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THE DISTRIBUTION OF THE GALATHEID CRAB *MUNIDA QUADRISPINA* (Benedict 1902) IN RELATION TO OXYGEN CONCENTRATIONS IN BRITISH COLUMBIA FJORDS

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Abstract: Using the manned submersible *Pisces IV*, depth, population density and size distributions of the galatheid crab *Munida quadrispina* (Benedict) were measured in relation to oxygen concentrations in Saanich Inlet and two other fjords in British Columbia. Sampling was done from May 1980 to June 1981, and September 1982 to April 1983.

M. quadrispina were consistently found at oxygen levels as low as 0.1 to 0.15 ml/l in Saanich Inlet, where population density was greatest. No adults were ever observed below 140 m in this 220-m deep fjord. Total estimated counts per transect and changes in depth–density distributions indicate that these epibenthic crabs remained within tolerable oxygen limits by vertical migration on the cliff. Carapace length of adults increased significantly ($P = 0.1$) with increasing depth and decreasing oxygen. Therefore, only the largest crabs were present at 0.1 to 0.15 ml/l oxygen, where food was abundant, and predation and interspecific competition were absent. Smaller crabs evidently could not tolerate these low oxygen conditions. In contrast, *M. quadrispina* were present to the bottom of the cliff in other, well oxygenated fjords (maximum 680 m). No size gradients or density peaks in population were found in these areas.

Key words: galatheid crab; population density; size distribution; oxygen concentration

INTRODUCTION

Isolated fjord basins are often geomorphologically shaped to act as nutrient sinks. Limited bottom water renewal and low mixing result in strong vertical stratification of temperature and salinity. The resultant stagnation of bottom water leads to deoxygenation, which can adversely affect the benthic community, limiting recycling of organic material and productivity of the fjord. Although bottom organisms in fjords can be readily sampled, remote studies of cliff invertebrates can be difficult below the depth accessible by SCUBA diving (see Jørgenson, 1980). Since a portion of the benthos in steep sided fjords can inhabit the cliff walls, the inability to sample these animals can seriously affect results of fjord studies.

In reviews on European anoxic basins, Pearson & Rosenberg (1978), Pearson (1979), and Rosenberg (1979) indicate that recovery from anoxia 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. This produces what Pearson & Rosenberg (1978) refer to as community instability. Tunnicliffe (1981) disputed this in her study of the cliff epifauna of Saanich Inlet, B. C., Canada, since the community maintained a high diversity and abundance in very low oxygen concentrations. Saanich Inlet has a long history of oxygen depletion (Herlinveaux, 1962), which may have allowed the benthic community to adapt.

Studies on European fjords indicate that polychaetes, lamellibranchs, anemones, and starfish are the groups most commonly found in low oxygen areas (Pearson & Rosenberg, 1978; Jørgenson, 1980; Tulkki, 1965; Leppakoski, 1969). These invertebrates may be capable of anaerobiosis for some period (Hochachka, 1980), followed by rapid reproduction upon recovery. Few crustaceans and no decapods are included in these low oxygen tolerant assemblages.

Galatheid crabs, however, have been found in oxygen deficient marine areas of North America. Childress (1975) and Boyd (1967), respectively, noted that *Pleuroncodes planipes* was present to oxygen levels of 0.1 ml/l in the plankton and <0.5 ml/l in the benthos off the coast of Baja California (an area affected by the mid-Pacific oxygen minimum layer). In Howe Sound, B.C., a fjord which experiences episodic anoxia similar to Saanich Inlet (Levings, 1980), the galatheid *Munida quadrispina* was consistently found (70% of samples) in low oxygen areas. Levings (1980) states that this species seemed better able to exploit low oxygen conditions than most invertebrates in Howe Sound. This species is also found in Saanich Inlet, B.C.

The present study deals with the effect of oxygen fluctuations on the distribution of *M. quadrispina* (Benedict) in Saanich Inlet, and two other fjords in British Columbia. Submersible dives made in Saanich Inlet in May 1980 revealed that *M. quadrispina* was the dominant mobile invertebrate species on the cliff. The crabs were found in large monospecific concentrations in severely oxygen depleted areas, with only one or two attached invertebrate species present (usually a small encrusting sponge and a small anemone). The hypothesis that the depth, density and size distributions of *M. quadrispina* were affected by oxygen was tested using remote sampling combined with in situ sampling from the submersible *Pisces IV*, stationed near Sidney, B.C.

There is no literature on the life history, habits or habitat of *M. quadrispina*, although it is widespread in waters bordering Pacific Canada and Alaska. The abundance of this species in B.C. suggests that it is an important contributor to nutrient recycling in B.C. fjords, especially in low oxygen areas.

