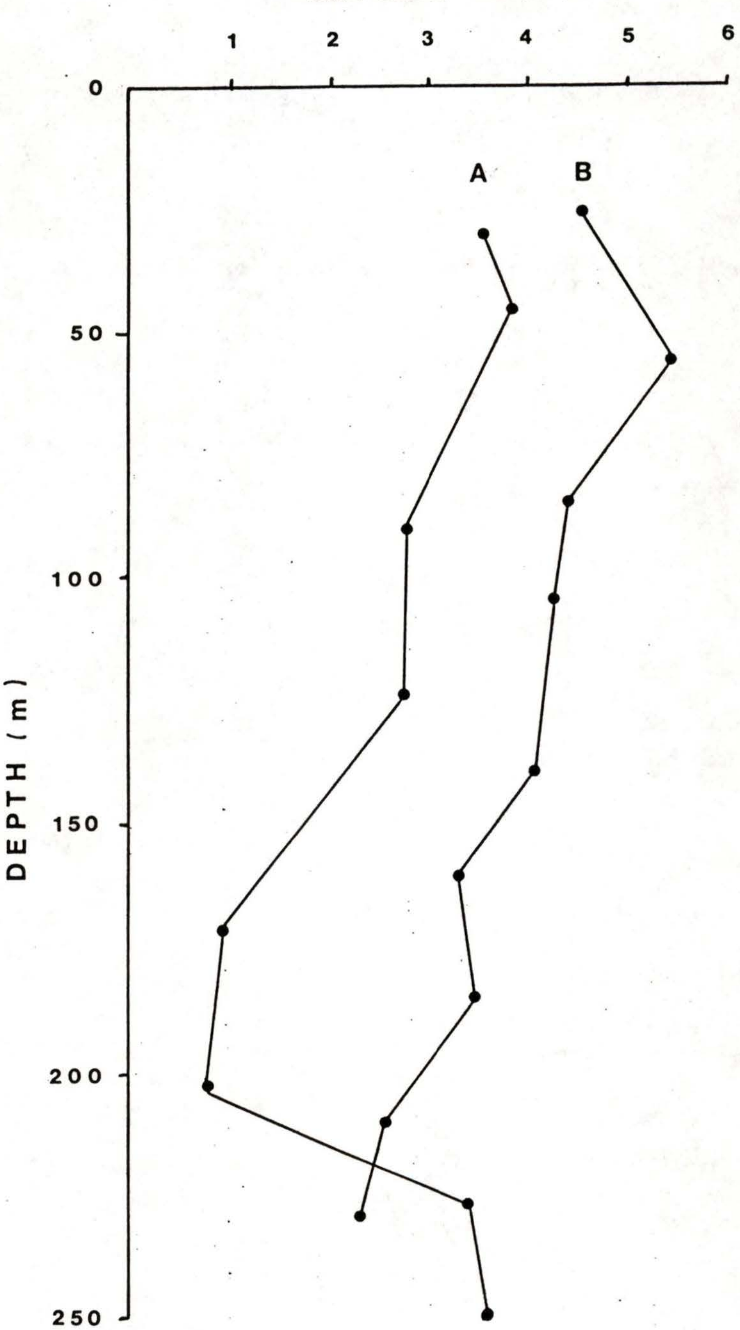

OXYGEN ml/l
1
2
3
4
5
6
0
50
100
150
200
DEPTH m

Figure 7. Oxygen profiles with depth for A = Brittania Beach and B = Port Mellon, Howe Sound in March 1981.


OXYGEN (ml/l)
1
2
3
4
5
6
0
50
100
150
200
250
DEPTH (m)
A
B

At Bamberton and Tozier Rocks in Saanich Inlet, oxygen valueswere lowest at 140 to 150m in September of 1980. However, the oxygen minimum did not go below 0.3 ml/l (Figure 6). At Port Mellon in Howe Sound oxygen was higher than 2.3 ml/l at all depths in March of 1981 (Figure 7), whereas the oxygen minimum was as low as 0.6 ml/l at Brittania Beach. Anoxia has been recorded at Brittania Beach (Levings 1980a) which is inside the inner sill of Howe Sound. Oxygen was greater than 2.8 ml/l at all depths at Dark Cove, Jervis Inlet in September 1980 and February 1981 (Tunnicliffe, unpublished data).

Salinity values for McCurdy Point, Elbow Point and Finlayson Arm ranged from 29.5 to 31.25 ppt (Figures 8,9 and 10) below 30m over the entire sample period. A fairly consistent pycnocline was evident from 20-40m at Elbow Point and Finlayson Arm (sampling at McCurdy Point was 40m and deeper only). The influence of surface fresh water input into Saanich Inlet (less that 50m) was evident in January and July at McCurdy Point, Elbow Point and Finlayson Arm, which conforms with past data collected by Herlinveaux (1962) and Pickard (1963). Salinity levels were similar throughout the sample period at other locations in Saanich Inlet, Jervis Inlet and Howe Sound (data not shown).

Figure 8 . Salinity profiles for McCurdy Point. A = July 1980, B = October 1980, C = November 1980, D = December 1980, E = January 1981, F = March 1981, G = July 1981, H = September 1981.

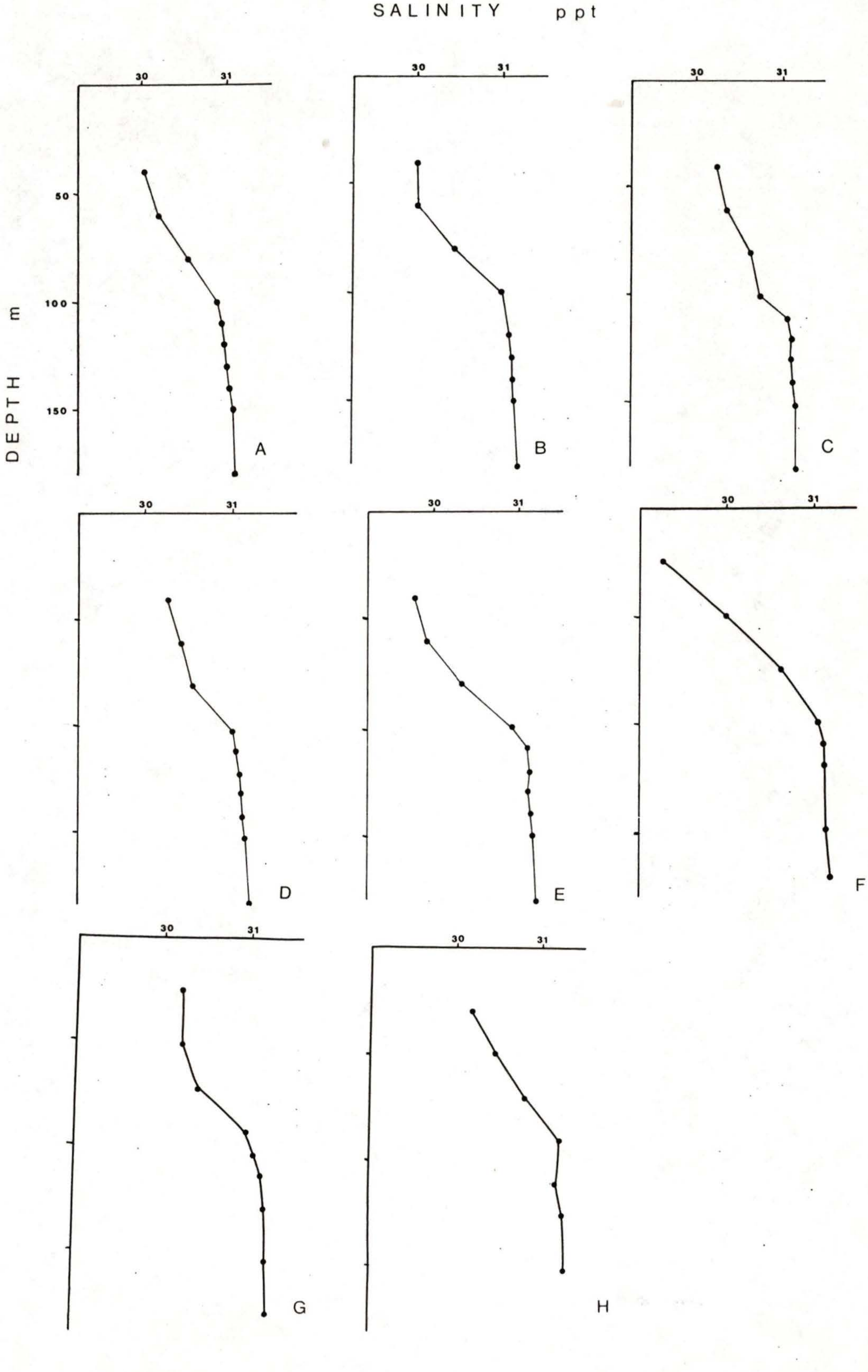

SALINITY ppt
DEPTH m
30
31
50
100
150
A
B
C
D
E
F
G
H

Figure 9. Salinity profiles for Elbow Point. A = July 1980, B = October 1980, C = November 1980, D = December 1980, E = January 1981, F = March 1981, G = July 1981, H = September 1981.

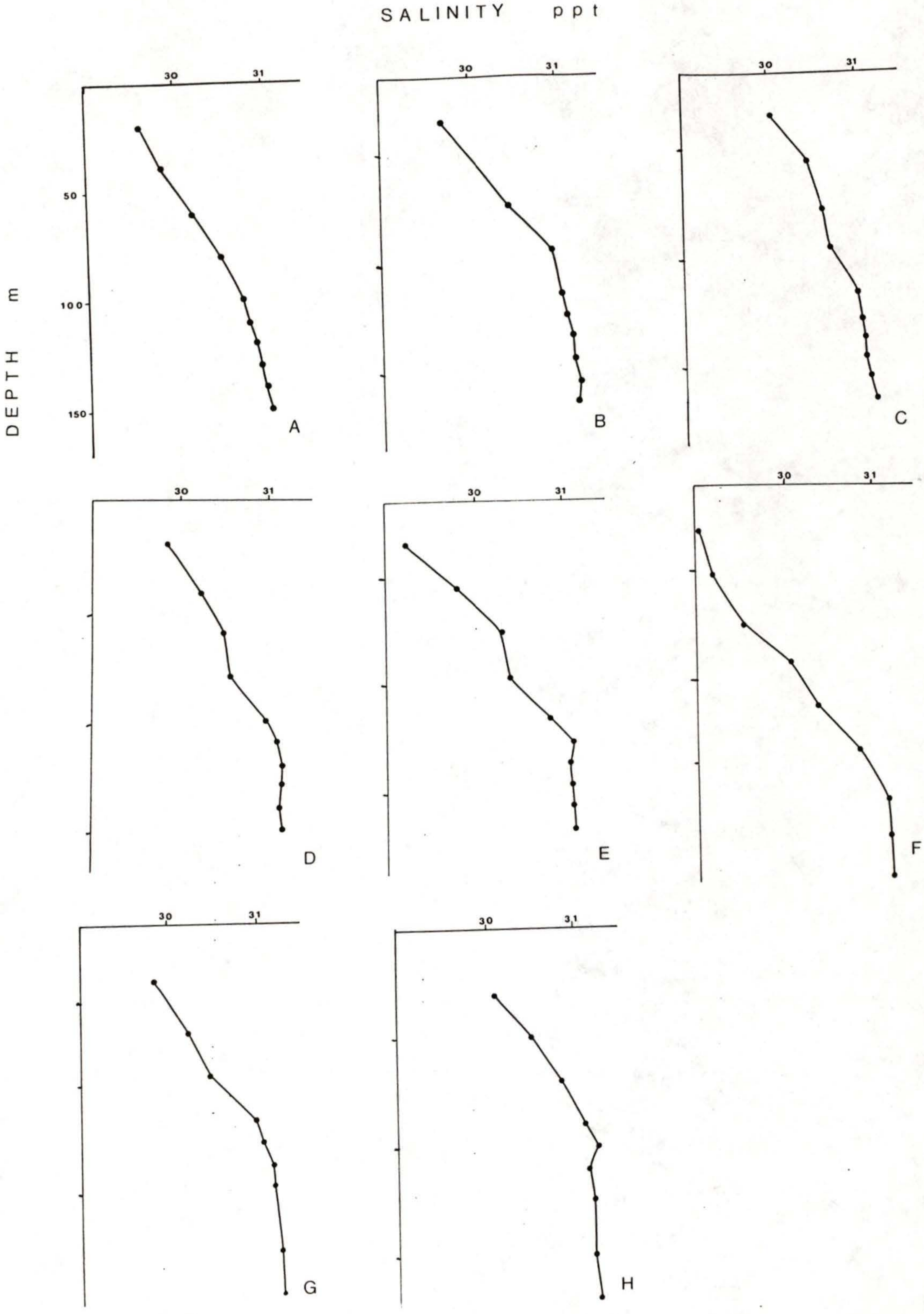
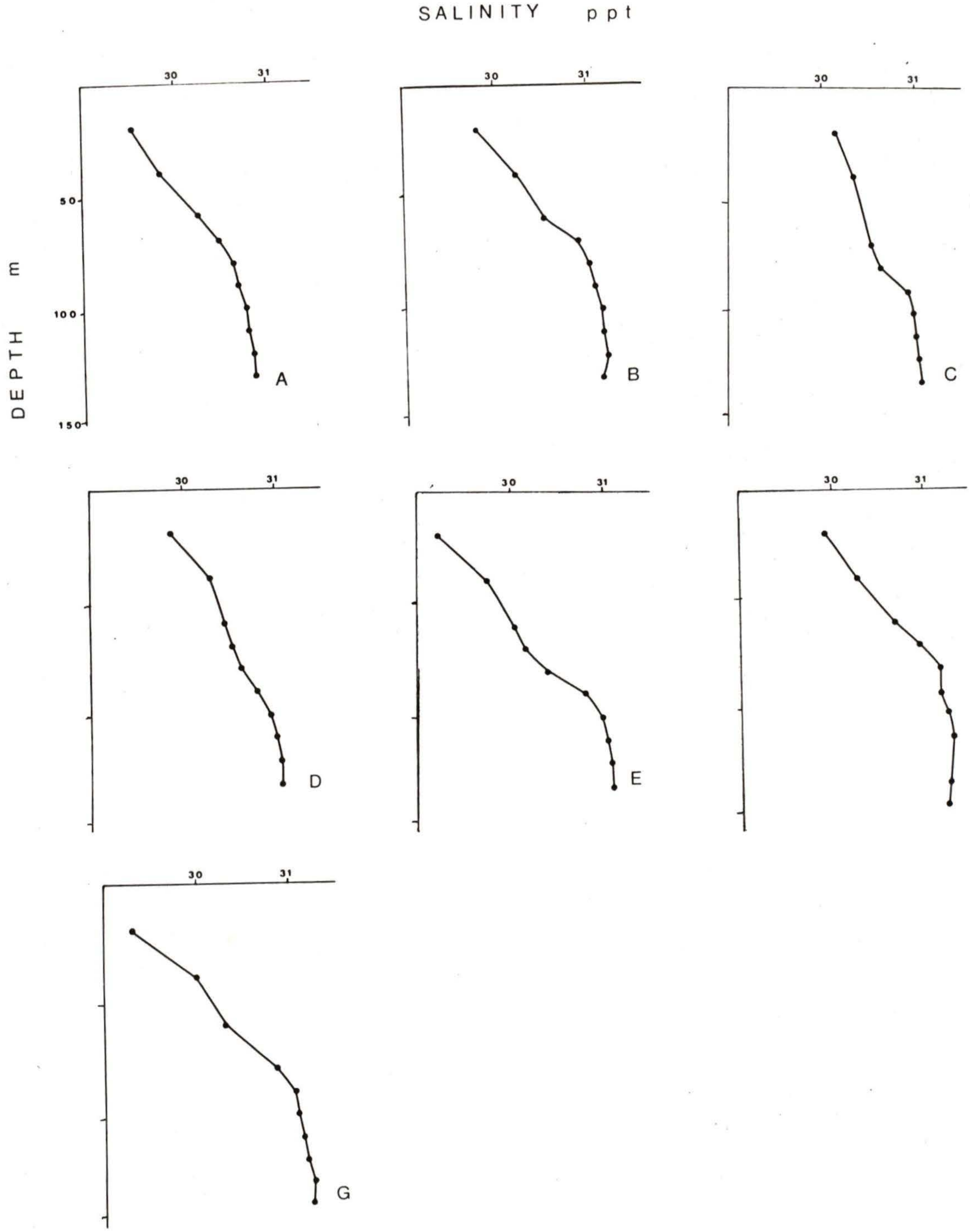

SALINITY ppt
DEPTH m
30
31
50
100
150
A
B
C
D
E
F
G
H

Figure 10. Salinity profiles for Finlayson Arm. A = July 1980 B = October 1980, C = November 1980, D = December 1980, E = January 1981, G = July 1981, H = September 1981.


SALINITY ppt
DEPTH m
30
31
50
100
150
A
B
C
D
E
F
G

Temperatures below 30m ranged from 8.5°C to 11.0°C (Figures 11,12 and 13) at the three main locations in Saanich Inlet. Warming of subsurface waters was maximal in October. There was little change in temperature from 100m to bottom throughout the year. In January of 1980, a reverse profile, with upper water colder that deep water was evident. A thermocline occurred at 20-40m in the summer. Temperature profiles for other sampled areas are not shown but were similar to those in Saanich Inlet.

Physical water characteristics of McCurdy Point, Elbow Point and Finlayson Arm were typical of patterns described for Saanich Inlet based on many years of data (Herlinveaux 1962, Anderson & Devol 1973, Pickard 1963). However, unlike the oxygen conditions described in previous years, the main basin of Saanich Inlet did not experience deoxygenation during this study (Guest, Whitney, Burd, unpublished data). This illustrates that the oxygen cycle in Saanich Inlet varies from year to year.

Adult Depth Distribution

Adult *Munida quadrispina* were limited to depths at which oxygen concentration was greater than 0.1 to 0.15 ml/l. The deepest penetration of the fjord by *M. quadrispina* in these areas therefore varied from month to month in relation to the oxygen cycle (Figures 3,4 and 5).

Figure 11. Temperature profiles for McCurdy Point. A = July 1980 B = August 1980, C = October 1980, D = November 1980, E = December 1980, F = January 1981, G = March 1981, H = May 1981, I = September 1981.

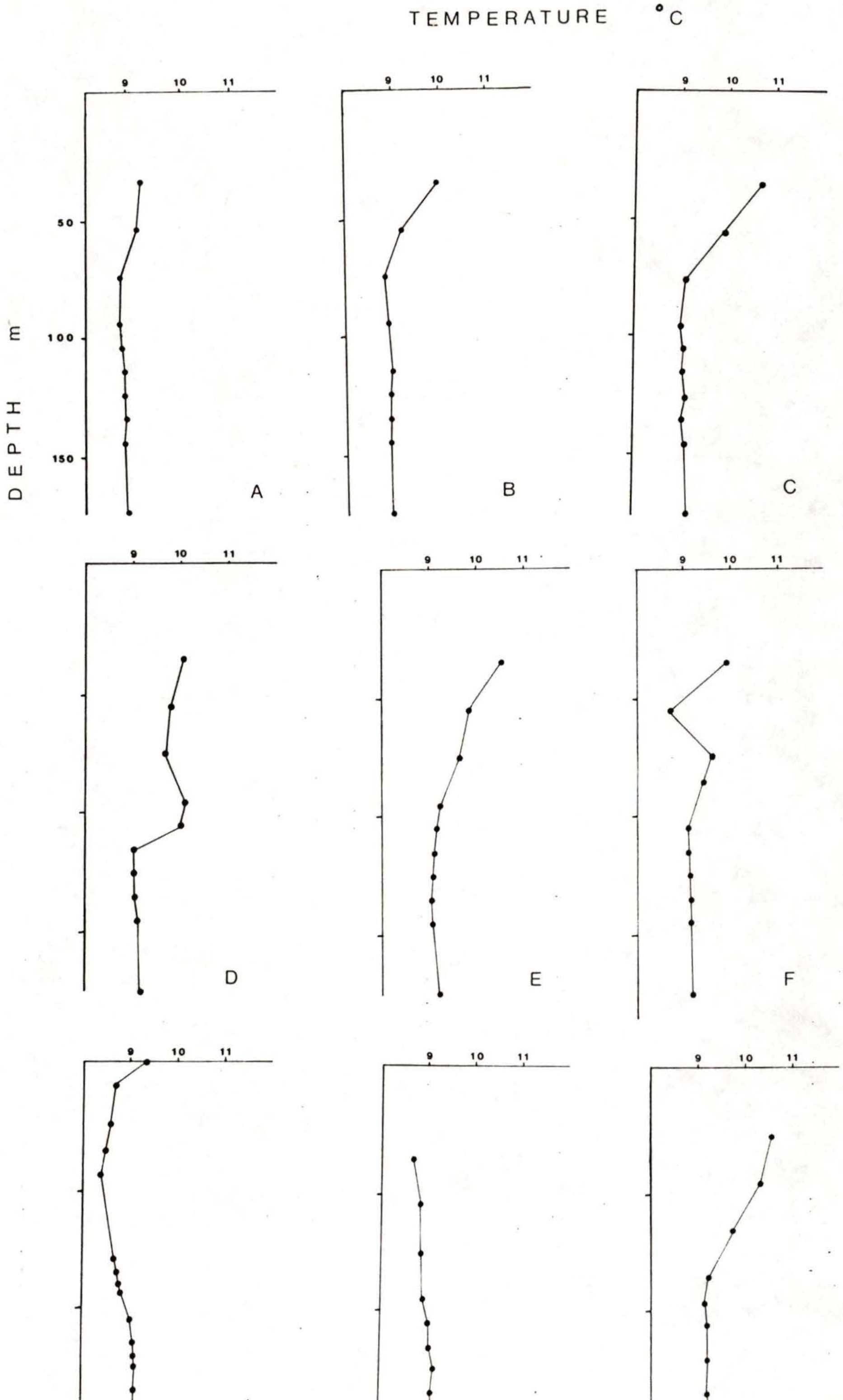

TEMPERATURE °C
DEPTH m
9
10
11
50
100
150
A
B
C
D
E
F
G
H

Figure 12. Temperature profiles for Elbow Point. A = July 1980 B = August 1980, C = October 1980, D = November 1980, E = December 1980, F = January 1981, G = May 1981, H = September 1981.