AREAS SAMPLED

Saanich Inlet is a fjord located on the southeastern side of Vancouver Island with a maximum depth of 236 m. The cliff walls are partially covered with fine silt which is often deoxygenated below a water depth of 150 m. Water characteristics of Saanich Inlet have been studied by Herlinveaux (1962), Pickard (1963), Richards (1965), Anderson & Devol (1973), and Emerson *et al.* (1979). The main basin is partially isolated from outside water by a shallow sill (70 m) at the mouth of the Inlet, which prevents bottom water renewal for most of the year. Consequently, the deep water stagnates through winter and summer, producing deoxygenation and a build-up of the metabolic by-products of anaerobic bacterial respiration (Emerson *et al.*, 1979). In late summer deep water with density greater than the bottom water of Saanich upwells off the coast of B.C., flows into Satellite Channel and over the sill into Saanich Inlet. This layer sinks to bottom, forcing deoxygenated water upwards to a midwater depth and finally dispersing it (Herlinveaux, 1962; Anderson & Devol, 1973). The flow characteristics of this flushing water were measured by Anderson & Devol (1973) using temperature–salinity characteristics and nitrate budget analysis.

Two locations in Howe Sound were sampled. Howe Sound is ≈300 m deep. Although anoxia often occurs inside the inner sill (Levings, 1980), bottom water is thought to be completely exchanged within the sill every 3 or 4 yr (Bell, 1973). The other fjord sampled during this study was Jervis Inlet (700 m), a well-oxygenated basin (Pickard, 1961).

MATERIAL AND METHODS

Locations in Saanich Inlet were sampled between February 1980 and March 1981, and from August 1982 to April 1983. Three locations were far from the sill or flushing source of the inlet, so that oxygen depletion was extensive and prolonged. Areas sampled (Fig. 1) were McCurdy Point (No. 1, 48°33.6′N : 123°31.5′W), Elbow Point (No. 2, 48°32.8′N : 123°31.9′W), and Finlayson Arm (No. 3, 48°31.5′N : 123°32.3′W). Tozier Rock and Bamberton (Nos. 4 and 5, 48°34.6′N : 123°31.1′W) in Saanich Inlet were sampled once.

Locations outside Saanich Inlet which were sampled one or more times included Port Mellon (No. 6, 49°31.3′N : 123°27.9′W) and Brittania Beach (No. 7, 49°37.3′N : 123°13.25′W) in Howe Sound and Dark Cove (No. 8, 49°48.5′N : 123°57.0′W) in Jervis Inlet (Fig. 1). Sampling methods, locations and dates are summarized in Table I.

WATER SAMPLES

Bottle casts were done from 20–200 m at Stations 1, 2 and 3 to determine temperature, salinity and dissolved oxygen. Oxygen sampling was also done in situ by obtaining water samples through a port in the submersible (usually within 2 m of the cliff). They were fixed and analysed aboard ship. Oxygen analysis was done using a Winkler method (Strickland & Parsons, 1972).

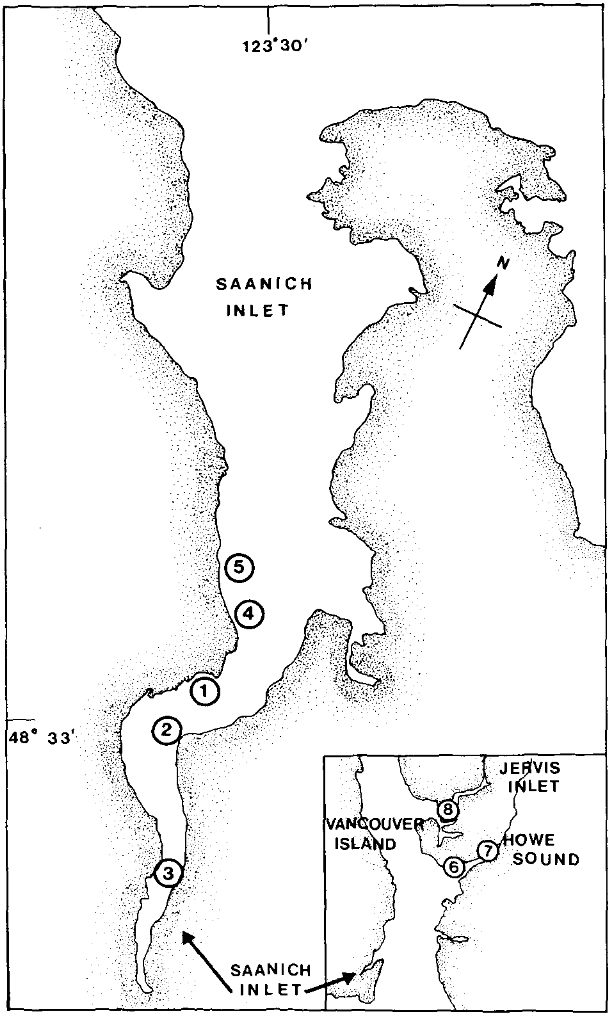

Fig. 1. Sampling stations in Saanich Inlet and other fjords in B.C. (see inset): 1, McCurdy Point; 2, Elbow Point; 3, Finlayson Arm; 4, Bamberton cement plant; 5, Tozier Rock; Station 6, Port Mellon, Howe Sound; Station 7, Brittania Beach, Howe Sound; Station 8, Dark Cove, Jervis Inlet.

SUBMERSIBLE DIVES

Sampling from the submersible consisted of taking several colour slides every 5 or 10 m up the cliff face, using two 35-mm cameras and 160–360 ASA tungsten film (external illumination on the submersible consists of tungsten lights). This sampling was done whenever possible, based on submersible availability. In phototransect dives a rubber bumper arm attached to the front of the submersible below the viewport supporting a 900-cm^2 frame on the distal end, was placed gently against the cliff and

TABLE I

Sampling methods, Stations and dates: +, –, operation carried out or not; *, bottle cast sampling; **, data supplied by V. Tunnicliffe or K. Bruce; *+, bottle cast and in situ oxygen sampling done.

Date	Station	Dives		Oxygen	Traps
		Phototransect	Observation		
1980					
May 15	1	–	+	*	–
May 15	2	–	+	*	–
June 15	8	–	+	–	–
July 16*	1	–	–	*	–
July 16*	2	–	–	*	–
July 16*	3	–	–	*	–
Aug. 19*	1	–	–	*	–
Aug. 19*	2	–	–	*	–
Aug. 19*	3	–	–	*	–
Sept. 3	1	+	+	+	+
Sept. 2, 4	2	+	+	+	+
Sept. 5	4	–	+	–	–
Sept. 5	5	+	–	+	–
Sept. 29, 30**	8	+	+	+	–
Oct. 16*, 23	1	+	–	*+	+
Oct. 16*, 23	2	+	–	*+	+
Oct. 16*	3	–	–	*	–
Nov. 13*, 20–27	1	+	+	*+	+
Nov. 13*, 18–27	2	+	+	*+	+
Nov. 13*, 18–19	3	+	+	*+	–
Dec. 4*	1	–	–	*	–
Dec. 4*	2	–	–	*	–
Dec. 4*	3	–	–	*	–
1981					
Jan. 15*	1	–	–	*	–
Jan. 15*	2	–	–	*	–
Jan. 15*	3	–	–	*	–
Feb. 3, 4, 18*	1	+	+	*+	+
Feb. 3, 5, 18*	2	+	+	*+	+
Feb. 2, 18*	3	–	+	*+	–
Feb. 23**	8	+	+	+	–
Mar. 23*, 24, 26	1	+	+	*+	+
Mar. 24, 25	2	+	+	+	+
Mar. 19	6	+	–	+	–
Mar. 17	7	–	+	+	–
May 26*	1	–	–	*	+
May 26	2	–	–	*	–
July 30*	1	–	–	*	–
July 30*	2	–	–	*	–
July 30*	3	–	–	*	–
Aug. 7*	1	–	–	*	–
Sept. 30*	1	–	–	*	–
Sept. 30*	2	–	–	*	–
Sept. 30*	3	–	–	*	–
Nov. 17*	1	–	–	*	–
Nov. 17*	2	–	–	*	–
Nov. 17*	3	–	–	*	–

Date	Station	Dives		Oxygen	Traps
		Phototransect	Observation		
1982					
Aug. 25	1	+	−	+	−
Aug. 25	2	+	−	+	−
Sept. 10	1	+	−	+	−
Sept. 10	2	+	−	+	−
Nov. 9	8	+	+	−	−
Nov. 11	1	+	−	+	−
1983					
Apr. 19–21**	1	+	+	+	−
Apr. 19–21**	3	+	−	+	−

Fig. 2. Example of scale photograph taken through the viewport of *Pisces IV* (Station 1, 10 Sept. 1982, 95 m): the scale encloses an area of 0.09 m^2.

photographed (Fig. 2). *M. quadrispina* did not move away from the frame unless touched. The area of the photograph, carapace length of visible animals and population density could be calculated by projection of the colour slides onto a screen, using the scale as a reference. Usable photographs were as vertical in plane as possible, although some distortion due to the photograph angle was unavoidable. Therefore, density is presented in ranges of 0–20, 21–50, 51–100, and > 100/m^2, to show relative abundance. Carapace length compared with depth was examined for each transect using regression analysis.

All *M. quadrispina* except newly settled juveniles were large enough to identify and measure from the photographs. These measurable animals will be referred to as adults, although they may also represent immature specimens. Depth of occurrence of benthic and pelagic juveniles was recorded during each dive although abundance could not be calculated from phototransects.

LIVE TRAPPING

Adult *M. quadrispina* were obtained by trapping at Stations 1 and 2 between May 1980 and June 1981. Traps made of 15-cm diameter PVC pipe were baited with fresh salmon. Nine traps were attached at 20-m intervals to a 554-m terylene line tied to shore. A pinger was attached to the deep end of the line and then located by sonar from the submersible *Pisces IV*. The line was followed from bottom to top, in order to photograph each trap. Depth, substratum and orientation of traps were recorded. Oxygen samples were taken from *Pisces* at each trap depth (traps set in June 1981 were lowered individually, with depth measured by line length and depth sounding; oxygen concentrations for these trap samples were analysed from bottle casts). The animals collected by trap were sexed, measured for carapace length and preserved in 70% alcohol.