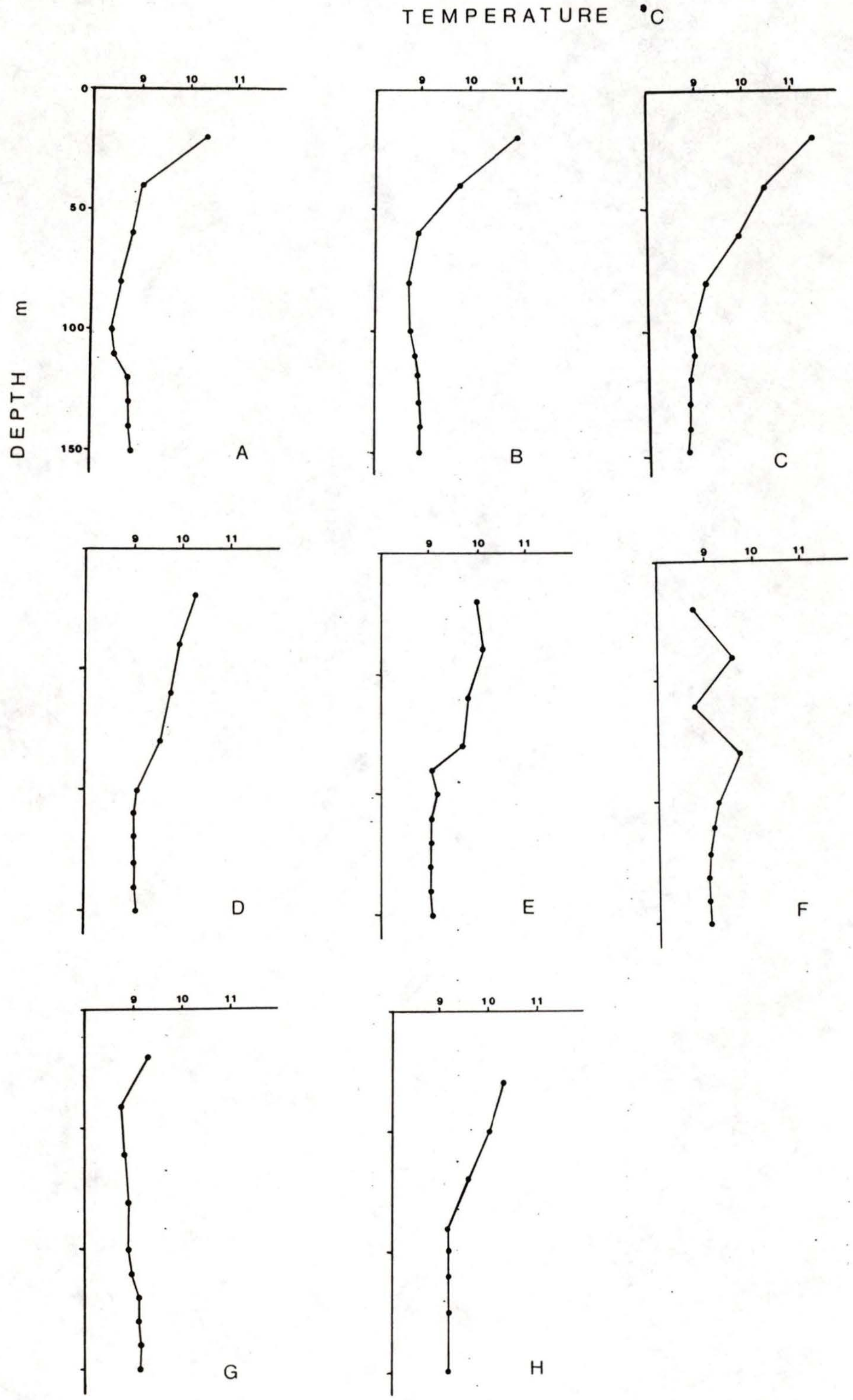
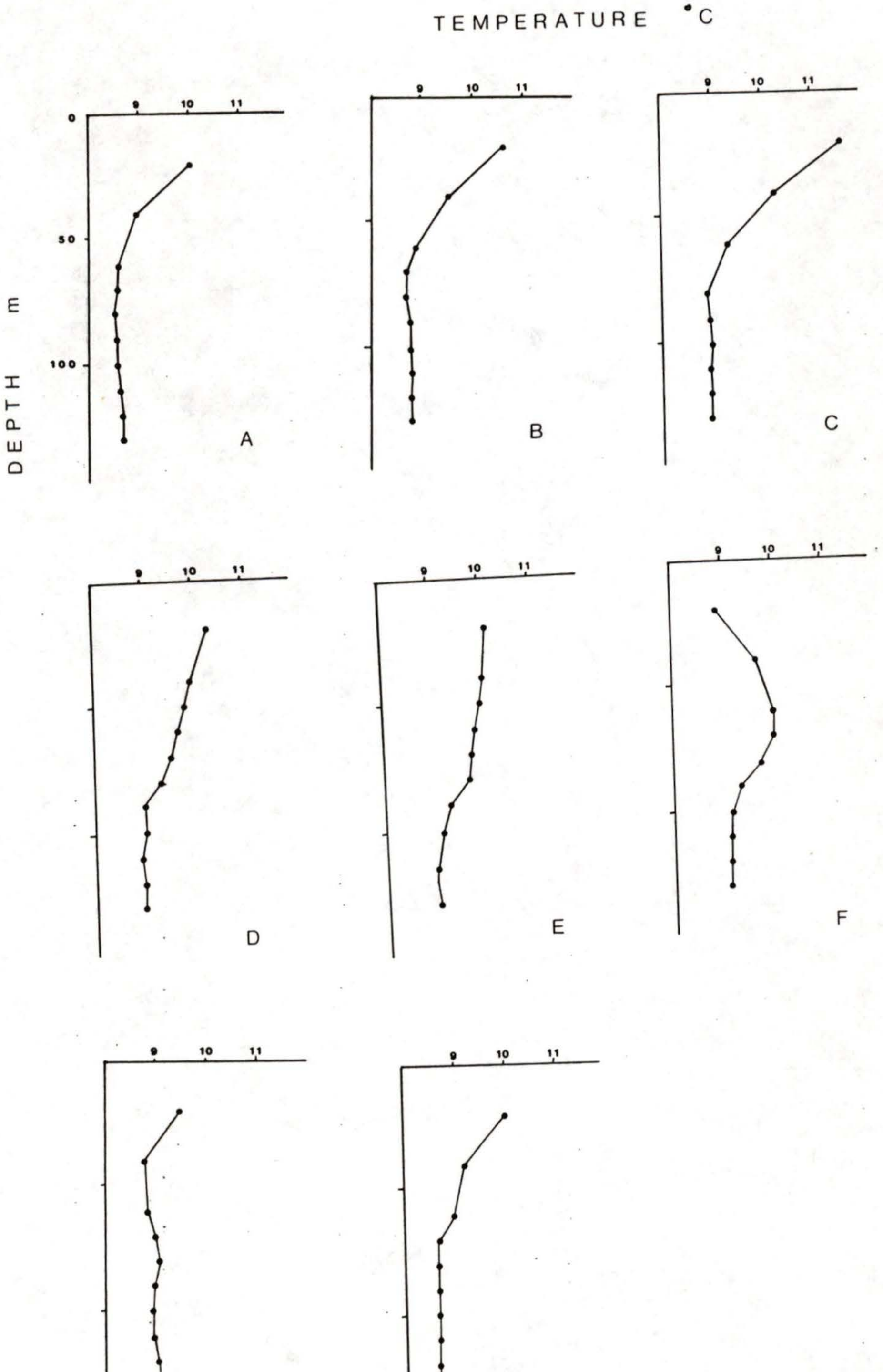

TEMPERATURE °C
DEPTH m
9
10
11
0
50
100
150
A
B
C
D
E
F
G
H

Figure 13 . Temperature profiles for Finlayson Arm. A = July 1980. B = August 1980, C = October 1980, D = November 1980, E = December 1980, F = January 1981, G = May 1981, H = September 1981.


TEMPERATURE °C
DEPTH m
0
50
100
9
10
11
A
B
C
D
E
F
G
H

At Dark Cove in Jervis Inlet, *Munida quadrispina* were found all the way to the bottom of the cliff (680m) in June and September 1980 and in February of 1981. *M. quadrispina* were also present at the bottom of the cliff at Port Mellon (230m) and Brittania Beach (280m) in March of 1981. At these three locations oxygen levels were above 0.65ml/1. At Bamberton and Tozier Rocks in Saanich Inlet *M. quadrispina* were also recorded at the bottom (190m) in September of 1980, at which time oxygen levels were greater than 0.3 ml/1.

Adult Population Density

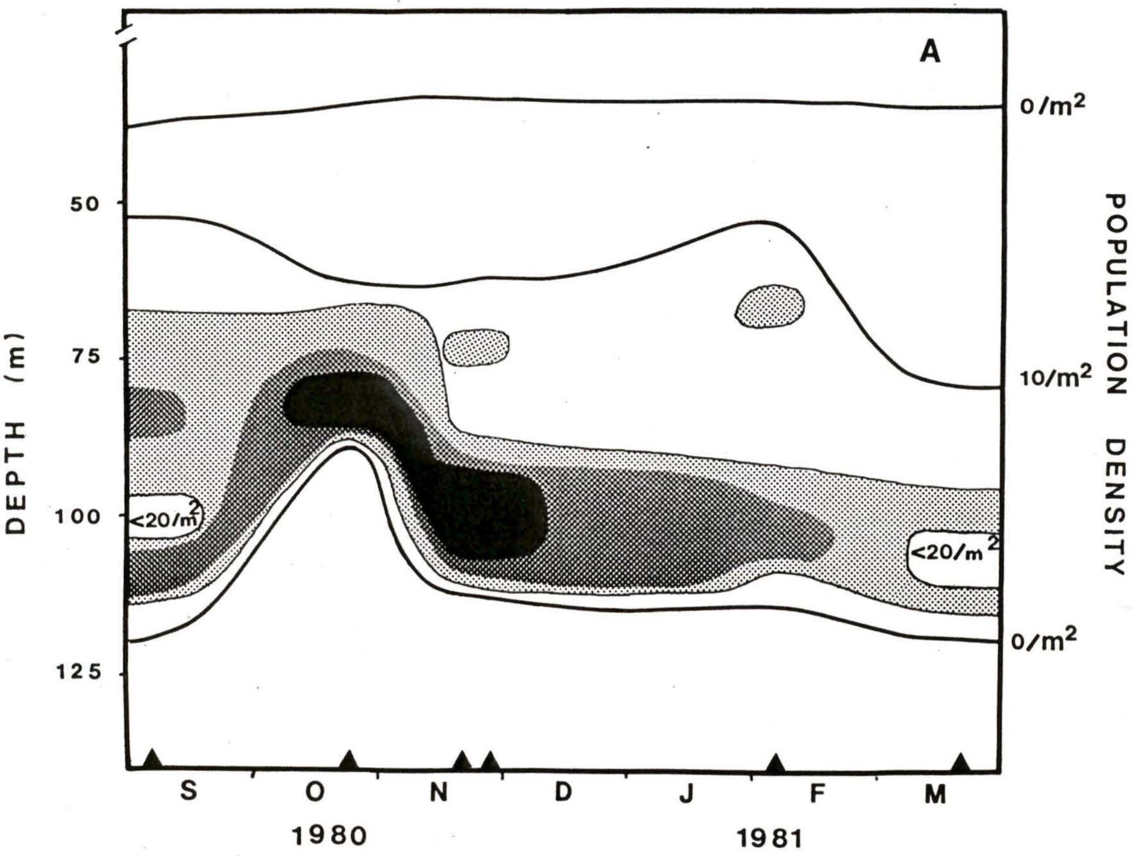
Maximum density of *Munida quadrispina* always occurred within the 0.1 to 0.15 ml/1 oxygen zone. The crab population appears to have been compressed upwards during upwelling of deoxygenated water (Figure 14) in October and November of 1980. A large number of dead adults were not observed just below the limiting oxygen concentration layer at that time. The density peak reached a maximum of >100 crabs per square metre in October and November at Elbow and McCurdy Points (Figure 15), when the limiting oxygen layer was shallowest. However, after the limiting oxygen layer moved downward, the population spread out again with the maximum density reduced to about 50 crabs per square metre.

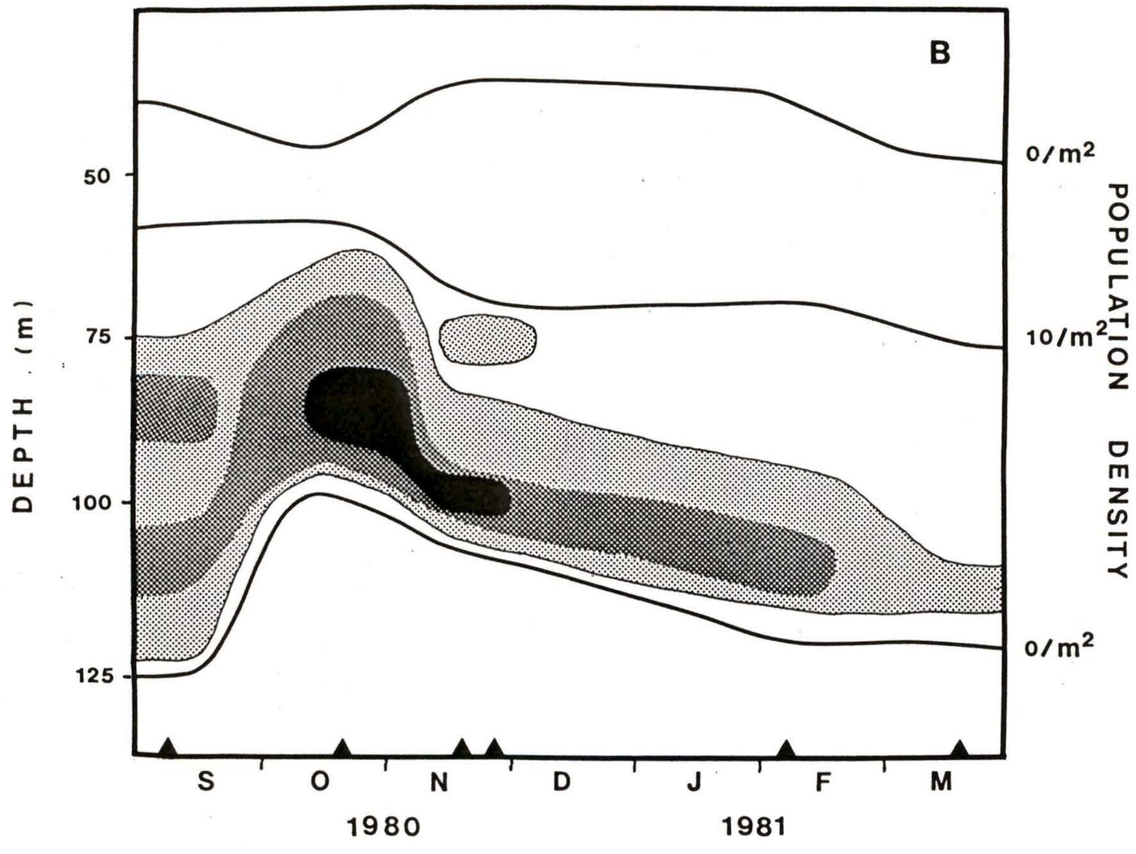
At Dark Cove in Jervis Inlet, density did not exceed 17 *Munida quadrispina* per square metre and at Port Mellon in Howe Sound, maximum density was less than 8 *M. quadrispina* per square metre

Figure 14. Photograph from *Pisces IV* showing high density of *Munida quadrispina* at 90m depth on October 23, 1980 on the cliff at McCurdy Point.

Figure 15 A. Profile showing density distribution (#/m^2) of Munida quadrispina from September 1980 to March 1981 at Elbow Point in Saanich Inlet. ■ => 100/m^2, ▦ => 50/m^2, ░ => 20/m^2 and □ =< 20/m^2. The 10/m^2 and 0/m^2 profiles are also included.

B. Profile showing the same distribution of *Munida* from McCurdy Point, Saanich Inlet. Sample dates are indicated by ▲ .


A
0/m²
10/m²
0/m²
<20/m²
<20/m²
POPULATION DENSITY
DEPTH (m)
50
75
100
125
S
O
N
D
J
F
M
1980
1981


B
0/m²
10/m²
0/m²
POPULATION DENSITY
DEPTH (m)
50
75
100
125
S
O
N
D
J
F
M
1980
1981

(Figure 16). No density maxima were observed at these locations.

An estimate of the total number of *Munida quadrispina* at all sample locations in a 1m wide vertical transect from 30m to bottom was done for each sample date (Table 2) based on the area under frequency curves of each phototransect. Total organic weight per transect was estimated by multiplying the organic weight (Appendix 3) of a *M. quadrispina* of average carapace length for a specific phototransect by the number of *M. quadrispina* per transect. Organic weight calculations are described in Gill Morphology methods.

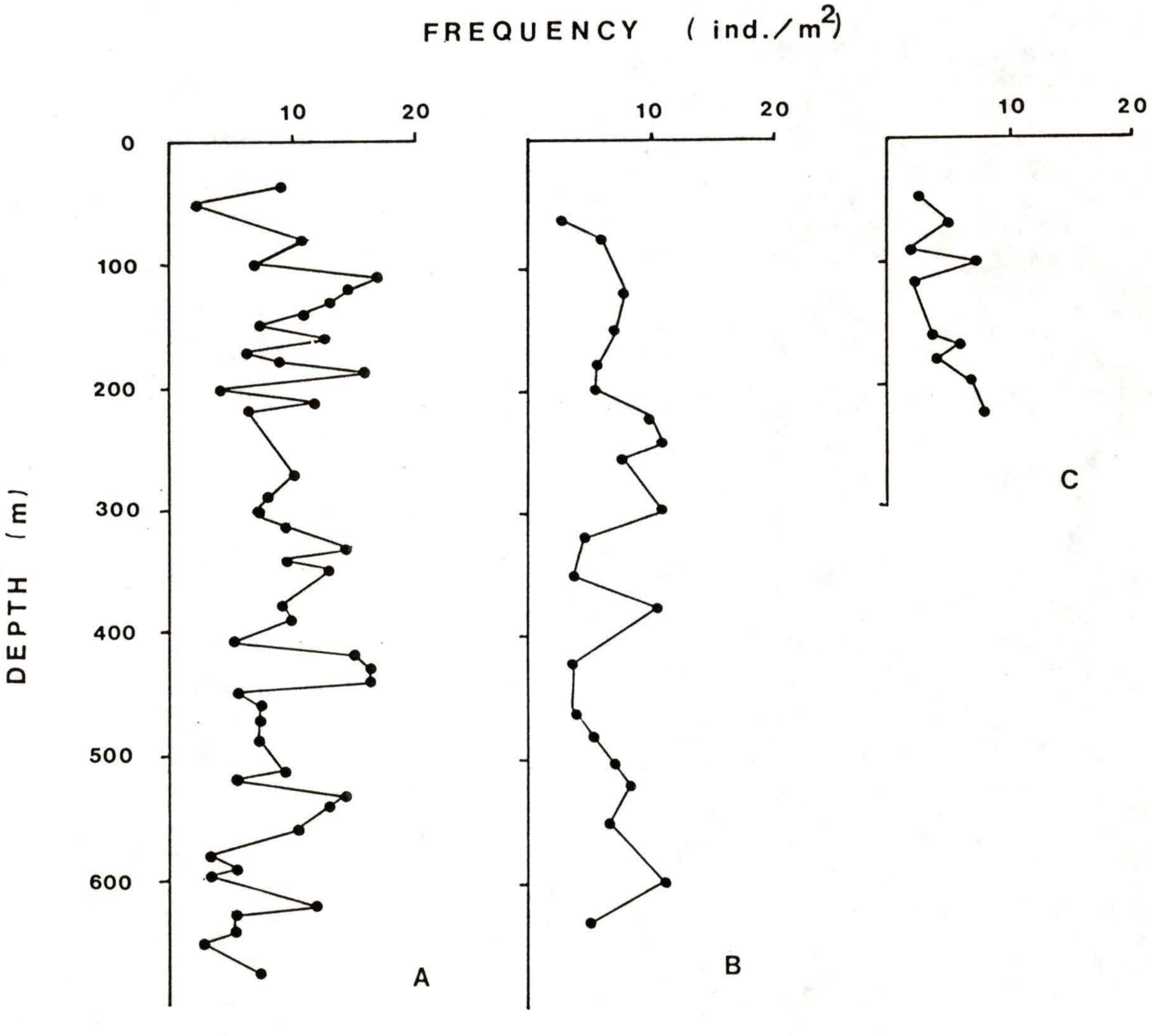
The total number of *Munida quadrispina* per transect at Elbow and McCurdy Points remained fairly constant from September 1980 to February 1981, but had declined 50% by March 1981 (Table 2), when a large number of dead *M. quadrispina* were observed at the depth limit of the population. This was evidently not related to any change in oxygen, but might be a life history phenomenon (see Appendix 5). Figure 15 suggests that this loss was due mainly to a reduction in the number of deep animals, since the density of crabs was greatly reduced below 100m in March 1981.