RESULTS

WATER SAMPLES

The oxygen cycle in Saanich Inlet is illustrated in Figs. 3, 4 and 5. Oxygen concentrations at Stations 1, 2 and 3 varied from 0 to 5.5 ml/l from the bottom up to 30 m (the upper limit of benthic *M. quadrispina*). At Stations 1 (Fig. 3) and 2 (Fig. 4) anoxia

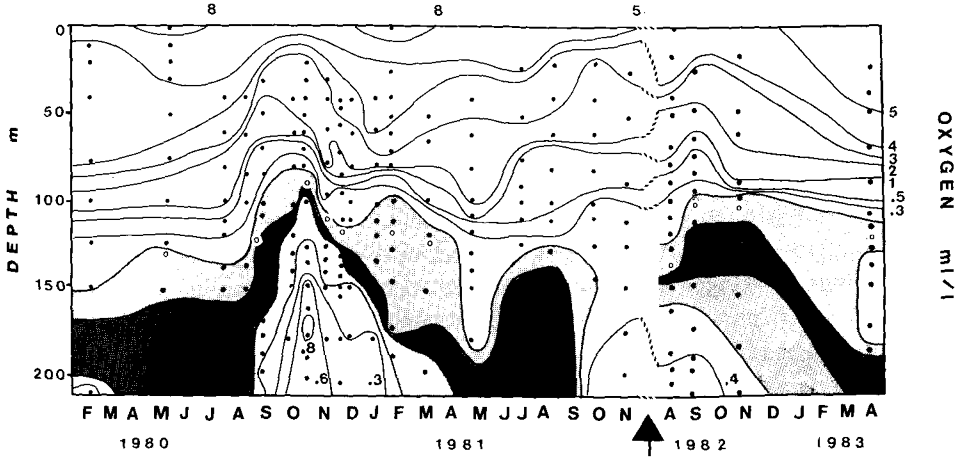

Fig. 3. Oxygen profile with depth from 15 February 1980 to 21 April 1982 for Station 1 (McCurdy Point): dotted profile lines and the arrow indicate a discontinuity in time as shown; light shading represents 0.15 to 0.1 ml/l oxygen, dark shading represents <0.1 ml/l, and black represents 0 ml/l; ○, maximum depth of the *M. quadrispina* population; note that this occurs within the 0.15 to 0.1 ml/l zone.

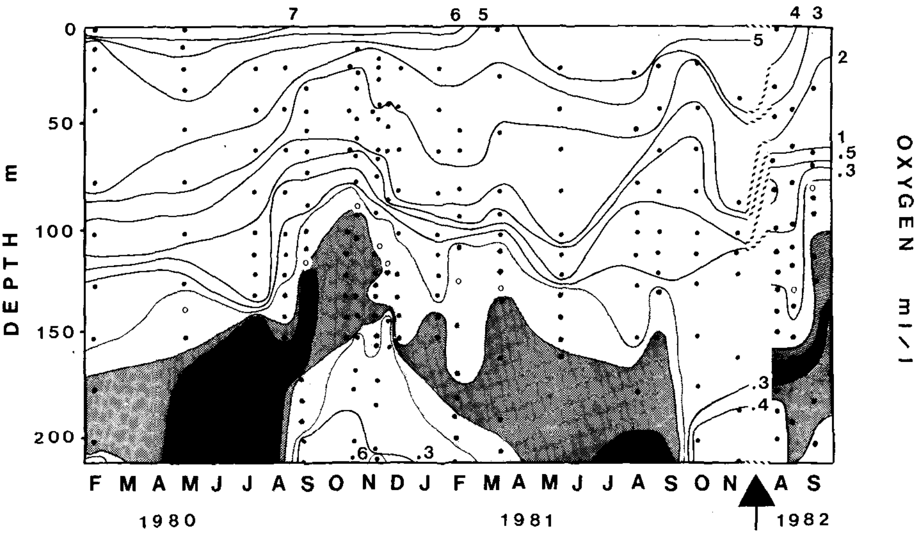

Fig. 4. Oxygen profile with depth from 15 February, 1980 to 10 September, 1982 for Station 2 (Elbow Point): dotted profile lines and arrow indicate a discontinuity in time as shown; light shading represents 0.15 to 0.1 ml/l oxygen, dark shading represents <0.1 ml/l, and black represents 0 ml/l; ○, maximum depth of the *M. quadrispina* population; note that this occurs within the 0.15 to 0.1 ml/l zone, except on 25 August, 1982.

developed in April 1980 and dissipated before 23 October. An influx over the sill of dense oxygenated bottom water began in August 1980, forcing the anoxic layer upwards to a midwater depth and dissipating it in October. Flushing ended in December, and progressive stagnation resulted in anoxia by May 1981. Flushing was again evident in fall 1981 and 1982. At Station 3 an anoxic layer developed in August 1980, and persisted until late November (Fig. 5). A second anoxic layer did not develop that year. At Stations 4 and 5 in Saanich Inlet the oxygen minimum was 0.3 ml/l in September 1980. The extent of flushing appears to decrease from Station 5 (close to the flushing source) to Station 3, the farthest site from flushing. Flushing water may not penetrate the entire inlet each year, depending on the volume of water entering the fjord.