Although there were twice as many *Munida quadrispina* per transect in Jervis Inlet as in Saanich Inlet, estimated biomass was slightly greater in Saanich Inlet. This indicates that the crabs were smaller overall in Jervis Inlet than in Saanich Inlet. In March of 1980 the number and organic weight of *M. quadrispina* at Port Melon in Howe Sound were comparable with Saanich Inlet.

Table 2. Estimated abundance of <u>Munida quadrispina</u> from each phototransect using density/depth distribution curves (data in Appendix 1). Organic weight was estimated from mean carapace length (Appendix 3) for each transect. Mean carapace length (CL) was estimated from size/depth regressions (Table 3). t = transect.

Location and Date	#/t	Org. Wt(g/t)	Mean CL
McCurdy Point			
Sept/80	2120	216	16.7
Oct/80	2200	216	16.5
Nov/80	2000	163	15.0
Feb/81	1960	184	15.7
Mar/81	920	131	17.8
Elbow Point			
Sept/80	2077	163	14.8
Oct/80	2400	259	17.0
Nov/80	2424	261	17.0
Feb/81	1500	125	15.1
Mar/81	775	83	16.4
Finlayson Arm			
Nov/80	2020	193	16.4
Dark Cove, Jervis			
Sept/80	3800	147	12.5
Feb/81	3500	107	10.6
Port Mellon, Howe			
Mar/81	730	51	14.2

Figure 16. Frequency distribution with depth of *Munida quadrispina* from A = Dark Cove, Jervis Inlet in September 1981 and B = Dark Cove in February 1981, and C = Port Mellon, Howe Sound in March 1981.


FREQUENCY (ind./m2)
10
20
10
20
10
20
0
100
200
300
400
500
600
DEPTH (m)
A
B
C

Size Distribution with Depth from Trap Data

Submersible observations suggested that the overall size of *Munida quadrispina* increased as depth increased. This was tested by trapping animals from various depths at McCurdy Point and Elbow Point.

The hypothesis that carapace length of the trapped *Munida quadrispina* was not related to depth was tested by regression analysis and rejected at the 1% level. Combined data from the entire sample period for McCurdy Point (Figure 17) and Elbow Point (Figure 18) respectively illustrate that carapace length increased significantly as depth increased.

Size Distribution Versus Oxygen from Trap Data

Since depth distribution of *Munida quadrispina* from Saanich Inlet varies seasonally in relation to fluctuations in oxygen concentrations, it would be expected that the correlation between carapace length and oxygen would be higher than the correlation between carapace length and depth. Therefore the hypothesis that carapace length was not related to oxgyen concentration was also tested by regression analysis. Since oxygen samples were taken at each trap depth this analysis was feasible. The hypothesis was rejected at the 1% level at both McCurdy and Elbow Points. The hypothesis that the slope was 0 was examined by t-test and rejected at the 1% level. The correlation coefficients of the inverse regression of carapace length to oxygen concentration were greater

Figure 17 A. Regression of carapace length (mean for each trap sample ± standard error shown) with depth for *Munida quadrispina* from McCurdy POint in Saanich Inlet. Total n = 272, r = 0.85, slope = 0.15, y intercept = 8.1.

B. Regression of log carapace length with habitat oxygen concentrations for *M. quadrispina* at McCurdy Point in Saanich Inlet. Carapace length data is identical for A and B. Total n = 272, r = 0.93, slope = -0.10, y intercept = 1.4.

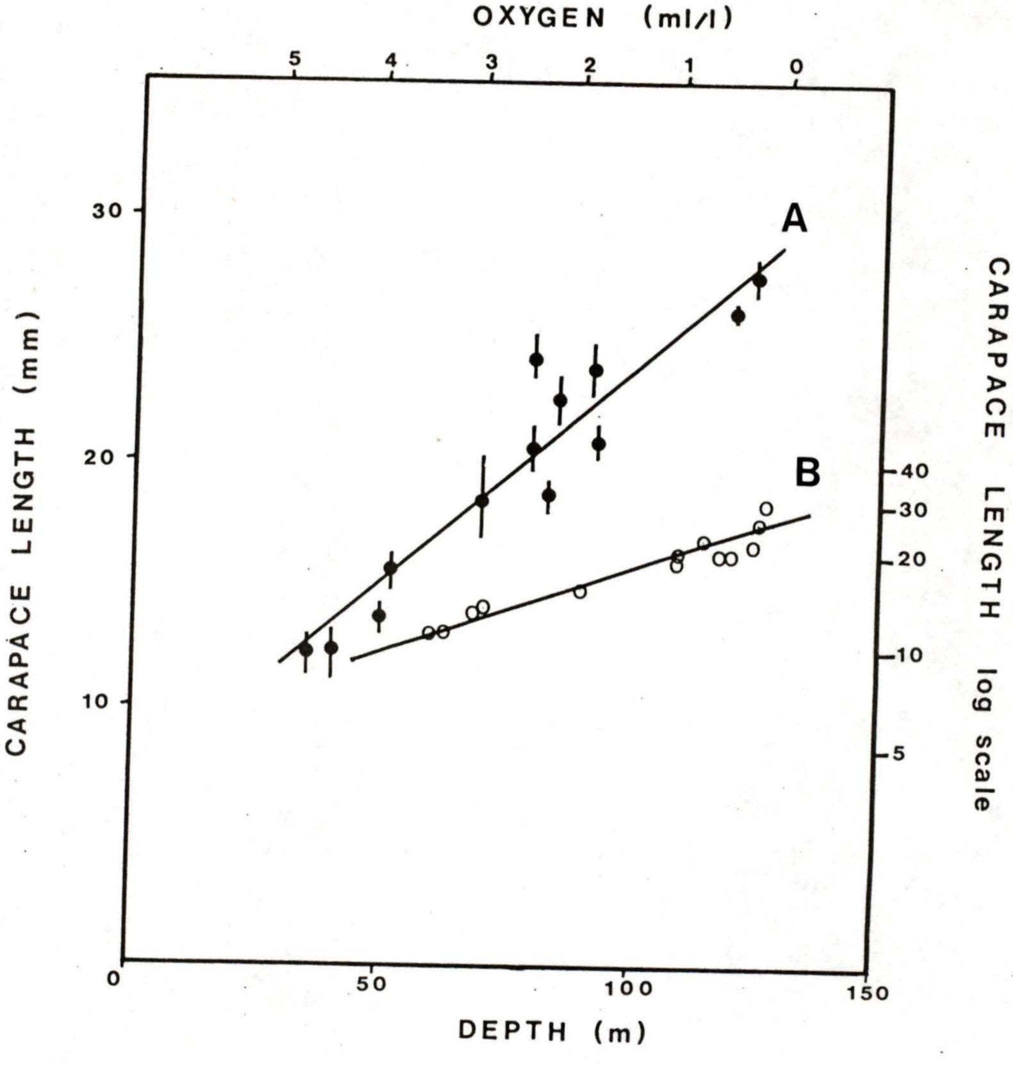
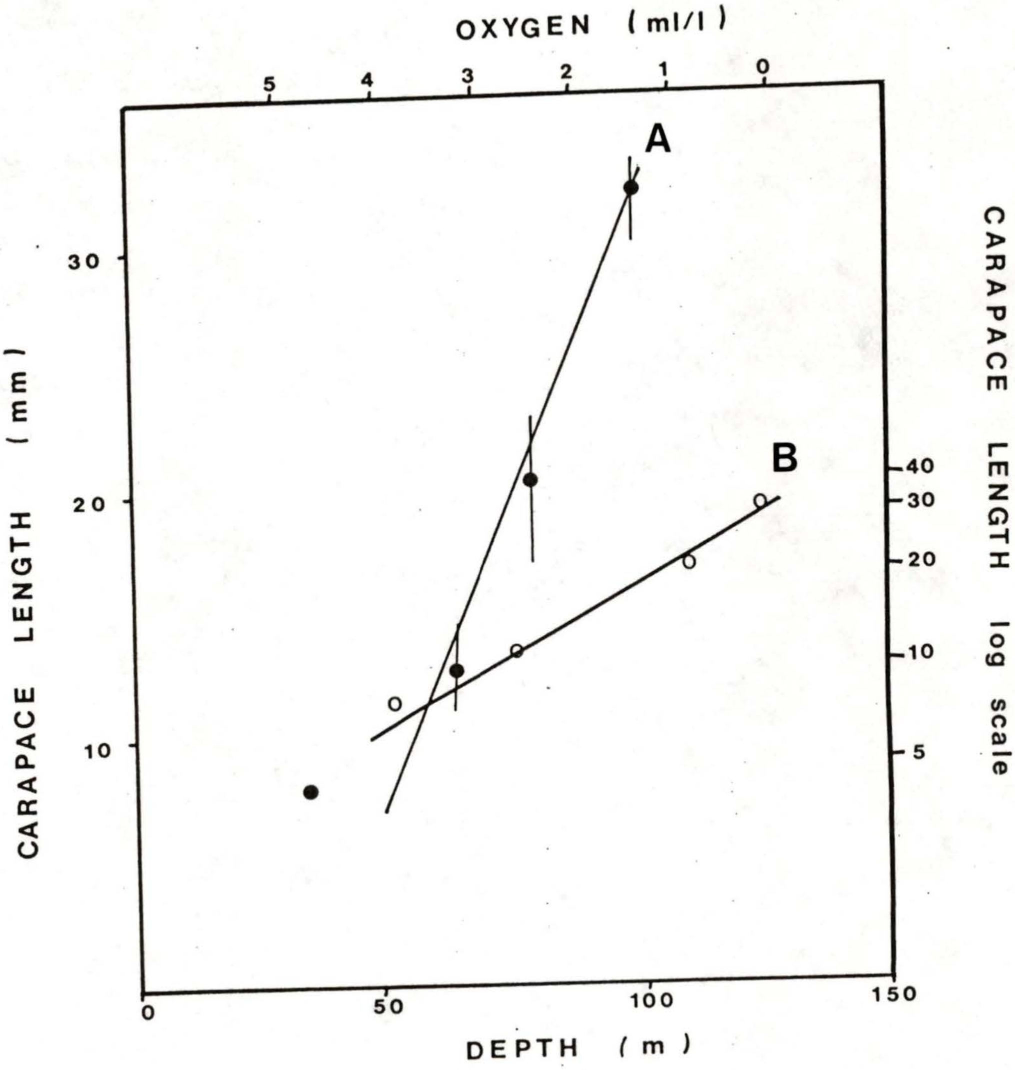

OXYGEN (ml/l)
5
4
3
2
1
0
30
20
10
0
CARAPACE LENGTH (mm)
A
B
40
30
20
10
5
CARAPACE LENGTH log scale
50
100
150
DEPTH (m)

Figure 18 A. Regression of carapace length (mean for each trap sample ± standard error shown) with depth for *Munida quadrispina* from Elbow Point in Saanich Inlet. Total n = 64, r = 0.83, slope = 0.50, y intercept = -21.

B. Regression of log carapace length (mean for each trap sample shown) with habitat oxygen concentration for *Munida* at Elbow Point in Saanich Inlet. Carapace length data is identical for A and B. Total n = 64, r = 0.89, slope = -0.20, y intercept = 1.5.


OXYGEN (ml/l)
5
4
3
2
1
0
A
B
CARAPACE LENGTH (mm)
30
20
10
CARAPACE LENGTH log scale
40
30
20
10
5
0
50
100
150
DEPTH (m)

in value than for the regression of carapace length to depth (r = 0.92 vs r = 0.85, Figure 17 for McCurdy Point, and r = 0.89 vs. r = 0.83 Figure 18 for Elbow Point). Carapace length was therefore more closely correlated with oxygen concentration than with depth. The sample sets from both sites were then pooled to calculate an overall regression of oxygen concentration to carapace length (log CL = -0.15(Oxygen)+1.46, n = 336, r =0.84) significant at 1%.

Size Distribution with Depth from Phototransects

The hypothesis that carapace length of Munida quadrispina was not related to depth in phototransects was tested by regression analysis and rejected at the 1% level for all locations and sample dates (Table 3) in Saanich Inlet, Jervis Inlet and Howe Sound. The carapace length of M. quadrispina at McCurdy and Elbow Points and Finlayson Arm increased significantly as depth increased (the hypothesis that the slope = 0 was rejected at the 5% level using a t-test, Table 2). However, the slopes of regression for Tozier Rock, Port Mellon and the February sample from Dark Cove were not significantly different from zero (p = 0.05). The slope of regression for Dark Cove in September 1981 was significantly different from zero at the 5% level, but was very small (slope = -0.003), indicating that carapace length decreased slightly as depth increased, the opposite trend to that observed in the low oxygen areas of Saanich Inlet.

The regression slopes of carapace length versus depth for

Table 3. Regression Equations for carapace length (CL) vs depth (D) in *Munida quadrispina* measured from phototransects.

Location and Date	N	Equation	p(reg)	Ho:b=0 (at 5%)
McCurdy Point				
Sept/80	505	$CL = .25D-7.4$	.1%	reject
Oct/80	284	$CL = .48D-25$	.1%	"
Nov/80	270	$CL = .28D-11.2$	.1%	"
Feb/81	155	$CL = .24D-7.2$	.1%	"
Mar/81	43	$CL = .28D-12.6$	.1%	"
Elbow Point				
Sept/80	167	$CL = .27D-10.5$	.1%	"
Oct/80	114	$CL = .52D-25$	.1%	"
Nov/80	648	$CL = .31D-12.1$	.1%	"
Feb/81	170	$CL = .21D-4.6$	.1%	"
Mar/81	157	$CL = .26D-9.5$	.1%	"
Finlayson Arm				
Nov/80	254	$CL = .24D-7.7$	.1%	"
Tozier Rock				
Sept/80	11	$CL = .09D+4$	1%	accept
Dark Cove, Jervis				
Feb/81	233	$CL = -.004D+11$	.1%	reject
Sept/81	70	$CL = -.003D+12$	.1%	accept
Port Mellon, Howe				
Mar/81	25	$CL = .009D+13$	5%	accept

McCurdy and Elbow Points for September 1980, February and March 1981 did not differ significantly (t-test, $p = 0.01$). The slopes for the October regressions were significantly steeper (t-test, $p = 0.01$) than those measured for any other month. This corresponded with the date on which the lower depth limit of benthic *M. quadrispina* was shallowest (see Figures 3 and 4). The regression slopes for carapace length versus depth at McCurdy and Elbow Points were significantly steeper in November of 1980 ($p = 0.01$) than the following February (1981), but were not significantly different from September 1980 or March 1981.

The relation of carapace length and oxygen concentration was not tested from the phototransects since oxygen samples were not taken at each photo depth and approximations of oxygen levels from some depths would introduce too great an error for this comparison. Figures 2 and 3 show that the difference in oxygen levels between two consecutive depths was sometimes 1.0 ml/l or more.

Depth Distribution of Juveniles

Pelagic juvenile *Munida quadrispina* were observed at Elbow Point and McCurdy Point from September 3, 1980 to March 23, 1981. Since juveniles were also found in plankton hauls taken in April and through the summer of 1981 (Mills, Larson, pers. comm.), some pelagic juveniles were present for most or all of the year.

Two distinct populations of pelagic juveniles were present at McCurdy Point and Elbow Point (Figures 19 and 20) from October 23

Figure 19. Oxygen profile (isopleths in ml/l) from August 1980 to May 1981 showing the distribution of juvenile *Munida quadrispina* at McCurdy Point in Saanich Inlet. The broken line represents the presence of pelagic juveniles, and the solid line represents the presence of settled juveniles. The black area is anoxic, while the 0.1 to 0 ml/l area is shaded.

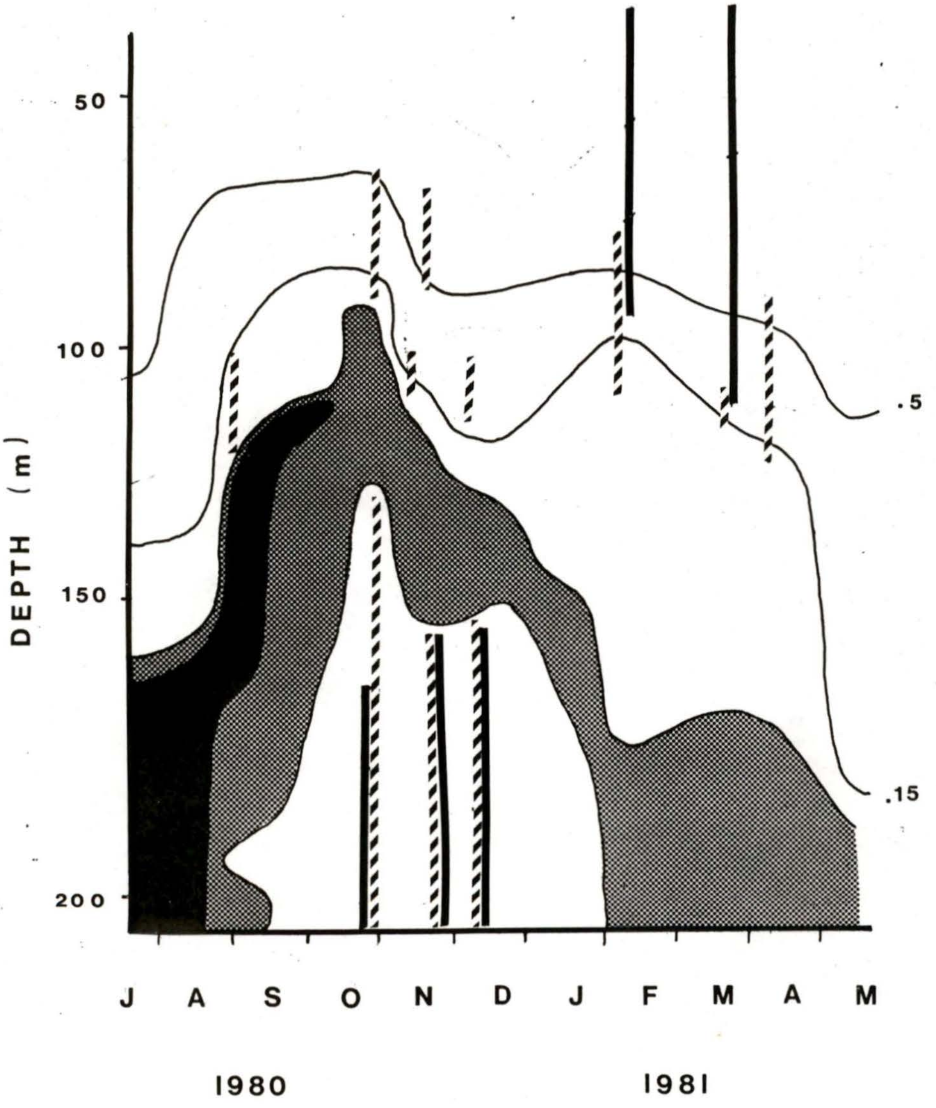
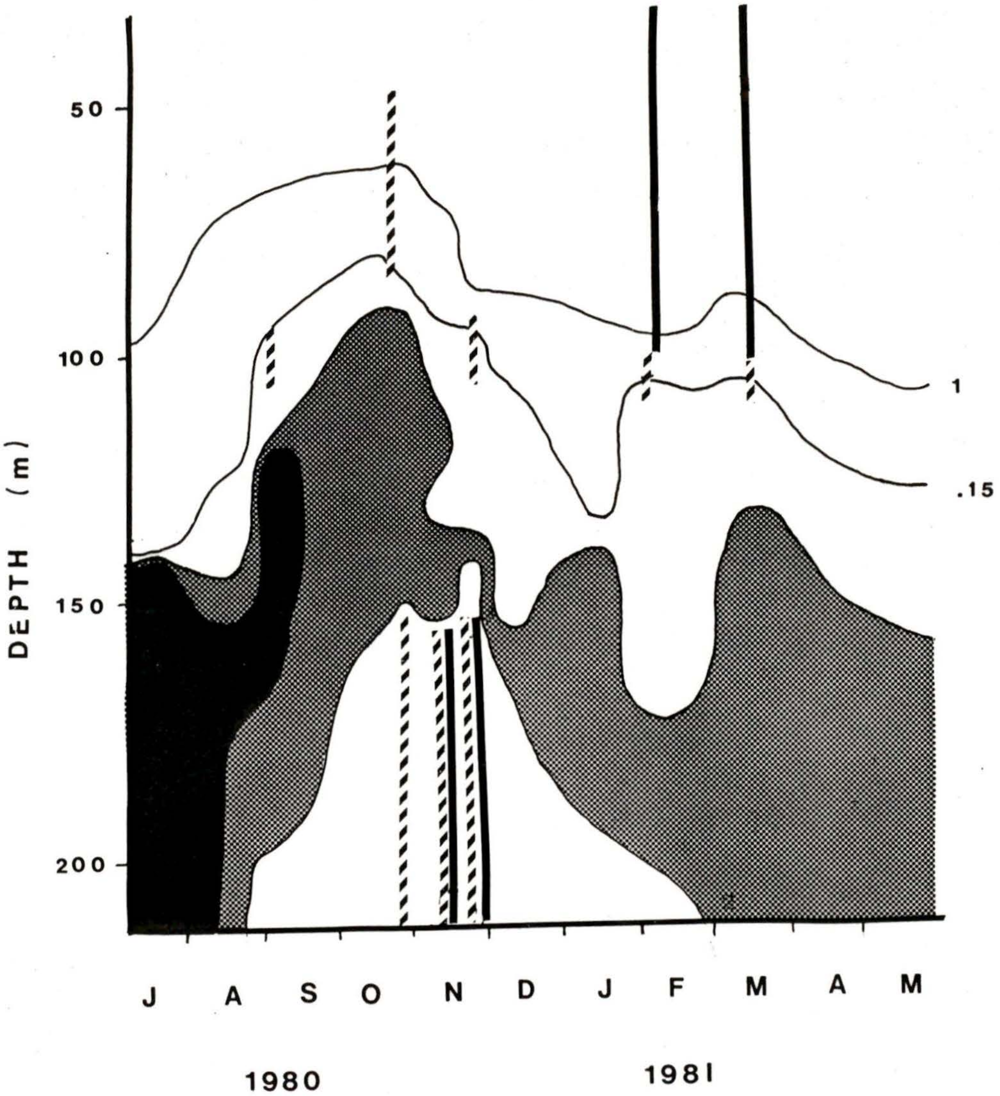

DEPTH (m)
50
100
150
200
.5
.15
J
A
S
O
N
D
J
F
M
A
M
1980
1981

Figure 20. Oxygen profile (isopleths in ml/l) from August 1980 to May 1981 showing the distribution of juvenile *Munida quadrispina* at Elbow Point in Saanich Inlet. The broken line represents the presence of pelagic juveniles, and the solid line represents the presence of settled juveniles. The black area is anoxic, while the 0.1 to 0 ml/l area is shaded.