In March 1981, the oxygen minimum was 2.3 ml/l at Station 6 and 0.6 ml/l at Station 7 in Howe Sound (Burd, 1983). Anoxia has been recorded at Station 6 (Levings, 1980). Minimum oxygen was 2.8 ml/l at Station 8, Jervis Inlet in November 1980, February 1981 (Tunnicliffe, unpubl. data), and November 1982 (Burd, 1983).

Salinity values in Saanich Inlet ranged from 29.5 to 31.25‰ over the entire sampling period. Temperatures below 30 m ranged from 8.5 to 11.0 °C in Saanich Inlet. Water chemistry at Stations 1, 2 and 3 was typical of patterns described for Saanich Inlet (Herlinveaux, 1962; Pickard, 1963; Anderson & Devol, 1973). Unlike conditions described in previous years, the main basin of Saanich Inlet (Stations 4 and 5) did not, however, experience deoxygenation during the 1980–1981 sampling period (Burd, unpubl. data).

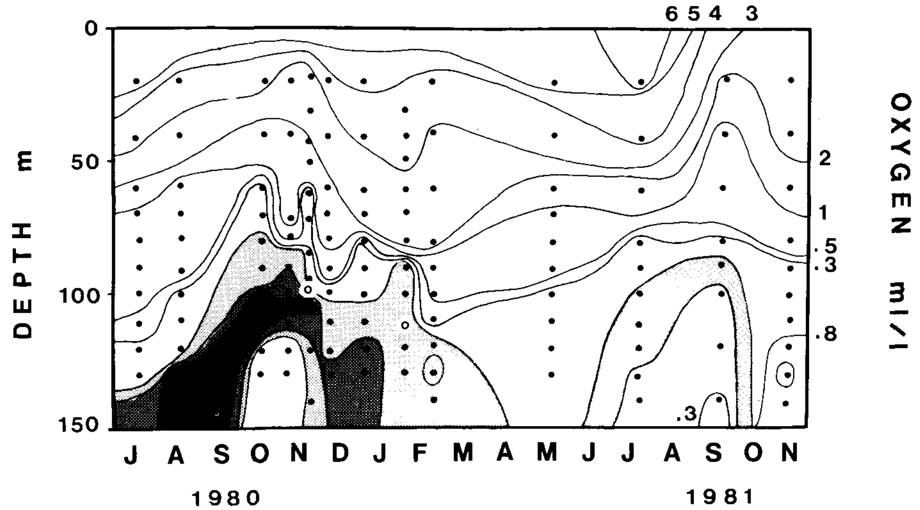

Fig. 5. Oxygen profile with depth from 15 July 1980 to 17 November, 1981 for Station 3 (Finlayson Arm): light shading represents 0.15 to 0.1 ml/l oxygen, dark shading represents <0.1 ml/l, and black represents 0 ml/l; ○, maximum depth of the *M. quadrispina* population; note that this occurs within the 0.15 to 0.1 ml/l zone.

ADULT DEPTH DISTRIBUTION

Adult *M. quadrispina* were limited to depths at which oxygen levels were >0.1 ml/l. Therefore the deepest penetration by *M. quadrispina* at Stations 1, 2, and 3 varied in relation to the oxygen cycle (Figs. 3, 4, and 5), but did not exceed 140 m during the study. At Stations 4 and 5 in Saanich, *M. quadrispina* were found at the bottom of the cliff (190 m) in September 1980. At Stations 6 (230 m), 7 (280 m), and 8 (680 m) outside Saanich Inlet, *M. quadrispina* were always present at the bottom of the cliff.

ADULT POPULATION DENSITY

A density peak of *M. quadrispina* occurred within the 0.1 to 0.15 ml/l oxygen zone at Stations 1, 2, and 3. The population retreated up the cliff ahead of upwelling deoxygenated water (Figs. 6 and 7) in fall 1980 and 1982. The density peak reached a maximum of $>100/m^2$ in October and November 1980 and September 1982 (Figs. 6, 7 and 8), when the limiting oxygen layer was shallowest. Dead crabs were only observed below the limiting oxygen concentration layer in August 1982 at Station 2 (young-of-the-year). This limiting oxygen layer diminished following flushing, and the population spread out again, resulting in reduced density peaks after November. This illustrates a compacting and spreading of the population with the rise and decline of the limiting oxygen layer. In contrast, no densities $>20/m^2$ and no peak densities were ever observed at Stations 4 through 8 (Burd, 1983).