DEPTH (m)
50
100
150
200
1
.15
J
A
S
O
N
D
J
F
M
A
M
1980
1981

to November 27, 1980, separated by a wedge of low oxygen water. The group below this layer first appeared during the flushing event and was only observed below 140m in October and November. By February, there were no pelagic juveniles below 120m, where oxygen had decreased to less than 0.2 ml/1. No deep group was observed at Finlayson Arm, where oxygen was consistently <0.2ml/1 below 100m.

Many of the deeper group of juveniles settled on the bottom between 140m and 210m at McCurdy Point and from 150m to 210m at Elbow Point in November and October of 1980. By February 5, 1981 only carcasses or cast off exoskeletons remained where these juveniles had settled. Concurrent with this disappearance oxygen levels decreased below 0.2ml/1 at both locations.

Some pelagic juveniles observed above the low oxygen water layer (above 125m) remained in the water column instead of settling, from September 3 through to March 23, 1981, and were observed from _Pisces_ at McCurdy Point in April (C. Mills, pers. comm.). This group was present to the same depth as the benthic adults, tolerating oxygen levels from 0.1 to 0.15 ml/1, but were observed to migrate diurnally (G. Mackie, pers. comm., pers. obs.). Pelagic juveniles were found at 5m during a night dive in February 1981, when a heavy diatom bloom was present. During the day these juveniles were always observed below 50m.

The upper group of juveniles settled above 100m, mostly between November 1980 and February 1981 in contrast with the group below the low oxygen layer that settled earlier. Since reproduction also occurs in March (see Appendix 5) these juveniles were settling at about one year of age, at the same time as a 50% decline in adult numbers occurred (Table 2).

No juveniles were ever observed settled on the cliff from 100m to 140m at McCurdy Point and from 100m to 150m at Elbow Point. Within these depth regions oxygen never increased above 0.2 ml/1 during the sample period. Therefore, settled benthic juveniles were never observed alive at oxygen levels below 0.2 ml/1, although pelagic juveniles were present at oxygen levels of 0.1 to 0.15 ml/1. In contrast to the gap in depth distribution of settled juveniles in Saanich Inlet, recruitment had occurred at all depths at Port Mellon and Brittania Beach in Howe Sound by March of 1981, where oxygen levels were higher than 0.2 ml/1 at all depths.

Behavioural Observations

Some important aspects of field and lab behaviour of *Munida quadrispina* were observed but not quantified during this study. The hour spent stationary in *Pisces IV* observing *M. quadrispina* at 85m at Elbow Point in February of 1981 revealed that settled adults and juveniles actively grasp and feed on zooplankton such as chaetognaths, copepods, euphasiids and amphipods. The chelipeds are used to grasp prey objects and bring them to the mouth.

Pelagic juveniles have also been observed from the submersible to grasp copepods and bring them to their mouths. In contrast, *M. quadrispina* in laboratory tanks have been kept alive for six months or more, with only sediment from the closed running seawater system for food. They will occassionally eat each other under crowded conditions making it necessary to provide shelter for moulting individuals.

Observations from the submersible made over the entire sample period indicate that *Munida quadrispina* living in low oxygen conditions (0.1 to 0.15 ml/1) were sedentary, even when so crowded that they overlapped (Figure 14). These *M. quadrispina* did not display any observable territoriality or aggression such as defending an individual space or crevice. In sharp contrast to this, the one hour spent at 85m showed that *M. quadrispina* living at higher oxygen concentrations with other invertebrate and fish species, occupied crevices and cracks, actively driving away other *M. quadrispina* by grabbing or pinching with the chelipeds. Many crabs observed in these shallower areas were missing one or both chelipeds and were evenly spaced so that they did not touch each other. These observations suggest that *M. quadrispina* are territorial in oxygenated areas, but not in low oxygen areas. On the four occassions that a large number of trapped *M. quadrispina* were dumped into a single tank, it was also observed that they separated themselves evenly and avoided touching each other, to the extent of climbing and clinging to the walls and screen of the tank. When an individual touched another, the same active pinching and grabbing behaviour as observed in the field at 83m occurred. Once the spacing pattern was established, individual *M. quadrispina* remained stationary for long periods.

DISCUSSION

As temperature in Saanich Inlet varied by only 2.5°C below 30m during this study and salinity varied only 2ppt below 30m, oxygen was the only unusual and widely fluctuating water characteristic measured that might affect the *Munida quadrispina* population of Saanich Inlet. The fluctuation in oxygen levels experienced at McCurdy and Elbow Points and Finlayson Arm did not occur to the same extent at any of the other sample locations, which allowed comparison of the effect of different oxygen regimes on the distribution of *M. quadrispina* populations.

Results of this study and Levings (1980a) study in Howe Sound indicate that *Munida quadrispina* is well adapted to exist in severely oxygen depleted areas (0.1 to 0.15ml/l oxygen concentrations) which cannot be inhabited by most other invertebrate species. Quetin & Childress (1976) indicated that other galatheid crabs can have oxygen tolerances similar to *M.*

quadrispina (see Introduction).

The change in depth distribution by adult *Munida quadrispina* in response to oxygen concentration without any concurrent change in overall population size (before recruitment) indicates that this species migrates vertically to avoid suffocation, rather than dying *en masse* during upwelling of hypoxic water.

An important aspect of the compression of the *M. quadrispina* population during upwelling was the uncharacteristic lack of aggression or territorial behaviour of individual *M. quadrispina* in low oxygen areas. This passive behaviour could be due to the fact that no predators are present in these areas to stimulate *M. quadrispina* to hide. Another possibility is that suppressed agression in high density areas is a result of the accumulation of catabolites from excretion. This was suggested by Vannini (1981) who found that group water from large concentrations of *Carcinus mediterraneus* decreased intraspecific aggressive encounters. Crabs kept in groups by Vannini had greater excretion and lower nitrogen output than isolated ones. Hazlett (1968) noted that after adjustment periods no increase in aggressive interactions ocurred in pagurid crabs when crowding was increased, however he didn't comment on what appearred to be a decrease in aggressive interactions in crowded conditions. Aggressive interactions increased in *Pagurus samuelis* upon isolation, as did dominance behaviour, as defined by Courchesne and

Barlow (1971). Although lobsters are normally considered to be solitary, highly territorial decapods, *Homarus americanus* has been observed to be less aggressive after group housing than after isolation (Dunham 1972). There were no measured differences between solitary and crowded group activity levels *per se*, indicating that this was a true group effect. These studies indicate that high density alone may cause the lack of aggressive territorial behaviour of *Munida quadrispina* that live in the low oxygen areas of Saanich Inlet.

Low aggression of *Munida quadrispina* in the low oxygen areas of Saanich Inlet might also be a result of a lowering of metabolic rates and consequently activity levels, as an adaptation for conserving oxygen during long term oxygen stress. A related species, *Munida bamffica* has been shown to have a high blood magnesium level (R.F. Uglow, pers. comm.), which is consideredto be indicative of low activity levels in crustaceans (Wolvekamp and Waterman 1960). This suggests that *Munida* may be a normally sluggish genus, a useful characteristic for the exploitation of oxygen depleted marine environments. However, it is probable that when the oxygen levels get too low in Saanich Inlet, inactivity is insufficient to conserve enough oxygen for survival and the *M. quadrispina* may then be stimulated to emigrate away from the area, producing the pronounced shift in the population distribution observed during upwelling anoxia.

Total Munida quadrispina adults per transect declined by 50% in March 1982 in the deepest and therefore largest animals. Since juvenile recruitment coincided with this event, it is likely that the population size remains stable, and that the decline in numbers is part of the life history. Several years data would be necessary to prove this hypothesis. The corresponding low number at Port Mellon may be affected by the wood fibre beds present in that area.

Settlement of juvenile Munida quadrispina below the low oxygen layer during flushing provided an effective mechanism for recolonization of previously anoxic cliff areas as noted in Howe Sound after anoxic recovery in 1977 (Levings 1980a). During the present study oxygen became too depleted to sustain the benthic juveniles that settled below 140m, but in years that anoxia does not redevelop after flushing (evidenced by traces of large attached fauna on deep cliff), juvenile M. quadrispina would quickly recolonize the dead areas. Therefore a long pelagic juvenile phase increases the opportunity for recolonization of anoxic habitats.

A size/depth gradient related to oxygen, such as that found in Munida quadrispina from Saanich Inlet, was hinted at in the benthic distributions of the galatheid Pleuroncodes planipes (Boyd 1967), and in king crab (Somerton 1981). Intertidal bivalves are often size distributed as well. McQuaid (1981) noted that shell length of Littorina africana decreased towards shore. Juveniles settle in high intertidal zones and migrate downshore with food availability, although only those which are large enough to resist predation survive in downshore areas. Adult limpets transplanted to upshore zones suffered weight loss due to limited food (McQuaid 1981). Bertness (1977) described a vertical size distribution in two species of gastropod. The high intertidal species increased in shell length upshore, whereas the low intertidal species increased in shell length downshore. He concluded that these distributions were initially determined at the time of larval settlement by photo-orthokinetic and geotactic responses and survival was therafter determined by predator/prey correlations.

Because the largest *Munida quadrispina* in Saanich Inlet live in high density in low oxygen areas, where there are virtually no other macroinvertebrates or fish, it is probable that predation and competition has little affect on *M. quadrispina* in these areas. Smaller *M. quadrispina* in shallower areas are exposed to potential predators, but do not move into the deeper areas. It is therefore likely that smaller *M. quadrispina* are unable to tolerate conditions in the deeper low oxygen areas. This is supported by the fact that carapace length of *M. quadrispina* was more closely related to oxygen than to depth alone.

A physiological explanation for the absence of small *Munida quadrispina* in low oxygen areas of Saanich Inlet is that metabolism increases as animals decrease in size (c.f. Bayne 1971, Leffler 1973, Taylor *et al.* 1975, Zeuthen 1953), which means that large animals consume less oxygen per unit weight. This possibility will be examined in the second part of the study.

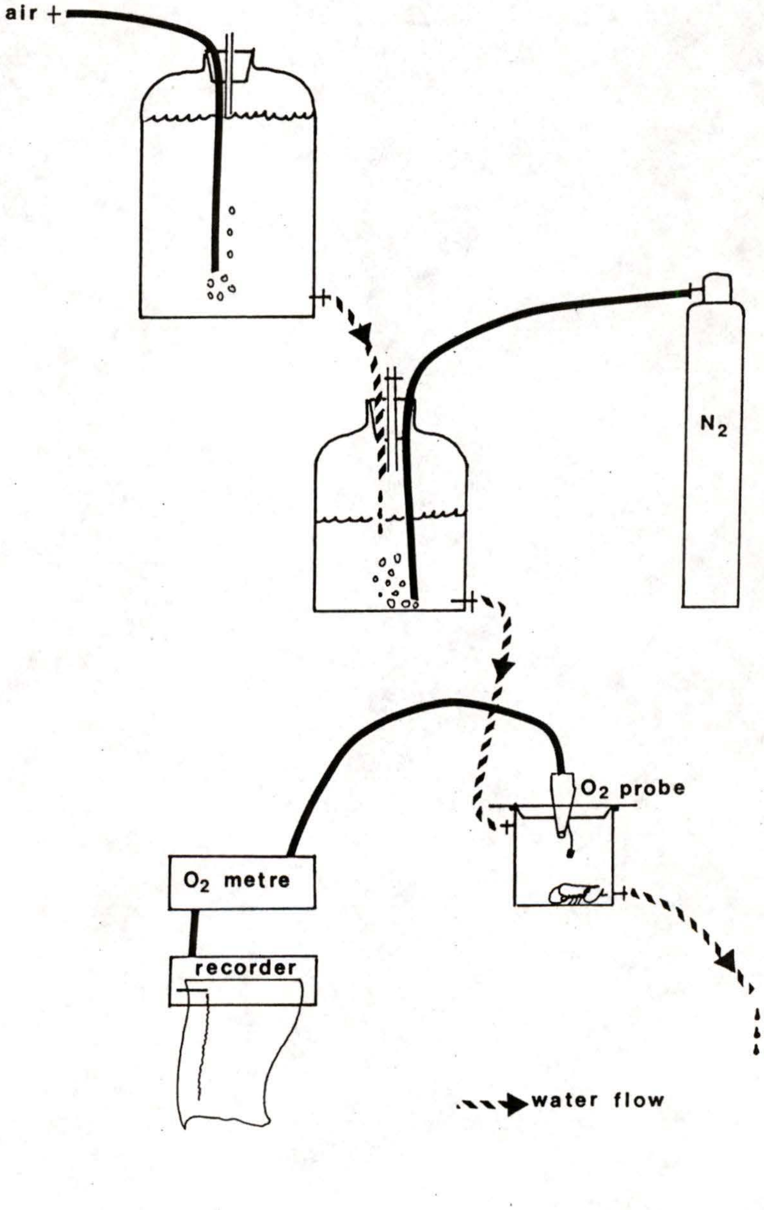
RESPIRATION OF *Munida quadrispina*

METHODS AND MATERIALS

Twelve benthic Munida quadrispina of all sizes were obtained from 52-92m depth by trap (see methods part I) from McCurdy and Elbow Points in Saanich Inlet, during May and June of 1980. These animals were kept for six months in an indoor running seawater system (about 10°c, 30ppt salinity) at the University of Victoria. Thirteen additional M. quadrispina were collected by vertical trawl up the cliff from 50-100m at McCurdy Point several days prior to experimentation. These were kept at 10°c in a thermally regulated room in filtered seawater of 30% salinity. The respiration of the 25 M. quadrispina thus collected was measured over a range of oxygen conditions. All 25 animals were in intermolt condition.

Respiration chambers consisted of cylindrical, 2 litre plexiglass chambers with O-ring sealed lids (Figure 21). A YSI oxygen probe (model 5420) with high sensitivity membrane was sealed into an opening of the lid. An electronic stirring rod attached to the probe maintained water circulation within the chamber. Inflow and outflow valves permitted addition and drainage of water. A 20 litre carboy with a N_2 gas cylinder connected to the lid was filled with seawater which had been pumped through a 250um Millipore filter. Nitrogen was bubbled through this container to reduce oxygen to the desired level. This carboy drained simultaneously into two respiration chambers.

Figure 21. Apparatus for measuring oxygen consumption of *Munida quadrispina*. Water flow was maintained by gravity as shown. The second respiration chamber is not shown.


air
N2
O2 probe
O2 metre
recorder
water flow

The oxygen probes and YSI meters (model 54) were calibrated using saturated seawater (10°C, 30ppt salinity), and with a series of oxygen depleted seawater samples. These calibration samples were then fixed and analysed for oxygen content using a modified Winkler titration method (Strickland & Parsons 1972). Probe membranes were changed and recalibrated periodically. The oxygen meters were connected to a dual channel chart recorder (Omniscribe) which was calibrated and zeroed with respect to the meters before each experiment and checked during the experiment.

Chambers were filled with O_2 saturated seawater (10-11°C,30ppt salinity), with all air bubbles excluded. Animals were not fed within 24 hours of a given experiment. Individuals were sexed, weighed to the nearest 0.01g using a Sartorius Analytical Balance and measured for carapace length, carapace width and volume (by water displacement), then placed within the experimental chambers. For three hours, low oxygen water from the container with the nitrogen tank attached was slowly introduced into the experimental chamber, to provide time for acclimation of the crabs to experimental conditions and to slowly decrease oxygen concentration. After this the oxygen level was adjusted slightly to 3.0mg/l, well within the range of habitat oxygen concentrations in Saanich Inlet. Twenty five mg per litre of streptomycin sulfate (after Quetin & Childress 1976) was added to the chambers and the valves closed. Oxygen concentrations were continuously recorded until the animals showed signs of stress (loss of equilibrium). Animals were then removed and placed in a lab tank to observe recovery. Those that died were preserved in 70% alcohol.

After removal of the animal, the oxygen concentration of the experimental water was monitored for several hours to determine if any bacterial or algal respiration was ocurring. Calibration of the probes and meters was then checked by analysing the oxygen content of the experimental water by Winkler titration. If calibration of the meter or chart recorder did not correspond with the Winkler titrations, or some bacterial respiration had ocurred, the experiment was discarded. This ocurred in only 3 out of 25 experiments. Pc could not be deterimined in one of the 22 remaining experiments due to outside interference with the experimental apparatus before completion of the experiments. Oxygen consumption was determined by measuring the change in O_2 levels during constant consumption and dividing this by water volume and time (ml/l/hr).

RESULTS

Munida quadrispina became inactive within several minutes after placement in the experimental chambers, probably because they are normally sedentary animals. They remained inactive throughout the experiments, except for ventilation of the gills. The high ratio of water volume to animal volume (200:1) prevented rapid depletion of oxygen. Experiments therefore took 24 to 96 hours to complete.

In the 22 usable experiments, oxygen consumption was constant before Pc was reached. The resting respiration rate ranged from 0.02 ml/g/hr to 0.07 ml/g/hr in animals of 12 to 0.5g wet weight. Pc could be precisely determined on the continuous chart recording since respiration declined abruptly thereafter (Figure 22). Pc ranged from 0.14 ml/l to 1.1 ml/l.

The hypothesis that weight specific oxygen consumption (above Pc) was not related to wet weight was tested by correlation (Figure 23). The relationship was best described by the equation:

$$\text{oxygen consumption (ml/g/hr)} = 0.055\ (\text{Wet Weight})^{-0.475}$$

The correlation coefficient of this relationship was $r = 0.86$ ($n = 22$). Therefore the hypothesis was rejected at the 1% level. Respiration rate decreased significantly as wet weight increased. A similar test showed that Pc increased significantly as wet weight decreased. The correlation coefficient of this relationship was $r = 0.79$ ($p = 0.01$, $n = 21$). The correlation between Pc and wet weight (Figure 23) was best described by the equation:

$$\text{Pc (ml/l)} = 1.36\ (\text{Wet Weight})^{-0.78}$$

In order to compare field and lab oxygen tolerance, a regression of

Figure 22. Examples of weight specific respiration rates (ml/g/hr) x 10^3 at different oxygen concentrations in five individual Munida quadrispina of different wet weights. Marked rate values are randomly selected points from a continuous chart recording.

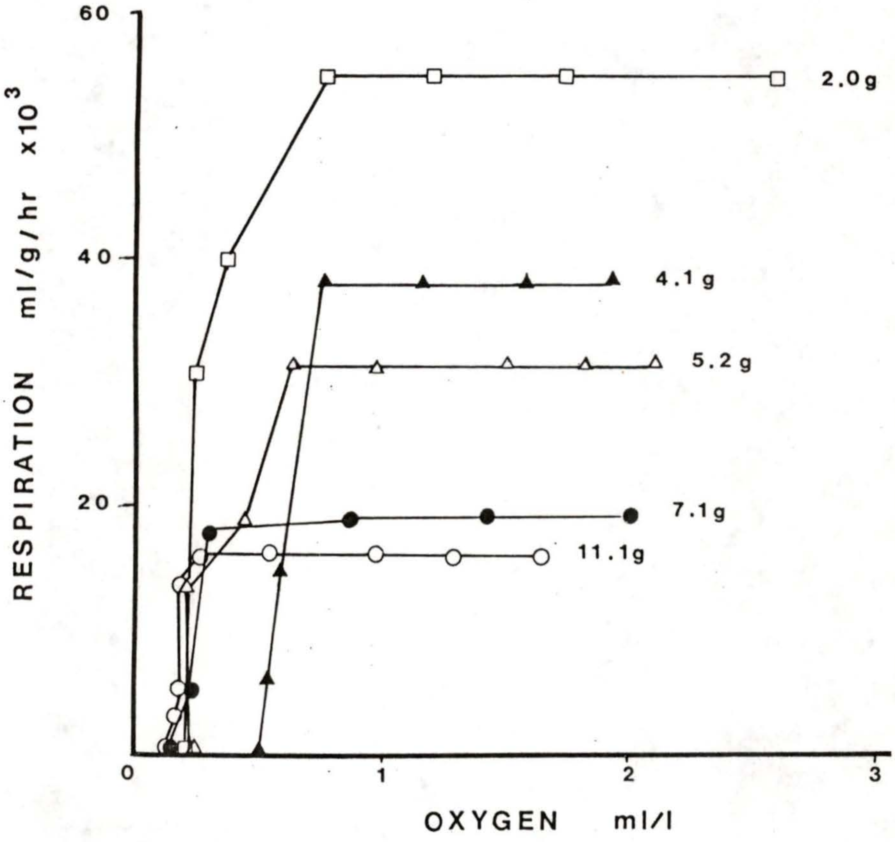
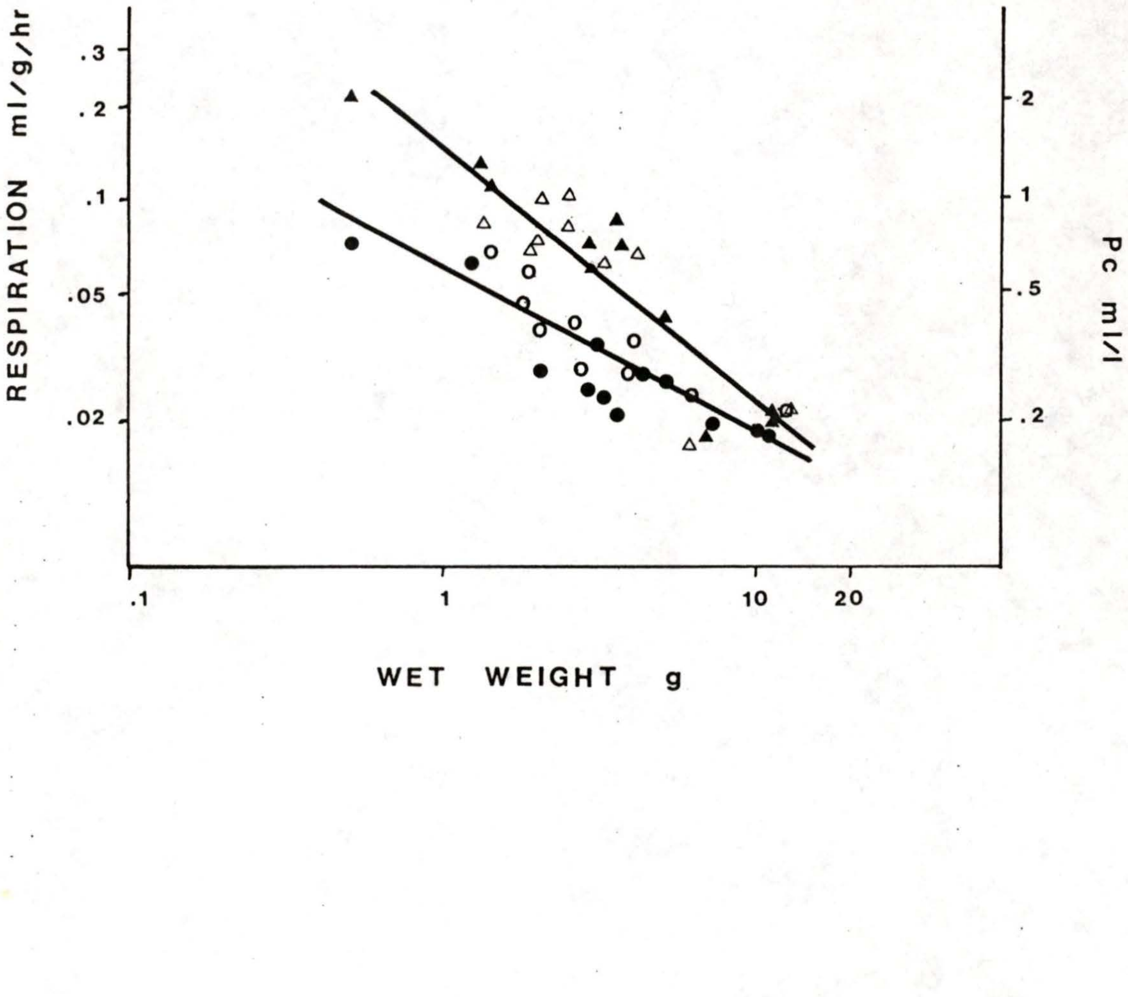

60
40
20
0
1
2
3
RESPIRATION ml/g/hr x10^3
OXYGEN ml/l
2.0g
4.1g
5.2g
7.1g
11.1g

Figure 23. Best fit line of the relationsip of weight specific respiration rate (ml/g/hr) and wet weight (g) of *Munida quadrispina*, in animals kept 6 months in the laboratory (open circles) and those kept several days only (solid circles). n = 22, r = 0.86.

Best fit line of the relationship of Pc (ml/l) and wet weight of *M. quadrispina* kept 6 months (open triangles) and those kept several days only (solid triangles). n = 21, r = 0.79.


RESPIRATION ml/g/hr
.3
.2
.1
.05
.02
Pc ml/l
2
1
.5
.2
.1
1
10
20
WET WEIGHT g

Pc versus carapace length was calculated producing the following regression equation:

log carapace length = -.18 (Pc) + 1.55

This regression was significant at the 1% level (n = 21, r = 0.86). When compared by analysis of covariance with the regression of carapace length and habitat oxygen:

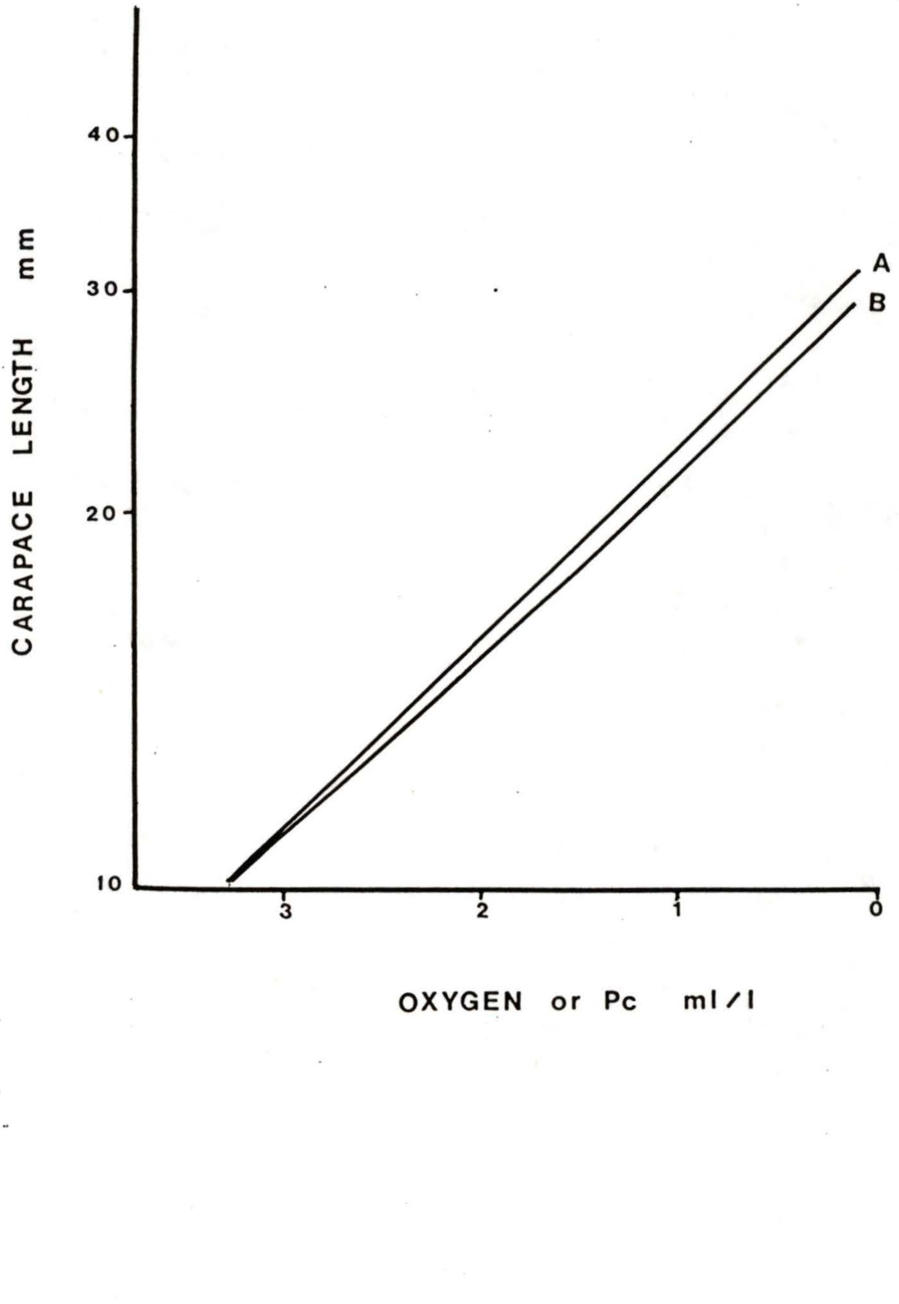
log carapace length = -.15 (Habitat oxygen) + 1.46

(from the combined trap data, Figures 17 and 18) no significant difference between the slopes (t = 0.15) and elevations (t = 0.16) of the two regressions were found at the 1% level (Figure 24).

There was no detectable difference in respiration rates of crabs acclimated in aquaria for six months and those acclimated 2 days. Pc values were not noticeably different in the two groups.

There were no behavioural changes during progressive hypoxia, except for increasing sluggishness (when container was disturbed) after Pc was reached. Oxygen stress was indicated by loss of equilibrium (animals rolled over). This always ocurred shortly after Pc was reached. If the animal was removed just after loss of equilibrium, it recovered temporarily but died within several days, indicating that permanent physiological damage had been done.

Figure 24. Comparison of regressions for A = log carapace length vs. Pc and B = carapace length vs. habitat oxygen concentration in *Munida quadrispina* from Saanich Inlet.


CARAPACE LENGTH mm
40
30
20
10
3
2
1
0
OXYGEN or Pc ml/l
A
B

DISCUSSION

Most terrestrial and aquatic animals regulate oxygen consumption over a range of ambient oxygen concentrations (Butler *et al*. 1978, Berg & Johannsen 1965, Bayne 1971, Bayne & Livingstone 1977, Davis 1975, Leffler 1973, Tang 1933, Taylor & Brand 1975, Taylor 1976, Taylor *et al*. 1977, Teal & Carey 1967, Thompson & Pritchard 1969). While Pc and weight specific respiration rates are affected by a number of physical and physiological factors in marine invertebrates and fish, there is an almost universal inverse relationship between weight and oxygen consumption per unit body weight (Zeuthen 1953). This relationship has been expressed for marine invertebrates by the equation metabolism = a $(\text{weight})^n$, where a is a constant and n is species specific. The relationship holds well for animals between 1g and 1000g regardless of taxonomic relationship (Leffler 1973). It is not surprising therefore, that *Munida quadrispina* in Saanich Inlet are largest at depths where oxygen concentration is lowest for the greatest periods of time (Figures 17 and 18). The largest *M. quadrispina* respired at the lowest respiration rate, while Pc values indicate that the largest animals regulate respiration down to the lowest ambient oxygen levels. It is not surprising that Pc is also weight related since Bayne (1971) showed that Pc also declined in lamellibranchs as they grew.

Quetin & Childress (1976) obtained results for respiration and Pc of another low oxygen tolerant galatheid crab, *Pleuroncodes planipes* (Table 4), which were very similar to those obtained in this study. Large *Munida quadrispina* and *P. planipes* both exhibit very low respiration rates in comparison with similar sized decapod species in which respiration has been measured at 10°C, including another galatheid species not found in low oxygen conditions.

Theoretically, Pc represents the oxygen tolerance of a species in its natural habitat. However, Pc has only rarely (Quetin & Childress 1976) been directly correlated with habitat oxygen levels (see Introduction). In *Munida quadrispina* the oxygen tolerance *in situ* was already known (see Part I), so that Pc could be compared with this to determine if it can indeed be used as a physiological indicator of respiratory tolerance in the natural habitat. The lowest Pc measured in the lab was 0.14 ml/l. Field tolerance of this species is 0.1 to 0.15 ml/l. The fact that there was no significant difference between the regressions relating carapace length to oxygen tolerance in the lab and carapace length to habitat oxygen at capture indicates that the lab experiments represent a valid measurement of the respiratory limits of *M. quadrispina* in their natural habitat, as well as explaining the size distribution observed in Saanich Inlet.

Table 4 Estimated respiration rates (Vo) at 10°C based on wet weights of comparably sized decapod crustaceans (Vo = ml/g/hr)

		Vo		
Species	Author	1g	10g	20g
Carcinus cassivelaunus	Bridges & Brand 1980a	.024	.018	.017
Nephrops norvegicus	"	.037	.027	.024
Pagurus bernhardus	"	.070	.040	.033
Callinectes sapidus	Laird & Haefner 1976	.052	.027	-
Upogebia africana	Hill 1981	.100	.078	.070
Uca pugettensis	Thompson & Pritchard 1969	-	.059	-
Callianassa californiensis	"	-	.029	-
Galathea strigosa	Bridges & Brand 1980a	.051	.028	.023
Pleuroncodes planipes	Quetin & Childress 1976	.051	.019	.014
Munida gregaria	McWhinnie & Marceniak 1964*	.074	.026	.024
Munida quadrispina	This Study	.055	.018	.013

*Note: Values estimated from dry weights based on fraction of total weight contributed by water in *Munida quadrispina*.

GILL MORPHOLOGY OF *Munida quadrispina*

METHODS AND MATERIALS

Adult Munida quadrispina obtained by trapping at depths between 40m and 125m from McCurdy Point (see first part) were used in determination of gill mass. 36 of these animals preserved in 70% alcohol were selected from a variety of habitat oxygen conditions. Eight animals trapped from 52 to 92m in May of 1981 and maintained in the University of Victoria aquarium, and nine animals trapped at 100m several days prior to use, were processed for comparison with the preserved animals. Therefore the gills of 36 preserved and 17 fresh animals from Saanich Inlet were examined.

Munida quadrispina were thoroughly rinsed with distilled water, sexed, and carapace length and width were measured. Half the gills were removed from all animals and counted using a dissecting microscope, then freeze dried for 48 hours. The remaining half of the gills were removed and saved intact in 8 animals of different sizes. The gills from legs I and IV of these 8 animals were fixed for one hour in 2.5% glutaraldehyde brought to pH 7.2 by the addition of sodium hydroxide. These gills were then dehydrated serially in concentrations of acetone from 10% to 100%. After drying in an OMAR critical point dryer, specimens were gold coated using the Hummer Sputtering system and examined with a JEOL 35 scanning electron microscope. Lamellar shape and surface features were compared. The bodies of the M. quadrispina (without gills) were dried for 24 hours, ground with pestle and mortar and freeze dried another 24 hours. Gills and bodies were weighed separately with a Sartorius Analytical balance to the nearest 0.1 milligram after freeze drying. Bodies were then ashed at 450°C for eight hours and reweighed. The bodies were ashed since ash free dry weight was considered to represent the weight of metabolizing tissue or organic weight, whereas ash was assumed to primarily represent calcification of the exoskeleton. The ash fraction of the gills was of no particular interest, but was considered to be the same proportion of the total dry weight as it was for the body (Belman & Childress 1976).

Twenty one Munida quadrispina from other coastal areas of B.C. and eleven specimens of alcohol preserved Munida gregaria, a pelagic galatheid crab from the east coast of New Zealand (compliments of J. Zeldis), were also measured for gill weight. Since the M. gregaria specimens were not collected from anoxic waters but may be found in New Zealand oxygen depleted fjords, they were used for comparison with M. quadrispina.

RESULTS

Both fresh and preserved Munida quadrispina from Saanich had the same percent body weight contributed by inorganic (ash) material. In animals less than 0.15g organic body weight, ash content was

63±2.9%(standard error) of dry weight. In animals greater than 0.20g, ash weight was 44±1.8% of dry weight. Calcification was therefore least in large M. quadrispina from Saanich Inlet. No crabs between 0.15 and 0.20g were measured. There was no detectable difference in ash fraction of males and females. M. quadrispina from other areas had a mean ash content of 49.6 ± 1.0% of dry weight regardless of size, whereas the mean ash content of M. gregaria was 51.1 ± 2.1% of dry weight.

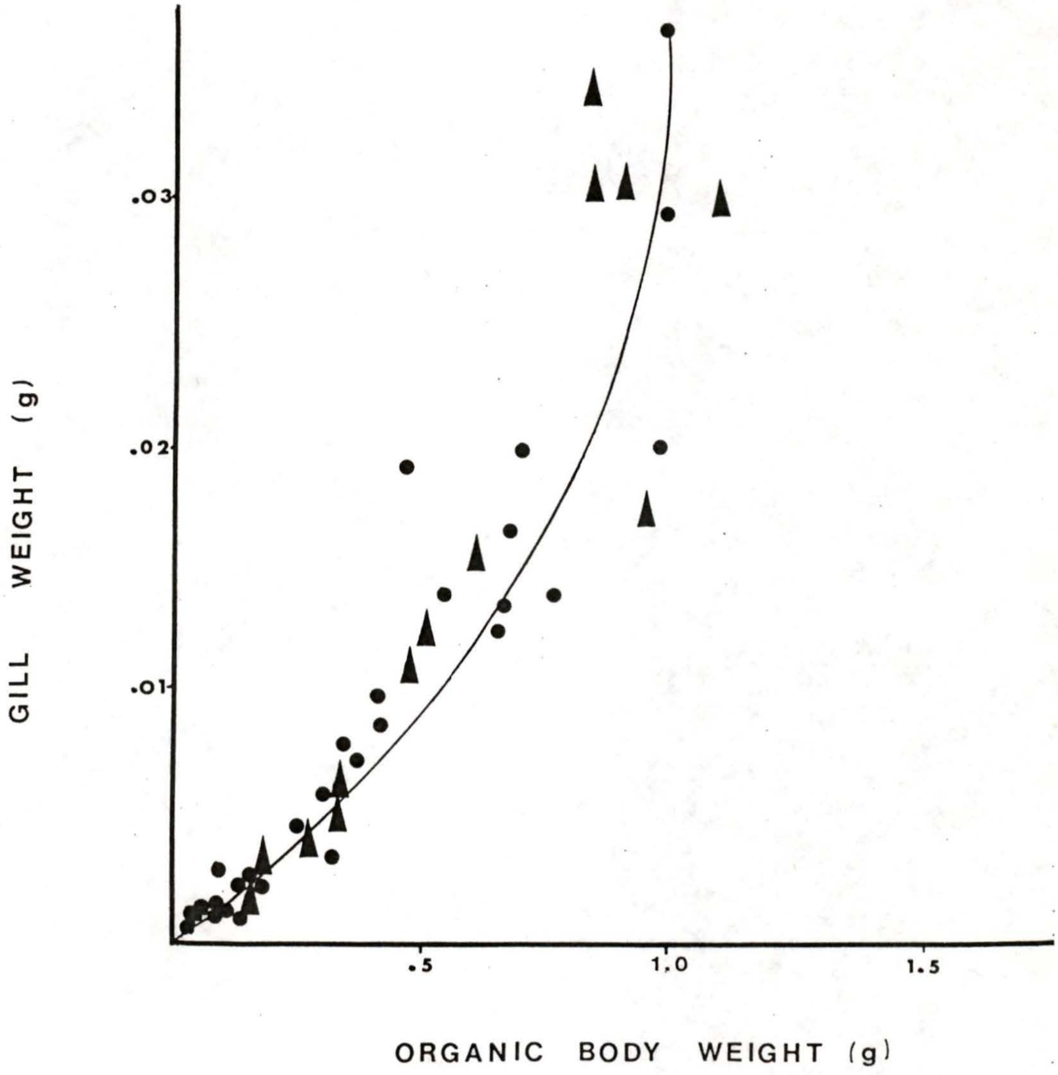
Figure 25 illustrates that large Munida quadrispina from Saanich Inlet had proportionately more gill tissue by weight than small ones. The hypothesis that gill weight was not related to body weight was tested by correlation in fresh and in preserved animals separately. Best fit lines of the correlation were:

(fresh) log gill weight = 1.48 (organic body weight) - 3.20

(preserved) log gill weight = 1.46 (organic body weight) - 3.20

The correlation coefficents were $r = 0.91$ ($n = 17$) for fresh and $r = 0.93$ ($n = 36$) for preserved animals. The hypothesis was rejected at the 1% level in both cases. The t-statistic for comparison of slopes was 0.89, while the t-statistic for the comparison of y intercepts was 0. Therefore there was no significant difference at the 1% level, in slopes or y intercepts

Figure 25. Relationship of gill weight to organic body weight of fresh (▲) and preserved (●) Munida quadrispina from Saanich Inlet, showing exponential increase of gill weight with increasing body weight.


GILL WEIGHT (g)
.03
.02
.01
.5
1.0
1.5
ORGANIC BODY WEIGHT (g)

for preserved and fresh animals. Males and females were not detectably different.