Estimates of total *M. quadrispina* adults in a 1-m wide transect from bottom to top

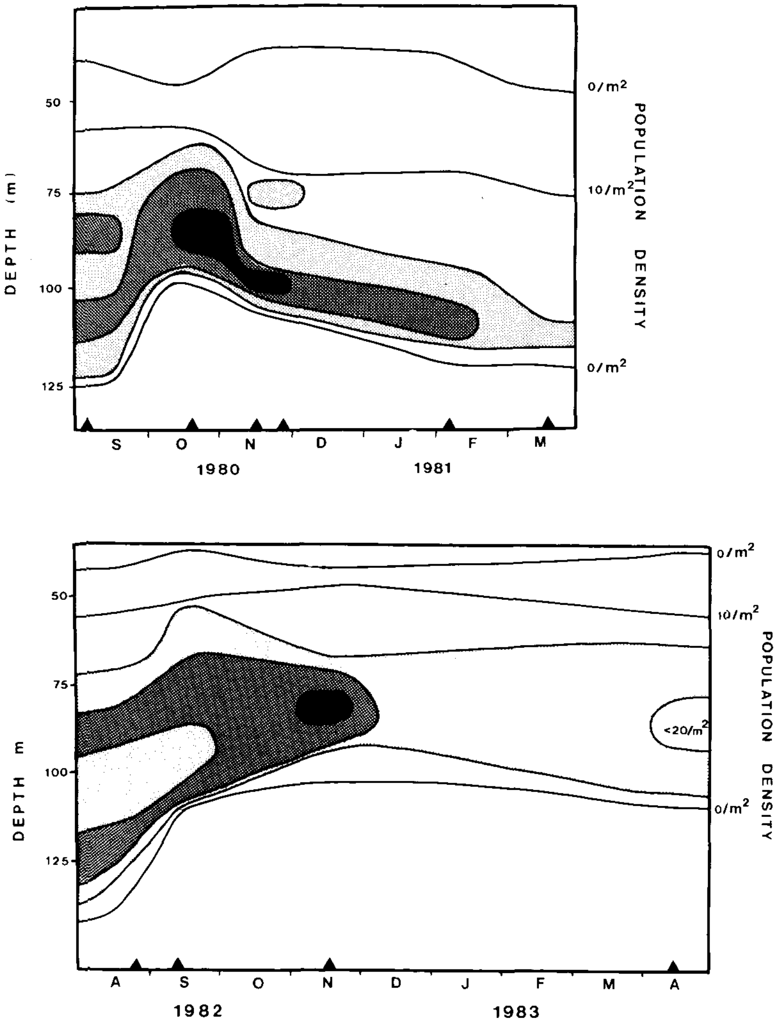

Fig. 6. Population density–depth profile of *M. quadrispina* from Station 1 between September 1980 and March 1981, and August 1982 and April 1983. Light shading represents 20–50; dark shading represents 50–100; black represents > 100 *M. quadrispina* per m^2; sampling dates are marked on the time axis.

of the cliff were calculated for each sampling date and Station (Table II) based on integration of population density–depth curves from phototransects. Total *M. quadrispina* per transect at Stations 1 and 2 remained stable from September 1980 to February 1981, but had declined 50% by March 1981. At this time a large number of dead *M. quadrispina* adults were observed at the depth limit of the population. This occurred again in spring 1983 but was not obviously related to changes in oxygen. The decline in adult numbers occurred mainly in those animals below 100 m (Figs. 6 and 7) and coincided with the major recruitment of juveniles to the benthos.

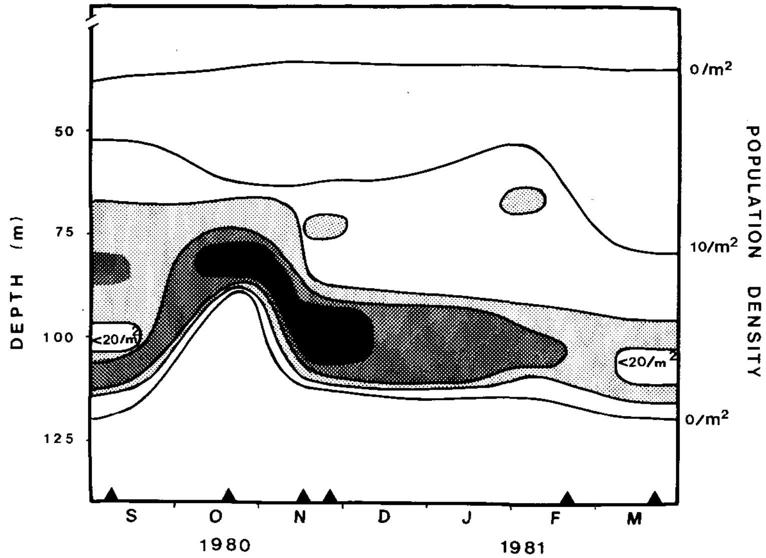

Fig. 7. Population depth–density profiles of *M. quadrispina* for Station 2 between September 1980 and March 1981: light shading represents 20–50; dark shading represents 50–100; black represents >100 *M. quadrispina* per m^2; sampling dates are marked on the time axis.

Fig. 8. Photograph taken from *Pisces IV* in November 1980 at Station 1: this illustrates high densities of *M. quadrispina* during upwelling low oxygen.

TABLE II

Estimated abundance of *Munida quadrispina* from each phototransect using integration of density–depth distribution curves: organic weights for the mean carapace lengths from each transect were estimated from ash-free dry weights of *M. quadrispina* (Burd, 1983); *t* = a 1-m wide phototransect; CL = carapace length; * the high number of *M. quadrispina* at Station 2 in August 1982 was caused by the survival of a narrow band of young-of-the-year below the largest adults.

Station and date	No./*t*	Org. wt. (g/*t*)	Mean CL (mm)
Station 1			
Sept. 1980	2847	367	16.7
Oct. 1980	3029	381	16.5
Nov. 1980	2600	315	15.0
Feb. 1981	2000	257	15.7
Mar. 1981	1188	166	17.8
Aug. 1982	3509	351	14.2
Sept. 1982	3045	461	18.0
Nov. 1982	2720	267	14.1
Apr. 1983	1658	149	14.6
Station 2			
Sept. 1980	2929	288	14.8
Oct. 1980	2800	381	17.0
Nov. 1980	3092	421	17.0
Feb. 1981	1901	201	15.1
Mar. 1981	928	112	16.4
Aug. 1982	4942*	412	13.1
Sept. 1982	3006	273	13.6
Station 3			
Nov. 1980	2600	315	16.4
Apr. 1983	2000	151	11.5
Station 6			
Mar. 1981	730	51	14.2
Station 8			
Sept. 1980	4400	333	12.5
Feb. 1981	2750	166	10.6
Nov. 1983	5800	340	10.4

SIZE DISTRIBUTION WITH DEPTH FROM TRAP DATA

Field observations suggested that the size of *M. quadrispina* increased as depth increased. To examine this possibility, the hypothesis that carapace length of the trapped *M. quadrispina* was not related to depth was tested by regression analysis and rejected at the 1% level for Stations 1 (Fig. 9) and 2 (Fig. 10). Carapace length increased significantly as depth increased.

SIZE DISTRIBUTION COMPARED WITH OXYGEN FROM TRAP DATA

Since the depth distribution of *M. quadrispina* from Saanich Inlet varies seasonally in relation to oxygen, it was expected that the correlation between carapace length and

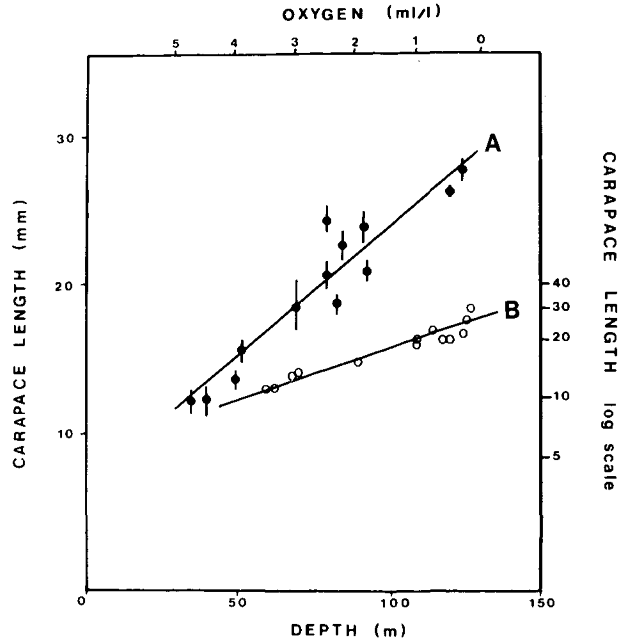

Fig. 9. A, regression of carapace length (mean for each trap sample ± SE) with depth for *M. quadrispina* from Station 1: total $n = 272$, $r = 0.85$, slope = 0.15, y intercept = 8.1. B, regression of log carapace length with habitat oxygen concentrations for *M. quadrispina* from Station 1. Carapace length data is identical for A and B; total $n = 272$, $r = 0.93$, slope = −0.10, y intercept = 1.4.