Gill weight increased linearly with increasing body weight in Munida quadrispina from areas other than Saanich Inlet (Figure 26B), in contrast with the curvilinear relation in Munida quadrispina from Saanich Inlet. The best fit line for this correlation in M. quadrispina from outside Saanich Inlet was:

$$\text{Gill Weight} = 0.0113(\text{Organic weight}) + 0.0015$$

The correlation coefficient for this equation was $r = 0.92$ ($n = 21$). The correlation was significant at the 1% level.

Gill weight was not as great in Munida gregaria as in similar sized Munida quadrispina (Figure 26A). Furthermore, gill weight was not proportionately greater in large M. gregaria than in small ones. The best fit line for this correlation was:

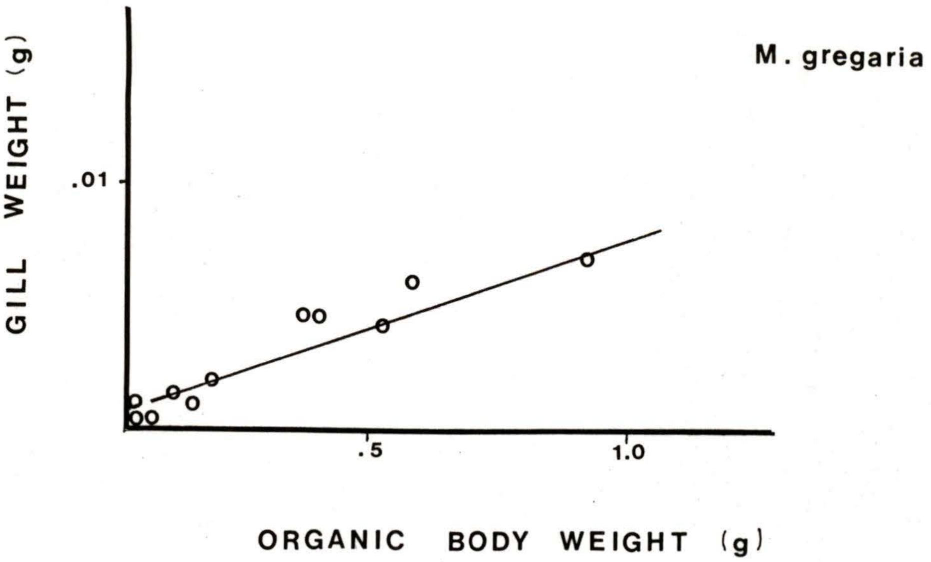
$$\text{Gill weight} = .0071\ (\text{organic weight}) + .00069$$

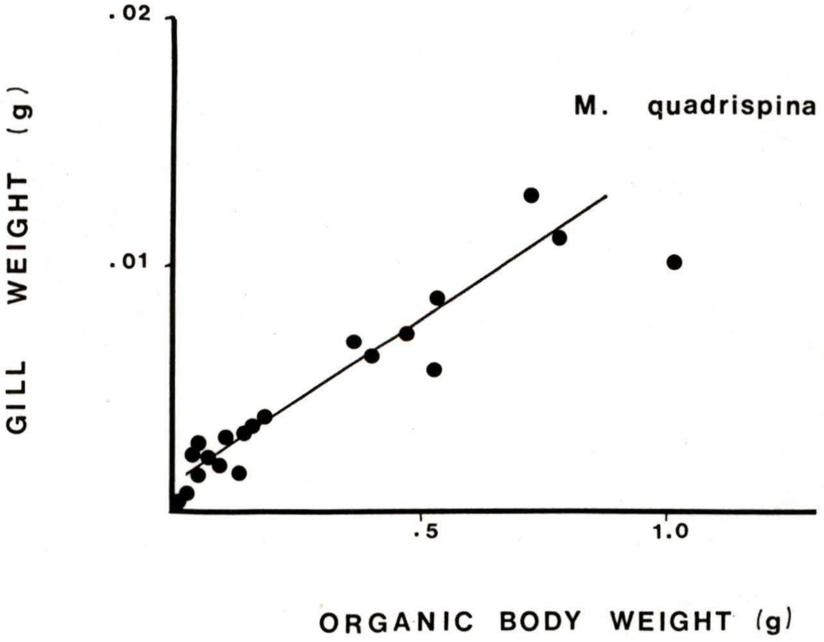
The correlation coefficient for the equation was $r = 0.93$ ($n = 11$) which was significant at the 1% level.

Percent gill weight of Munida quadrispina from Saanich Inlet as a fraction of total dry body weight ranged from 1.3 to 2.8 in crabs from environments with oxygen levels of 3.0 to 0.1 ml/l (Figure

Figure 26 A. Relationship of gill weight to organic body weight in *Munida gregaria* from eastern New Zealand.

B. Relationship of gill weight to organic body weight of *Munida quadrispina* from coastal areas other than Saanich Inlet.


M. gregaria
GILL WEIGHT (g)
.01
.5
1.0
ORGANIC BODY WEIGHT (g)


M. quadrispina
GILL WEIGHT (g)
.02
.01
.5
1.0
ORGANIC BODY WEIGHT (g)

27). The hypothesis that percent gill weight was not related to habitat oxygen concentration was tested by regression analysis. This test was done for 4 _M._ _quadrispina_ from each of seven different oxygen concentrations. The regression equation was:

percent gill weight = 0.45 (oxygen concentration) + 2.69

The correlation coefficient of the regression was $r = 0.85$ ($n = 28$). This hypothesis was rejected at the 1% level. The hypothesis that the slope of this regression was zero was tested using an F statistic. F for slope = 0 was 15.5. Therefore the slope of the regression was significantly different from zero, and the hypothesis was rejected at the 1% level. Therefore the percent gill weight of _Munida_ _quadrispina_ increased as habitat oxygen concentration decreased.

The number and types of gills did not vary in the two _Munida_ species, or in _M._ _quadrispina_ of different sizes or habitat oxygen concentrations. The gill complement of the two _Munida_ species is listed in Table 5. The gills were phyllobranche (Figure 28), with 14 gills per side, or 28 gills total. The shape and structure of lamellae fixed for scanning electron microscopy were the same in all _Munida_ _quadrispina_ examined. Lamellae were flat and ovoid, and attached to the filament at a narrowing of the lamellar plate, unlike the subtriangular gill lamellae described by Kaestner (1970)

Figure 27. Regression of percent gill weight measured as a fraction of total dry weight (mean of 4 values ± standard error shown) of *Munida quadrispina* with different habitat oxygen concentrations. n = 28, r = 0.85.

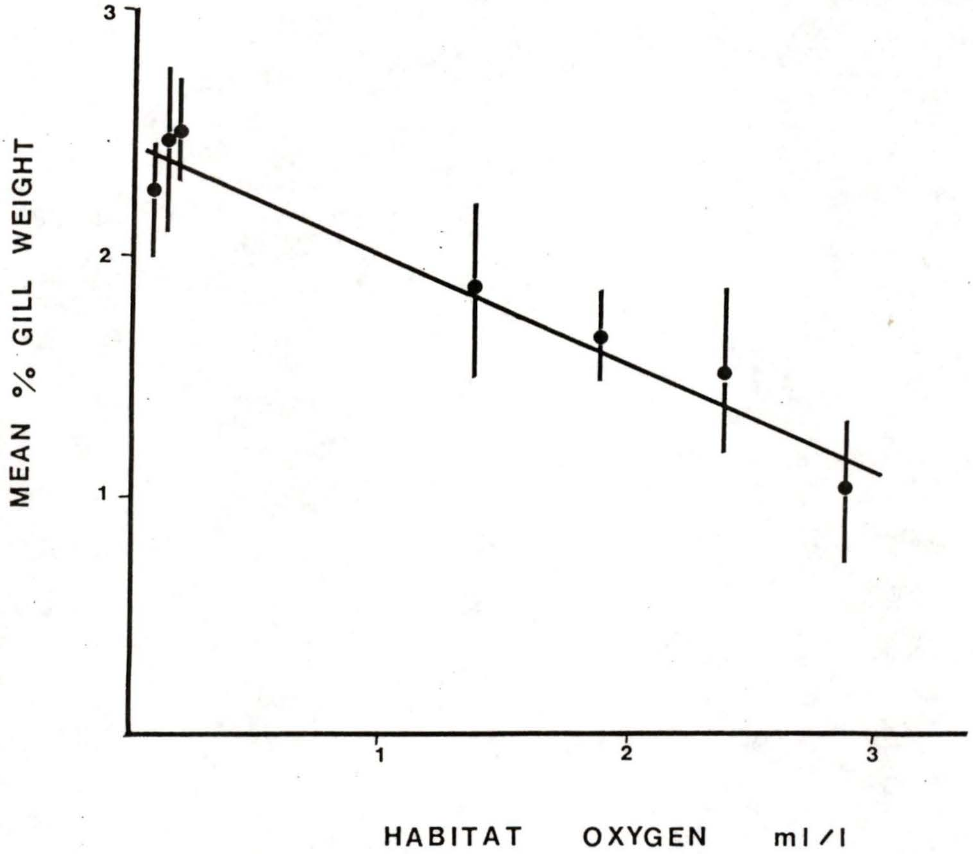
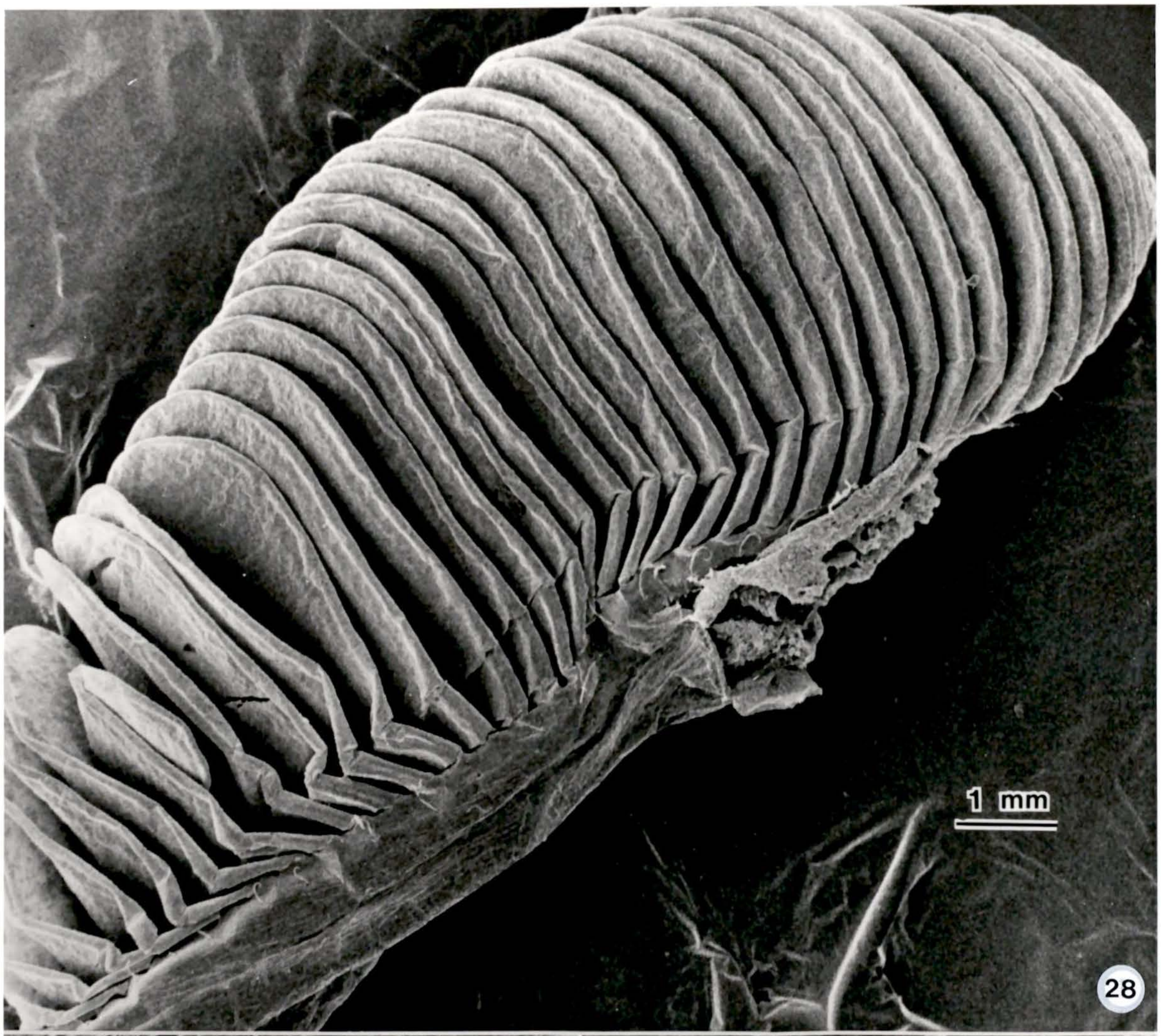

3
2
1
MEAN % GILL WEIGHT
1
2
3
HABITAT OXYGEN ml/l

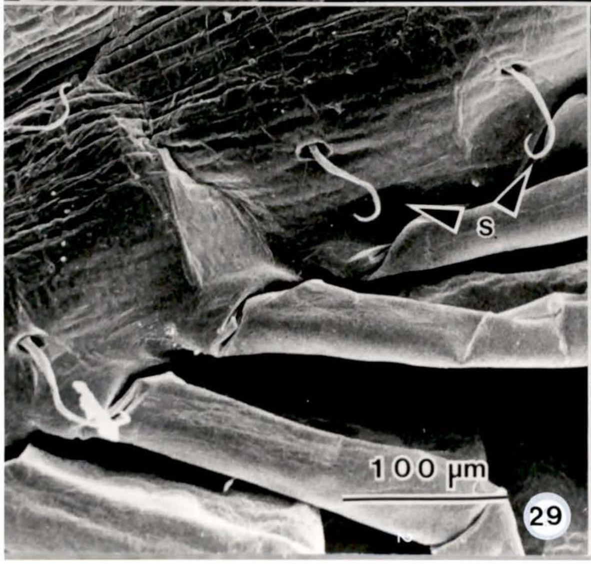
Figure 28. Phyllobranche gill from leg IV of Munida quadrispina. Magnification = 40x.

Figure 29. Setae on the filament of an arthrobranch gill of Munida quadrispina. s = setae. Magnification = 320x.

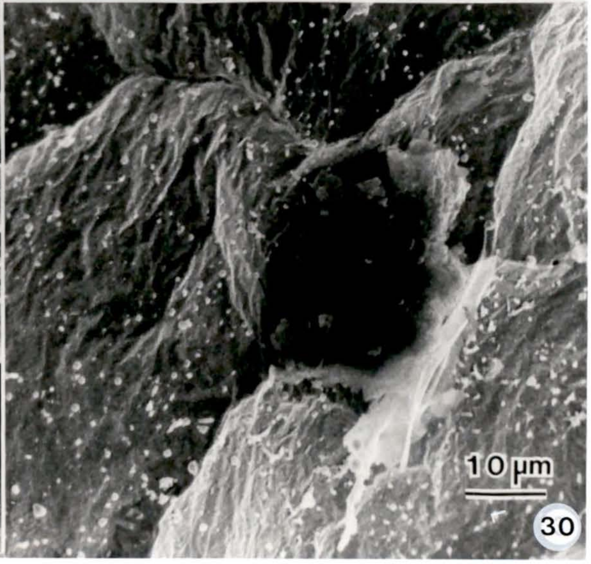
Figure 30. Pore canal on the lamellar surface of the gill of Munida quadrispina. Magnification = 2600x.



28



29



30

Table 5. Types and Numbers of Phyllobranche gills of Munida quadrispina and Munida gregaria

Appendage	Podobranch	Arthrobranch	Pleurobranch
Maxilliped I	0	0	0
Maxilliped II	0	0	0
Maxilliped III	0	2	0
Cheliped	0	2	0
Leg I	0	2	1
Leg II	0	2	1
Leg III	0	2	1
Leg IV	0	0	1
Total	0	10	4

Gills per side = 14

for Brachyura. The epicuticle was covered by rounded, hill shaped projections, though this may have been due to fixation. Setae were spaced every second or third lamella along the filament (Figure 29). Figure 30 illustrates a typical pore canal.

DISCUSSION

The measurement of gill weight instead of gill surface area as an index of change in size of gills with respect to size of animal was prompted by several considerations. The only crustaceans with phyllobranche gills in which gill measurements have been done are brachyurans (Gray 1957, Pearse 1929). These gills may have 20 or more various sized lamellae per gill. Gray (1957) measured gill surface area of 16 species of crabs by arbitrarily selecting average sized lamellae and making camera lucida projections of one side. The projections were traced by planimetry with the resultant area doubled, then multiplied by the total number of lamellae. Gray neglected the lamellar thickness, the surface area of any setae or projections, and surface area of the gill filaments.

The surface area of individual gill filaments of Astacus leptodactylus, a crayfish, was found to make up from 4 to 20% of the total gill surface area, depending on the specific gill examined (Burggren et al. 1974). This represents a sizable portion of the gill to ignore. In Munida quadrispina the gill filaments also represented a considerable portion of the gill structure (Figure 29), and could not be considered unimportant.

Babula _et_ _al_. (1978) were able to make consistent gill surface area measurements on _Mesidothea_ _entomon_ (Isopoda), but they also neglected gill setae and thickness. In spite of this, the simple flat gills of this species were easily measured by camera lucida projection onto a grid. Belman & Childress (1976) calculated gill surface area of _Gnathophausia_ _ingens_ (Mysidacea) by measuring mass and average thickness of cast gill cuticle, and density of carapace cuticle. However, the thickness of gill cuticle can vary considerably around pore canals, or if the surface of the gill is not smooth. In crayfish, pores can reach a density of 4×10^6 per square meter, and penetrate the cuticle up to 75% of its thickness (Burggren _et_ _al_. 1974). In _Carcinus_ _maenus_ the pore canals are actually continuous with the underlying epithelium (Wolvekamp & Waterman 1960). These pore canals could therefore enhance oxygen exchange considerably by increasing exposed surface area, and by decreasing diffusion distance across the gill cuticle (Burggren _et_ _al_. 1974).

It is clear that setae, filaments, gill thickness, pore canals and any surface projections of the gill cannot be included in gill surface area measurements. Furthermore the internal epithelium of the gill can be highly folded and convoluted (Burggren _et_ _al_. 1974). This and other internal characteristics of gills have been found to be important factors in gas diffusion characteristics of crayfish gills (Burggren *et al*. 1974).

Alternatively, gill weight measurements quantify all of the gill. Assuming that gill shape and structure do not change within a species, as is true in *Munida quadrispina*, differences in gill weight with respect to body weight may convey important ecological information about the habitat of a species. For instance, does gill weight increase at a faster rate than body weight in species of crustaceans that are oxygen stressed, and in species that are not? Studies on crustacean and fish gills indicate that gills grow at the same rate as the body. Proportionate characters such as gill volume/body volume in crabs (Pearse 1929, Nicol 1967, Gurney 1960) and gill surface area/body area in fish (Gray 1954), are constant irrespective of size. However, gill surface area usually decreases relative to increasing body mass (Bergmiler and Bielawsky 1970, Bock 1925, Gray 1957, Hughes 1966). However, this is not too surprising since the relative surface area of an entire organism decreases as mass and volume increase. Changes in gill surface area in fact say very little about the nature of the gills.

Therefore from the general findings of the literature, gill weight would be predicted to be a constant proportion of body weight in *Munida quadrispina*. This was true in those specimens collected from oxygenated areas outside of Saanich Inlet and in the *Munida gregaria* examined. However, gill weight increased exponentially relative to body weight in *M. quadrispina* from oxygen depleted areas of Saanich Inlet. The exponential increase in gill weight in these *M. quadrispina* may allow the largest crabs to survive the chronic low oxygen in which they live. An example of this phenomenon was recorded in *Gnathophausia ingens*, a hypoxia tolerant mysid which was shown to have proportionately more gill surface area in large animals than in small (Belman & Childress 1976). In spite of inaccuracies in the method of measurement, the differences in gill surface area relative to body weight were considerable, and in direct contrast to other invertebrate species which have been studied.

Since salinity varies little subtidally in Saanich Inlet, osmotic stress cannot be considered to be a factor in gill development. Temperature changes in the depth range of this species in Saanich Inlet are about 2.5°C annually, and probably do not influence gill development. Oxygen, however, does vary substantially over depth and time in Saanich Inlet, conceivably affecting gill development.

The change in relative size of gills along with the ability of large adult *Munida quadrispina* to live at low oxygen concentrations may partially explain the unusual size distribution observed in Saanich Inlet. These adaptations would in fact be very useful for the invasion of low oxygen basins by other deep subtidal galatheid crabs such as *Pleuroncodes planipes*, in which the largest individuals are found at oxygen levels of less than 0.5ml/l (Boyd 1967). The strong correlation between habitat oxygen concentration and percent gill weight in M. quadrispina from Saanich Inlet further suggests that some functional relationship exists between development of gills and long term oxygen levels. This would only be useful if oxygen uptake could be enhanced by an increase in gill tissue. An example of this can be seen in a study by Anderson (1970), in which a positive correlation between the amount of respiratory surface area of booklungs and the rate of oxygen uptake in spiders was established.

A decrease in body calcification was observed only in the largest Munida quadrispina from Saanich Inlet, and did not occur in those specimens collected outside of Saanich Inlet, or in Munida gregaria. This may be related to the calcium carbonate dissolution of the skeleton for internal buffering of carbon dioxide accumulated during oxygen stress, as hypothesized by McMahon et al. (1978) and subsequently demonstrated in Cancer productus by Defur et al. (1980). Defur et al. measured the various components of carbonate and carbon dioxide equilibrium in the blood during emersion and hyperoxia and determined the diffusion rate of carbonate through the gills. Since diffusion was slower than expected across the gills, Defur et al. (1980) concluded that the exoskeleton was contributing calcium carbonate for buffering of blood acidosis. This has been observed in bivalves as internal etching of the shell during hypoxia (Robertson 1941).

The final gill characteristics examined in *Munida quadrispina* were number and type, structure and lamellae. Most marine crabs (from all depths) with phyllobranche gills have 8 or 9 gills per side (Barnes 1980, Kaestner 1970, Kerkut 1958, Wolvekamp & Waterman 1960, Pearse 1929). Gill number is decreased to 6 in species that are more land oriented (Pearse 1929), such as the air breathing anomurans (Kaestner 1970). *M. quadrispina* and *Munida gregaria* had 14 gills per side (Table 5), as do the galatheids *Galathea squamifera*, *Ptychogaster* and *Uroptychus* (Gurney 1960). The large number of gills in this family relative to Brachyurans and other anomurans may allow galatheids to exploit a wide range of environmental oxygen conditions which other decapod species cannot tolerate.

SUMMARY

1. *Munida quadrispina* are tolerant of oxygen levels as low as 0.1 to 0.15ml/l in Saanich Inlet. This oxygen range limits their vertical distribution in Saanich Inlet, but does not occur in Jervis Inlet or Howe Sound, where they are found at the bottom.

2. The greatest density of *Munida quadrispina* always occurred within the zero to 0.15ml/l oxygen range in Saanich Inlet, whereas no abundance peaks occurred in Jervis Inlet or Howe Sound.

3. The total population size of *Munida quadrispina* was fairly stable over time in Saanich Inlet, except in March 1980, when a 50% decrease occurred mainly in the largest animals in the population. This coincided with the greatest recruitment of juveniles.

4. *Munida quadrispina* were distributed in a size gradient with depth in Saanich Inlet such that the largest animals were deepest, and therefore living in the lowest oxygen concentrations. This did not occur in Jervis Inlet or Howe Sound.

5. The carapace length of *Munida quadrispina* was related to metabolism such that the largest animals has the lowest weight specific oxygen consumption.

6. There was no significant difference in the laboratory oxygen tolerance (Pc) and the field oxygen tolerance of *Munida quadrispina* from Saanich Inlet, indicating that the size distribution in Saanich was caused by size specific oxygen tolerances.

7. Gill weight increased exponentially with organic body weight only in those Munida quadrispina from the oxygen depleted areas of Saanich Inlet, indicating that gill development is affected by long term oxygen depletion, and may be a survival advantage in Saanich Inlet.

8. Distribution of Munida quadrispina seems to be partially controlled by oxygen conditions, such that changes in the oxygen regime from year to year could seriously affect the population structure of this species.

Literature

~~REFERENCES~~ CITED

AMBLER, J.W. 1980. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent Waters. Biol. Bull.78:13-34.

ANDERSON, J.F. 1970. Metabolic rates of spiders. Comp. Biochem. Physiol. 33:51-72.

ANDERSON, J.J. and A.H. DEVOL. 1973. Deepwater renewal in Saanich Inlet, an intermittently anoxic basin. Estuarine & Coastal Mar. Sci.:1-10.

AYERS, J.C. 1938. Relationship of habitat to oxygen consumption in certain estuarine crabs. Ecology 19:523-527.

BABULA, A., J. BIELAWSKI and J. SOBIESKI. 1978. Oxygen consumption and gill surface area in *Mesidothea entomon* (L) (Isopoda, Crustacea). Comp. Biochem. Physiol. 61A:595-597.

BALLARD, R.D. 1979. The Incredible World of the Deep-Sea Rifts. Nat. Geog. 156:680-705.

BARNES, R.D. 1980. Invertebrate Zoology. Holt, Rinehart and Wilson, Saunders College, Philadelphia. 1089p.

BAYNE, B.L. 1971. Oxygen consumption by three species of Lamellibranch mollusc in declining ambient oxygen tension. Comp. Biochem. Physiol. 40:955-970.

BAYNE, B.L. and D.R. LIVINGSTONE. 1977. Responses of *Mytilus edulis* L. to low oxygen tension: allcimation of the rate of oxygen consumption. J. Comp. Physiol. 114:129-142.

BELL, W.H. 1973. The exchange of deep water in Howe Sound basin. Pac. Mar. Sci. Rep. 73-13, Institute of Ocean Sciences, Sidney, B.C. 35p.

BELMAN, B.W. and J.J. CHILDRESS. 1973. Oxygen consumption of the larvae of the lobster *Panulirus interruptus* (Randall) and the crab *Cancer productus* (Randall). J. Biochem. Physiol. 44:821-828.

BELMAN, B.W. and J.J. CHILDRESS. 1976. Circulatory adaptions to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. Biol. Bull. 150:15-37.

BERG, K. and P.M. JOHANSSEN. 1965. Oxygen consumption of profundal lake animals at low oxygen content of water. Hydrobiol. 26:131-143.

BERGMILER, E. and J. BIELAWSKI. 1970. Role of the gills in osmotic regulation of the crayfish Astacus leptodactylus (Esch). Comp. Biochem. Physiol. 37:85-91.

BERTNESS, M.D. 1977. Behavioural and ecological aspects of shore-level size gradients in Thais lamellosa and Thais emarginata. Ecology 58:86-97.

BLACKBURN, M. 1977. Temporal changes in pelagic biomass of Pleuroncodes planipes Stimpson (Decapoda, Anomura, Galatheidea) off Baja California, Mexico. Crustaceana 32:178-184.

BOCK, F. 1925. Die Respirationsorgane von Potamobus astacus Leach (Astacus fluviatilis Fab.) Ein Bietrag zur morphologie des Decapoden. Z. wiss. Zool. 124:51-117.

BOYD, C.M. 1967. The benthic and pelagic habitats of the red crab, Pleuroncodes planipes. Pac. Sci. 21:394-403.

BRATTEGARD, T. 1979. Why biologists are interested in fjords. In: Fjord Oceanography. Edited by H.J. Freeland, D.M. Farmer and C.D. Levings. Plenum Press, New York. pp.53-66.

BRIDGES, C.R. and A.R. BRAND. 1980a. Oxygen consumption and oxygen independance in marine crustaceans. Mar. Ecol. Prog. Ser. 2:133-141.

BRIDGES, C.R. and A.R. BRAND. 1980b. Effects of hypoxia on oxygen consumption and blood lactate levels of some marine crustacea. J. Biochem. Physiol. 65:399-409.

BURGGREN, W.W., B.R. McMAHON and J.W. CASTERTON. 1974. Branchial water and blood-flow patterns and the structure of the gill of the crayfish Procambarus clarkii. Can. J. Zool. 52:1511-1521.

BUTLER, P.J., E.W. TAYLOR and B.R. McMAHON. 1978. Respiratory and circulatory changes in the lobster (H. vulgaris) during long-term exposure to moderate hypoxia. J. Exp. Biol. 73:131-146.

CHAPMAN, P.M., M.A. FARRELL and R.O. BRINKHURST. 1982. Relative tolerances of selected aquatic oligochaetes to combinations of pollutants and environmental factors. Aqu. Toxicol. 2:69-78.

CHILDRESS, J.J. 1975. The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off southern California. Comp. Biochem. Physiol. 50:787-799.

COURCHESNE, E. and G.W. BARLOW. 1971. Effect of isolation on components of aggressive and other behaviour in the hermit crab Pagurus samuelis. Z. Vergl. Physiol. 75:32-48.

✓ DAVIS, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J.Fish Res. Board Can. 32:2295-2332.

DEFUR, P.L., P.R.H. WILKES and B.R. McMAHON. 1980. Non-equilibrium acid-base status in Cancer productus: Role of exoskeleton carbonate buffers. Respir. Physiol. 42:247-261.

DUNHAM, P. 1972. Some effects of group housing upon aggressive behaviour of the lobster H. americanus. J.Fish. Res. Board Can. 29:598-601.

EMERSON, S., R.E. CRANSTON and P.S. LISS. 1979. Redox species in a reducing fjord: Equilibrium and kinetic considerations. Deep Sea Res. 26:859-878.

FAMME, P. 1982. An open system respirometer for measuring steady-state oxygen uptake by aquatic animals, applied to the marine mussel, Mytilus edulis L. J. Exp. Mar. Biol. Ecol. 56:257-266.

FELDER, D.L. 1979. Respiratory adaptations of the estuarine mud shrimp Callianassa jamaicense (Schmitt, 1935) (Crustacea, Decapoda, Thallasianidae). Biol. Bull. 157:125-137.

FOX, H.M. 1949. Haemoglobin in crustacea. Nature 164:59.

✓ GADE, H.G. and A. EDWARDS. 1979. Deep water renewal in fjords. In Fjord Oceanography. Edited by H.J. Freeland, D.M. Farmer and C.D. Levings. Plenum Press, New York. pp. 453-490.

✓ GILMARTIN, M. 1962. Annual cyclic changes in the physical oceanography of a British Columbia fjord. J.Fish. Res. Board Can. 19:922-974.

GNAIGER, E. 1980. Energetics of invertebrate anoxibiosis: Direct Calorimetry in aquatic oligochaetes. Fish. Res. Board Letters 112:239-242.

GRAY, I.E. 1954. A comparative study of the gill area of marine fishes. Biol. Bull. 107:219-225.

GRAY, I.E. 1957. A comparative study of the gill area of crabs. Biol. Bull. 112:34-42.

GURNEY, R. 1960. Larvae of decapod crustacea. Adland and Son Ltd., London. 306 p.

HAGERMAN, L. 1976. The respiration during the moult cycle of *Crangon vulgaris* (Fabricius) (Crustacea, Natantia). Ophelia 15:15-21.

HAZLETT, B.A. 1968. Effects of crowding on the agonistic behaviour of the hermit crab *Pagurus bernhardus*. Ecology 49:573-575.

HERLINVEAUX, R. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. J. Fish. Res. Board Can. 19:6-26.

HILL, B. 1981. Respiratory adaptations of three species of *Upogebia* (Thallasinidea, crustacea) with special reference to low tide periods. Biol. Bull. 160:272-279.

HOCHACHKA, P.W. 1980. Living without oxygen: closed and open systems in hypoxia tolerance. Harvard University Press, Cambridge Mass. 182p.

HUGHES, G.M. 1966. The dimensions of fish gills in relation to their function. J. Exp. Biol. 45:177-195.

JONES, J.D. 1972. Comparative physiology of respiration (Special topics in biology series). Edward Arnold Ltd. London. 201 p.

JORGENSON, B.B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. Oikos 34:68-76.

JUDKINS, D.C. 1979. Vertical distribution of zooplankton in relation to the oxygen minimum layer off Peru. Deep-Sea Res. 27:475-487.

KAESTNER, A. 1970. Invertebrate Zoology Volume 3:Crustacea. Wiley Interscience, New York. 523 p.

KERKUT, G.A. 1958. The invertebrata, third edition. Cambridge University Press. 795p.

LAIRD, C.E. and P.A. HAEFNER Jr. 1976. The effect of intrinsic and environmental factors on oxygen consumption in the blue crab, Cancer sapidus (Rathbun). J. Exp. Mar. Biol. Ecol. 22:171-178.

LARIMER, J.L. 1961. Measurements of ventilation volume in decapod crustacea. Physiol. Zool. 34:158-166.

LAZIER, R.B.M. 1973. Some aspects of the oceanographic structure in the Jervis Inlet system. MSc thesis, University of British Columbia.

LEFFLER, C.W. 1973. Metabolic rate in relation to body size and environmental oxygen concentration in two species of Xanthid crabs. Comp. Biochem. Physiol. 44:1047-1052.

LEPPAKOSKI, E. 1969. Transitory return of the benthic fauna of the Bornholm Basin after extermination by oxygen insufficiency. Cah. Biol. Mar. 10:163-172.

LEVINGS, C.D. 1980a. Demersal and benthic communities in Howe Sound Basin and their responses to dissolved oxygen deficiency. Can. Tech. Rep. Fish. Aqu. Sci. 951:27p.

LEVINGS, C.D. 1980b. Benthic biology of a dissolved oxygen deficiency event in Howe Sound, British Columbia. In: Fjord Oceanography. Edited by H.J. Freeland, D.M.Farmer and C.D. Levings. Plenum Press, New York pp.515-522.

MANGUM, C.P. 1972. pH of body fluids of marine invertebrates. Comp. Biochem. Physiol. 42:693-698.

MANGUM, C.P. and W. VAN WINKLE. 1973. Responses of aquatic invertebrates to declining oxygen conditions. Am. Zool. 13:529-541.

MAYO, B.S. 1972. Biological results of the University of Miami deep sea expeditions 90: Three new species of the family Galatheidae (Crustacea, Anomura) from the western Atlantic. Bull. Mar. Sci. 22:522-535.

McDANIEL, N.G., R.D. MACDONALD, J.J. DOBROCKY and C.D. LEVINGS. 1977. Biological surveys using in-water photography at three ocean disposal sites in the strait of Georgia. Dept. Fish. Envir. F.M.S. Tech. Rep. 713. 49p.

McDANIEL, N.C., C.D. LEVINGS, D. GOYETTE and D. BROTHERS. 1978. Otter trawl catches at disrupted and intact habitats in Howe Sound, Jervis Inlet and Bute Inlet, British Columbia. Dept. Fish. Envir. F.M.S. Data Rep.92. 78p.

McQUAID, C.D. 1981. The establishment and maintenance of vertical size gradients in populations of *Littorina africana kysnaensis* (Phillipi) on an exposed rocky shore. J. Mar. Biol. Ecol. 54:77-89.

McMAHON, B.R. and J.L. WILKENS. 1974. Respiratory and circulatory responses to hypoxia in the lobster (*H. americanus*). J. Exp. Biol. 62:637-655.

McMAHON B.R. P.J. BUTLER and E.W. TAYLOR. 1978. Acid-base changes during recovery from disturbance and during long-term hypoxic exposure in the lobster *H. vulgarus*. J. Exp. Zool. 205:361-370.

McWHINNIE, H.A. and P. MARCENIAK. 1964. Temperature responses and tissue respiration in Antarctic crustacea with particular reference to the krill *Euphausia pacifica*. In Biology of the Antarctic Seas. Edited by M. Lee. Pridemark Ltd. pp. 63-72.

NICOL, E.A.T. 1932. The feeding habits of the Galatheidae. J. Mar. Biol. Assoc. U. K. 18:78-106.

NICOL, J.A.C. 1967. The biology of marine animals. Pitman, London. 699 p.

PEARSE, A.S. 1929. Crustacean gills and habitat. Carn. Inst. of Wash. Totugas Papers 391:205-223.

PEARSON, T.H. and R. ROSENBERG. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16:229-311.

PEARSON, T.H. 1979. The macrobenthos of fjords. In Fjord Oceanography. *Edited by* H.J. Freeland, D.M. Farmer and C.D. Levings. Plenum Press, New York pp.569-602.

PEQUENAT, L.H. and W.E. PEQUENAT. 1970. Deep sea anomurans of the subfamily Galatheoidea with descriptions of three new species. In Contributions on the Biology the the Gulf of Mexico. *Edited by* W.E. Pequenat and F.A. Chase, Jr. Texas A&M U. Oceanogr. Stud. I(suppl).pp.1-24.

PICKARD, G.L. 1961. Oceanographic Features of Inlets in the British Columbia mainland coast. J.Fish. Res. Board Can. 18:907-999.

______, 1963. Oceanographic characteristics of inlets of Vancouver Island, British Columbia. J.Fish. Res. Board Can. 20:1109-1144.

PRITCHARD, A.W. and S. EDDY. 1979. Lactate formation in C. californiensis and U. pugettensis. Mar. Biol. 50:249-253.

QUETIN, L.B. and J.J. CHILDRESS. 1976. Respiratory adaptations of Pleuroncodes planipes to its environment off Baja California. Mar. Biol. 38:327-334.

RICHARDS, F.A. 1965. Anoxic basins and fjords. In Chemical Oceanography Vol.1. Edited by J.P. Riley and O. Skirrow. New York Academic Press pp.611-645.

ROBERTSON, J.D. 1941. Calcium in the invertebrata. Biol. Rev. 16:106-133.

ROSENBERG, R. 1979. Effect of oxygen deficiency on benthic macrofauna in fjords. In. Fjord Oceanography. Edited by H.J. Freeland, D.M. Farmer, C.D. Levings. Plenum Press, New York. pp. 499-514.

SCHOTTLER, U. 1979. On the anaerobic metabolism of three species of Nereis (Annelida). Mar. Ecol. Prog. Ser. 1:249-254.

STRICKLAND, J.D.H. and T.R. PARSONS. 1972. A practical handbook of seawater analysis. Fish. Res. Board Bull. 167. 309pp.

TANG, P.S. 1933. Oxygen consumption as a function of oxygen pressure. Q. Rev. Biol. 8:260-274.

TAYLOR, A.C. and A.R. BRAND. 1975. Effects of hypoxia and body size on the oxygen consumption of the bivalve Arctica islandica L. J. Exp. Mar. Biol. Ecol. 19:187-196.

TAYLOR, A.C. 1976. The respiratory responses of Carcinus maenus to declining oxygen tension. J. Exp. Biol. 65:309-322.

TAYLOR, A.W., P.J. BUTLER, and A. AL-WASSIA. 1977. Some responses of the shore crab Carcinus maenas to progressive hypoxia at different acclimatory temperatures and salinities. J. Comp. Physiol. 122:391-402.

SOMERTON, D.A. 1981. Contribution to the life history of the deep-sea king crab, Lithodes couesi, in the Gulf of Mexico. Fish. Bull. 79:259-269.

TEAL, J.M. and F.G. CAREY. 1967. The metabolism of marsh crabs under conditions of reduced oxygen pressure. Physiol. Zool. 40:83-91.

THEEDE, H., A. PONAL, K. HIROKI and C. SCHLIEPER. 1969. Studies on the resistance of marine bottom dwelling invertebrates to oxygen deficiency and hydrogen sulfide. Mar. Biol. 2:325-337.

THOMPSON, R.K. and A.W. PRITCHARD. 1969. Respiratory adaptations of two burrowing crustaceans, C. californiensis and U. pugettensis. Biol. Bull. 136:274-287.

TULKKI, P. 1965. Disappearance of the benthic fauna from the basin of Bornholm (S. Baltic) due to oxygen deficiency. Cah. Biol. Mar. 6:455-463.

TUNNICLIFFE, V. 1981. High species diversity and abundance of the epibenthic community in an oxygen deficient basin. Nature 294:354-356.

VANNINI, M. 1981. Notes on some factors affecting aggressive behaviour in Carcinus mediterraneus. Mar. Biol. 61:235-241.

VERNBERG, J.F. 1956. Oxygen consumption of excised tissues of certain marine crustacea in relation to habitat. Physiol. Zool. 29:227-234.

WILKIE, D.W. 1971. Short Communication: The carotenoid pigmentation of Pleuroncodes planipes (Stimpson) Crustacea:Decapoda Galatheidae. Comp. Biochem. Physiol. 42:731-734.

WILLIAMS, B.G. 1971. The effect of the environment on the morphology of Munida gregaria (Fabricus)(Decapoda, Anomura). Crustaceana 24:197-210.

WILLIAMS, B.G. 1980. The pelagic and benthic phases of post-metamorphic Munida gregaria (Fabricius)(Decapoda, Anomura). J. Exp. Mar. Biol. Ecol. 42:125-141.

WINGET, R.R. 1969. The oxygen consumption and respiratory energetics in the spiny lobster P. interruptus (Randall). Biol. Bull. 136:301-312.

WOLVEKAMP, H.P. and T.H. WATERMAN. 1960. Respiration. In The Physiology of Crustacea Vol. 1:Metabolism and Growth. Edited by Waterman, T.H. Academic Press, New York pp.1-100.

ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. Q. Rev. Biol. 28:1-12.

Appendix 1r. Density distribution of <u>Munida</u> <u>quadrispina</u> from phototransects in Saanich Inlet. Values represent means calculated from two or more photographs at each depth.

McCurdy Point

Date	Depth (m)	Density (#/m^2)	Standard Error (±)
September 1980	35	0	-
	45	3	1
	70	14	3
	80	41	5
	85	50	7
	90	28	3
	100	26	1
	110	64	3
	115	32	5
	120	32	6
	125	0	-
October 1980	45	0	0
	60	26	-
	75	50	5
	85	102	22
	90	137	27
	92	22	-
	95	0	-
November 1980	35	0	-
	40	5	3
	45	2	0.5
	60	9	2
	75	38	4
	80	13	4
	90	23	5
	95	33	6
	100	137	19
	107	20	5
	112	0	-
February 1981	35	0	-
	42	6	1
	60	4	1
	65	1	0.5
	70	11	1
	80	10	2
	100	41	9
	105	54	3
	110	72	3
	115	7	-
	120	0	

Date	Depth (m)	Density (#/m^2)	Standard Error (±)
March 1981	45	0	-
	60	3	1
	80	12	2
	105	18	2
	110	30	2
	117	12	4
	122	0	-
Elbow Point			
September 1980	40	0	0
	60	16	6
	70	25	5
	82	57	-
	90	46	8
	100	16	3
	110	53	4
	115	14	4
	120	0	-
October 1980	35	0	-
	44	4	-
	60	4	-
	70	44	-
	75	49	-
	85	220	-
	90	0	-
November 1980	35	0	-
	40	1	1
	50	1	0.5
	67	12	7
	75	22	7
	85	19	3
	100	163	35
	105	169	15
	117	0	-
February 1981	35	0	-
	40	2	1
	55	13	3
	65	22	1
	75	6	1
	85	14	4
	95	25	5
	105	51	3
	115	4	1
	120	0	-

Date	Depth (m)	Density (#/m^2)	Standard Error (±)
March 1981	35	0	-
	55	4	1
	60	1	1
	75	5	1
	85	15	4
	100	38	14
	105	19	3
	110	16	3
	115	43	2
	122	0	-
Finlayson Arm			
November 1980	45	0	-
	58	24	11
	68	40	14
	76	28	3
	88	26	7
	94	32	6
	100	140	60
	105	0	-

Appendix 2. Number and average size (Folded length) of *Munida quadrispina* from each photograph. Data from V.Tunnicliffe not included (see Table I).

Date and Location	Depth	N	Length
September 1980 McCurdy Point	126	0	-
	122	11	26.4
	122	16	25.6
	122	7	32.3
	122	0	-
	122	0	-
	122	0	-
	115	5	26
	110	20	28.0
	110	23	23.2
	110	23	23.2
	98	9	26.0
	96	9	23.2
	93	8	28.0
	93	10	28.0
	93	14	28.0
	93	15	28.0
	92	13	21.4
	90	6	17.0
	82	21	17.3
	82	32	15.3
	81	5	18.0
	78	15	-
	78	16	17.6
	76	18	15.3
	76	12	15.6
	76	15	13.0
	76	15	15.8
	75	3	8.0
	70	4	6.5
	65	6	6.4
	41	2	5.1
	41	1	5.1
	38	1	-
	38	0	-
	38	0	-
	32	0	-
	19	0	0

Appendix 2 . Continued.

Date and Location	Depth	N	Length
October 1980 McCurdy Point	95	10	31.9
	90	62	26.0
	90	100	25.8
	90	25	21.0
	85	48	25.5
	85	14	24.5
	70	8	13.5
	70	8	13.5
	63	2	12.7
	60	9	6.4
	52	0	–
	52	0	–
November 1980 McCurdy Point	122	0	–
	122	0	–
	120	0	–
	114	0	–
	107	1	25.0
	107	10	33.0
	105	2	24.0
	105	2	27.0
	105	4	27.0
	105	7	27.0
	101	27	25.0
	101	34	26.0
	99	7	22.0
	95	19	18.0
	95	20	18.0
	95	21	18.0
	95	11	18.2
	94	11	–
	94	–	–
	94	–	–
	93	9	15.0
	93	–	–
	89	8	16.0
	89	9	15.0
	86	7	13.8
	84	9	16.0
	77	7	15.0
	77	2	14.5
	74	8	13.5
	71	1	13.0
	70	10	13.0
	70	14	11.0
	38	2	10.0

Appendix 2. Continued.

Date and Location	Depth	N	Length
February 1981 McCurdy Point	130	0	-
	128	0	-
	119	0	-
	118	4	25.1
	118	3	25.4
	113	38	23.9
	113	39	23.5
	107	6	23.5
	105	12	23.5
	102	16	23.0
	102	24	27.1
	102	22	-
	94	4	19.7
	91	0	-
	90	2	18.8
	84	4	22.4
	84	6	13.4
	82	5	19.8
	82	3	16.9
	82	1	14.3
	81	9	12.0
	71	5	12.2
	71	5	10.7
	65	3	11.8
	65	1	5.1
	58	3	5.1
	58	2	5.1
	38	2	11.8
	38	0	-
	33	0	-
March 1981 McCurdy Point	124	0	-
	119	2	28.1
	118	2	30.6
	118	4	28.2
	118	5	26.7
	112	5	28.0
	112	5	21.4
	106	15	25.1
	106	3	25.1
	102	2	18.9
	100	0	-
	93	1	14.3
	86	5	13.0
	86	5	13.0
	83	4	13.0
	68	1	8.5
	46	0	-
	19	0	-

Appendix 2. Continued.

Date and Location	Depth	N	Length
September 1980 Elbow Point	124	0	-
	124	0	-
	118	30	-
	115	1	-
	115	11	24.0
	115	7	24.0
	115	8	27.0
	108	5	20.0
	106	20	21.0
	104	8	21.0
	104	8	18.0
	103	5	22.7
	99	12	23.0
	93	16	18.0
	90	25	17.5
	83	30	17.9
	71	13	8.3
	58	3	7.0
	48	0	-
	43	2	6.8
October 1980 Elbow Point	84	80	26.0
	75	10	18.6
	70	22	13.0
	60	6	7.0
	60	0	-
	45	1	7.0
	45	0	-
	45	0	-
November 1980 Elbow Point	116	1	34.4
	111	0	-
	105	80	27.0
	105	68	30.0
	105	20	26.0
	103	3	21.0
	101	14	17.0
	100	52	24.0
	100	43	21.0
	97	45	24.0
	97	7	26.0
	95	8	23.0
	93	37	28.0
	93	37	25.0
	93	46	-
	93	44	30.0
	92	17	21.0
	90	4	20.0
	85	4	20.0

Appendix 2. Continued.

Date and Location	Depth	N	Length
	85	2	19.0
	85	6	15.0
	85	8	19.0
	85	9	19.0
	82	11	18.8
	82	13	17.6
	82	8	19.0
	76	7	13.3
	75	9	14.3
	75	6	15.3
	72	-	13.0
	72	-	-
	66	3	9.0
	64	19	12.0
	52	2	6.4
	52	0	-
	51	0	-
	37	1	7.6
	37	0	-
	35	0	-
	21	0	-
February 1981 Elbow Point	127	0	-
	127	0	-
	117	0	-
	115	0	-
	115	1	22.0
	115	1	22.0
	112	15	26.0
	112	15	26.0
	110	25	25.0
	109	29	23.0
	105	20	26.0
	99	9	21.3
	99	11	21.3
	95	3	21.8
	95	6	19.9
	92	3	16.0
	90	8	17.9
	86	2	14.3
	86	3	14.6
	86	8	15.8
	80	1	16.0
	80	1	14.0
	80	3	10.0

Appendix 2. Continued.

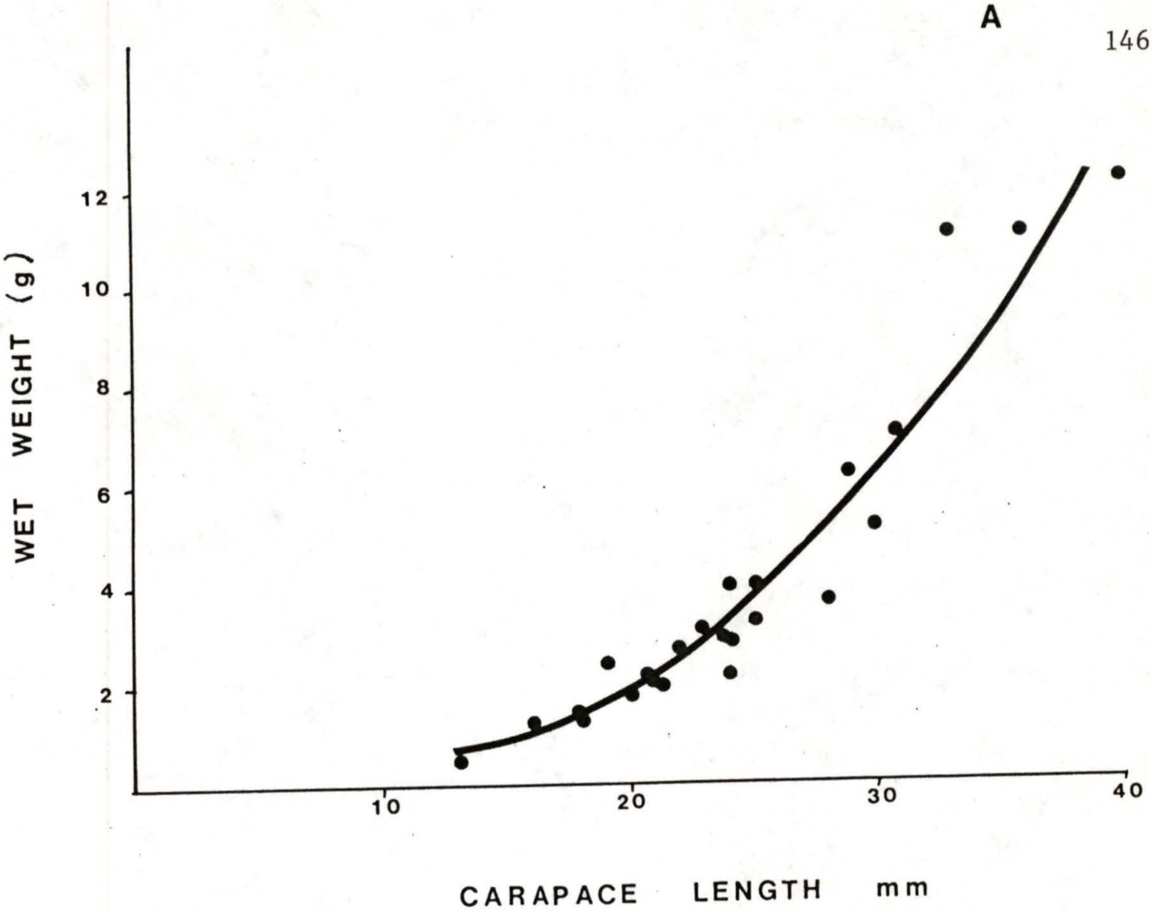
Date and Location	Depth	N	Length
	75	1	14.0
	74	3	14.0
	74	2	14.0
	68	6	12.0
	68	7	12.0
	65	1	9.3
	65	0	-
	56	3	10.5
	35	3	8.5
	35	1	9.0
March 1981 Elbow Point	130	0	-
	125	0	-
	122	1	-
	118	1	34.0
	114	14	27.9
	114	15	27.7
	111	3	23.7
	111	5	24.6
	110	4	21.8
	110	1	23.0
	110	26	26.5
	104	3	20.6
	104	7	22.0
	104	4	22.0
	102	2	14.5
	102	3	19.3
	102	2	23.0
	100	6	17.8
	100	18	16.2
	93	1	19.4
	92	1	18.6
	91	2	20.1
	90	3	20.9
	86	4	17.0
	86	5	17.0
	83	5	18.9
	76	2	13.4
	75	2	15.0
	75	4	13.4
	64	1	8.5
	64	1	8.5
	61	1	8.5
	57	1	8.5
	57	1	8.5

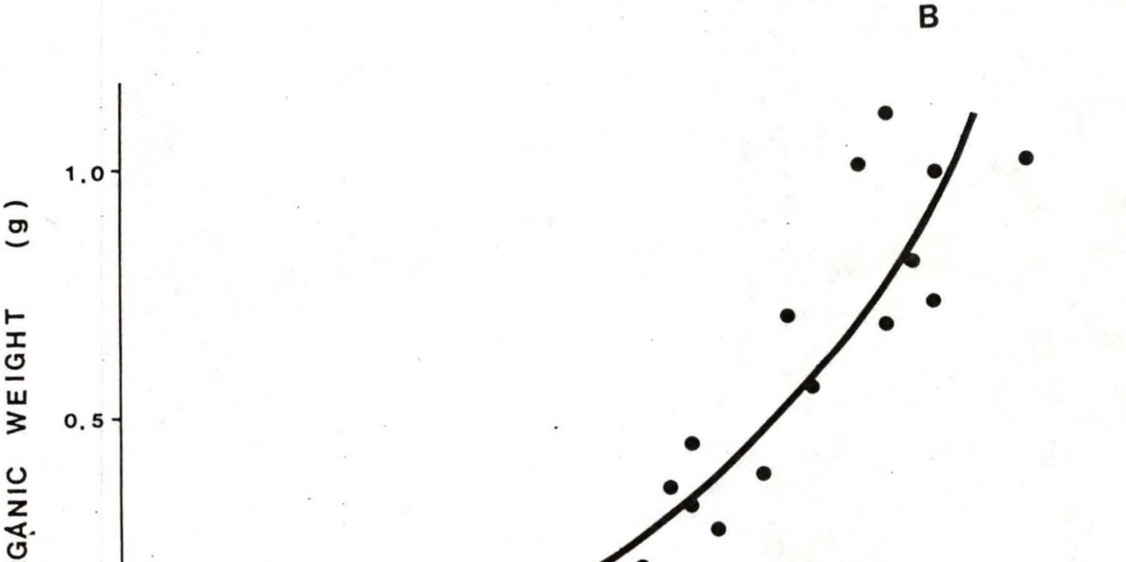
Appendix 2. Continued.

Date and Location	Depth	N	Length
November 1980 Finlayson Arm	98	26	26.4
	96	82	22.2
	94	16	24.9
	94	10	17.7
	94	8	19.4
	88	9	16.3
	88	15	12.9
	88	16	12.8
	78	11	15.0
	76	14	12.0
	76	7	10.2
	70	20	8.9
	67	9	7.6
	60	6	10.2
	60	18	13.9
	57	4	5.5
March 1981 Port Melon, Howe Sound	218	3	19.7
	201	2	22.3
	182	1	19.7
	182	2	19.7
	170	0	-
	170	2	19.7
	162	1	16.1
	162	1	19.7
	162	1	19.7
	160	2	19.1
	157	1	15.0
	119	2	18.0
	103	0	-
	103	1	19.7
	89	4	19.5
	89	1	19.5
	70	2	18.6
	70	2	19.1
	52	1	15.3
	27	0	-

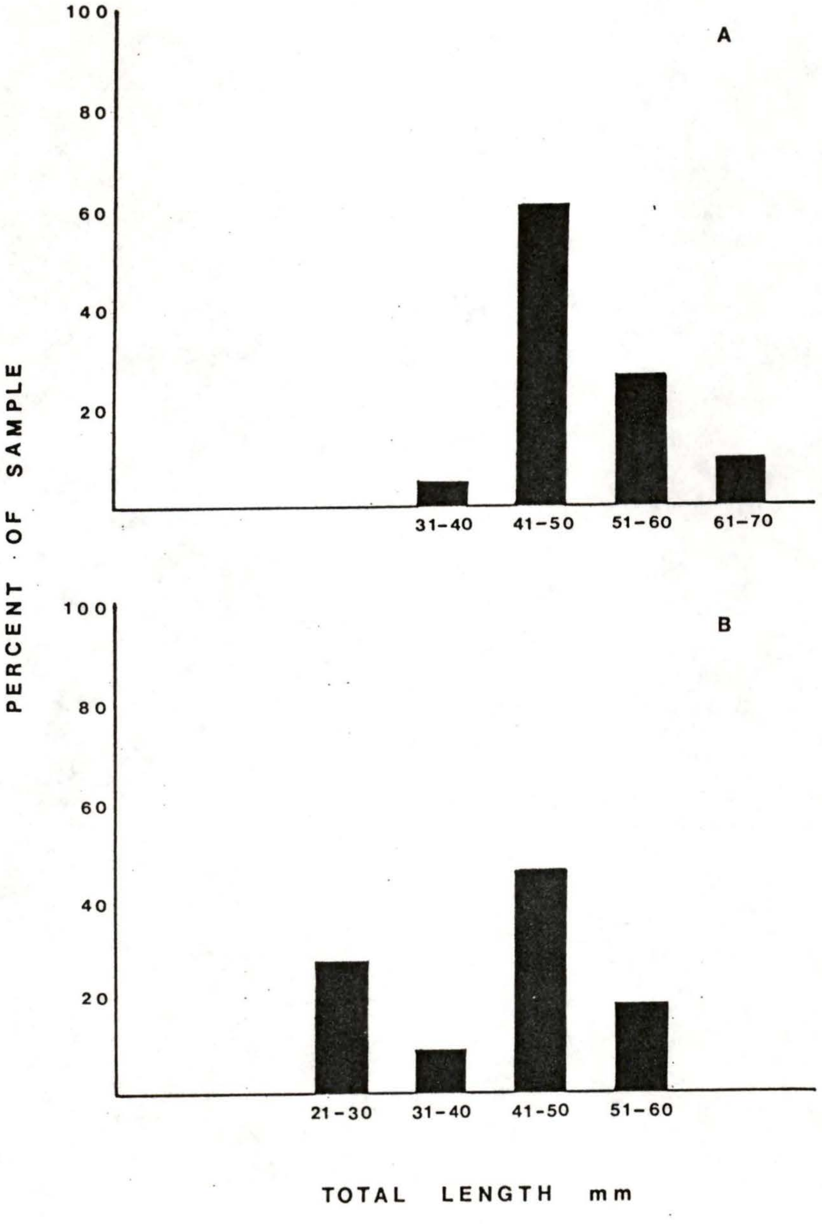
Appendix 3. A. Exponential relationship of wet weight (g) to carapace length (mm) in Munida quadrispina from Saanich Inlet. $n = 25$, $r = 0.95$.

B. Exponential relationship of organic weight (g) to carapace length (mm) in Munida from Saanich Inlet. $n = 36$, $r = 0.95$.


A
WET WEIGHT (g)
2
4
6
8
10
12
10
20
30
40
CARAPACE LENGTH mm


B
ORGANIC WEIGHT (g)
0,5
1,0
10
20
30
40
CARAPACE LENGTH (mm)

Appendix 4. Size distribution of Munida quadrispina trapped from 85m depth at McCurdy Point. A = November 20 1980, n = 24. B = March 23 1981, n = 12.


PERCENT OF SAMPLE
A
100
80
60
40
20
31-40
41-50
51-60
61-70
B
100
80
60
40
20
21-30
31-40
41-50
51-60
TOTAL LENGTH mm

Appendix 5. Life History Extrapolations

It is difficult to deduce the life history of *Munida quadrispina* from a study such as this, without background information on growth from lab studies. However, the information gathered during this study provides a basis from which some of the life history of this species can be inferred, as a starting point for future research.

The growth of this species can undoubtedly be affected by physical and biological environmental conditions, so that it is only possible to discuss the life history of *Munida quadrispina* from Saanich Inlet. It should be noted however, that this species is widespread in British Columbia and Alaska (Kozloff 1980).

Reproduction seems to occur only in late winter, when berried females can be captured. This occurs in *Munida quadrispina* from Jervis Inlet and other coastal areas besides Saanich Inlet (J. Hart, pers. comm.). Juvenile settlement is most extensive at this time, as is the evidence of a mass mortality in the largest adults. This suggests that the oldest year class reaches the end of its life span just after reproduction, and/or at the end of the production year in Saanich (i.e. just before spring bloom). The actual cause of this mortality cannot be discerned from this study, but the *Munida* which disappear at this time corresponds with the maximum size of *Pleuroncodes planipes* (Boyd 1967) and *Munida gregaria* (Williams 1971) that have been captured, suggesting that all three species probably have the same life span.

Boyd and Williams stated that M. gregaria and P. planipes live a maximum of 3 to 4 years. The first year class appears to remain pelagic until about 1 year of age. Therefore, can the second year class, presumably benthic, be found?

An examination of the density distributions of the benthic Munida quadrispina from Saanich Inlet (Figures 15A,B and Appendix 1) indicates that a secondary, shallower peak in abundance can occasionally be observed. By examining the carapace length of animals found at the depth of this secondary peak in each phototransect (Table 3), a comparison of the size of animals from each of these secondary peaks can be made (Table 6). It turns out that in all cases the carapace length is approximately 10mm. It is most likely that this represents a size class between 1 and 3 three years old.

The population structure of Munida quadrispina in Saanich Inlet seems to be heavily weighted with the largest size class. This does not occur in Jervis Inlet or Howe Sound, where the average size of Munida is noticeably smaller than in Saanich. Mortality of the largest animals in Saanich Inlet is probably reduced by the lack of predators in the severely oxygen depleted areas of the cliff.

Table 6. Estimated carapace length of Munida quadrispina (from Table 3) at the depth of the secondary peak of abundance observed in some phototransects (Figures 15 and Appendix 1).

Location	Date	Depth	Carapace Length
McCurdy Point	September 1980	80m	9.0mm
	October 1980	--	--
	November 1980	72m	9.3mm
	February 1981	70m	9.3mm
	March 1981	--	--
Elbow Point	September 1980	80m	10.7mm
	October 1980	--	--
	November 1980	74m	11.1mm
	February 1981	70m	9.7mm
	March 1981	100m	14.7mm
Finlayson Arm	November 1980	68m	9.6mm

Mean = 9.8mm

Standard Error = 0.3

Vita

Surname: BURD Given Names: BRENDA JEAN

Place of Birth: LONDON, ONTARIO Date of Birth: February 8, 1957

Educational Institutions Attended, with Dates of Entering and Leaving:

PRINCE EDWARD COLLEGIATE INSTITUTE, PICTON, ONTARIO 1970 to 1975

QUEEN'S UNIVERSITY, KINGSTON, ONTARIO 1975 to 1979

UNIVERSITY OF VICTORIA, VICTORIA, B.C. 1980 to 1983

Degrees, Diplomas, Etc., Awarded, with Dates and Names of Institutions:

B.Sc. (Honours) 1979 Queen's University, Kingston, Ontario

Honours and Awards:

Ontario Scholarship 1975

University Women's Club Scholarship 1974, 1975

B.C. G.R.E.A.T. Award 1980-1982

Publications:

Title of Thesis

The distribution, respiration and gills of a low oxygen tolerant Galatheid crab, *Munida quadrispina* (Benedict, 1902)in an intermittently anoxic basin.

Author [redacted]

BRENDA JEAN BURD