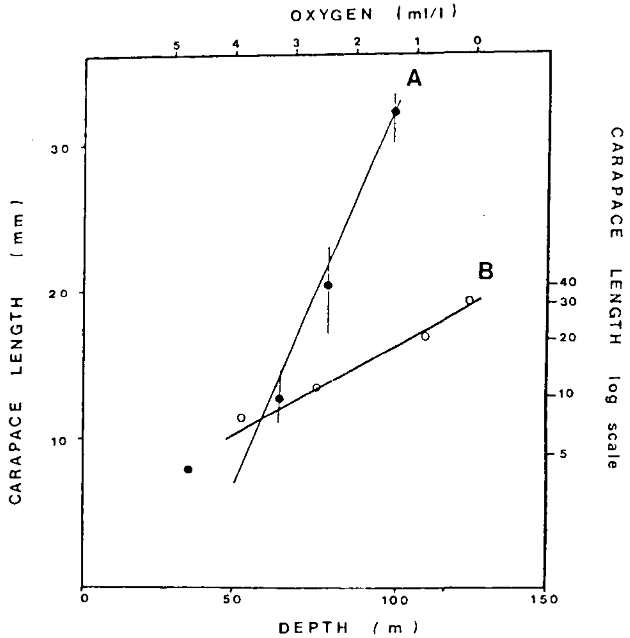

Fig. 10. A, regression of carapace length (mean for each trap sample ± SE) with depth for *M. quadrispina* from Station 2: total $n = 64$, $r = 0.83$, slope = 0.50, y intercept = −21. B, regression of log carapace length with habitat oxygen concentrations for *M. quadrispina* from Station 2. Carapace length data is identical for A and B; total $n = 64$, $r = 0.89$, slope = −0.20, y intercept = 1.5.

oxygen would be higher than the correlation between carapace length and depth. Therefore, the hypothesis that carapace length was not related to oxygen concentration was 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 Stations 1 and 2 (Figs. 9 and 10). The hypothesis that the slope was zero was examined by t-test and rejected at the 1% level.

The correlation coefficients of the inverse regressions of carapace length to oxygen concentration were greater than for the regressions of carapace length to depth ($r = 0.92$ compared with $r = 0.85$, Fig. 9 for Station 1, and $r = 0.89$ compared with $r = 0.83$, Fig. 10 for Station 2). Carapace length (CL) was, therefore, more closely correlated with oxygen concentration than with depth. Data from both sites were pooled to calculate the regression of oxygen concentration to carapace length ($P = 0.01$) for all trap animals:

$$\log \mathrm{CL} = -0.15\,(\text{oxygen}) + 1.46 \qquad (n = 336,\ r = 0.84)$$

SIZE DISTRIBUTION COMPARED WITH DEPTH FROM PHOTOTRANSECTS

To examine the stability of the size gradient over time, the hypothesis that carapace length of *M. quadrispina* from phototransects was not related to depth was tested by regression analysis and rejected at the 1% level for all Stations and sampling dates (Table III) in Saanich Inlet, Jervis Inlet and Howe Sound. The carapace length of *M. quadrispina* at Stations 1, 2, and 3 increased significantly as depth increased on all dates. In August 1982 some young-of-the-year were, however, present below the depth of the large adults at Station 2, considerably reducing the slope of the regression (Table III). These juveniles disappeared by 10 September, returning the size gradient to expected proportions. The slopes of regression for Stations 5 and 6 and for Station 8 (February 1981 and November 1982) were not significantly different from zero ($P = 0.05$). The slope of regression for Station 8 in September 1981 was significantly different from zero, but was very small (slope = -0.003) and probably meaningless.

The relationship between carapace length and oxygen concentration was not tested from phototransects since oxygen samples were not taken at each "photo" depth. This was considered to introduce too great a source of error for regression analysis.

DEPTH DISTRIBUTION OF JUVENILES

Pelagic juvenile *M. quadrispina* were observed at Stations 1, 2, and 3 on all sampling dates. Since juveniles were found in plankton hauls through the summer of 1981 (R. Larson, pers. comm.) pelagic juveniles seem to be present for most of the year.

Two distinct populations of pelagic juveniles were present at Stations 1 and 2 in fall 1980 and 1982, separated by a wedge of low oxygen water. The smaller group below the low oxygen layer first appeared during flushing (possibly carried into the area by flushing water). Many of these juveniles settled on the bottom below 140 m in fall 1980 and 1982 (and presumably in fall 1981). By 5 February, 1981 and 19 April, 1982 only

TABLE III

Regression equations for carapace length (CL) against depth (D) in *Munida quadrispina*, measured from phototransects (b = slope of regression): Ho : $b = 0$ was tested by F test; * data contributed by K. Bruce; ** reduced slope of size distribution due to surviving juveniles below deepest adults.

Station and date	N	Equation	P (reg)	Ho : b = 0 (P = 5%)
Station 1				
Sept. 1980	505	CL = 0.25D − 7.4	0.1%	reject
Oct. 1980	284	CL = 0.48D − 25	0.1%	reject
Nov. 1980	270	CL = 0.28D − 11.2	0.1%	reject
Feb. 1981	155	CL = 0.24D − 7.2	0.1%	reject
Mar. 1981	43	CL = 0.28D − 12.6	0.1%	reject
Aug. 1982	157	CL = 0.34D − 12.7	0.1%	reject
Sept. 1982	140	CL = 0.35D − 3.7	0.1%	reject
Nov. 1982	311	CL = 0.34D − 13.2	0.1%	reject
Apr. 1983*	162	CL = 0.29D − 6.5	0.1%	reject
Station 2				
Sept. 1980	167	CL = 0.27D − 10.5	0.1%	reject
Oct. 1980	114	CL = 0.52D − 25	0.1%	reject
Nov. 1980	648	CL = 0.31D − 12.1	0.1%	reject
Feb. 1981	170	CL = 0.21D − 4.6	0.1%	reject
Mar. 1981	157	CL = 0.26D − 9.5	0.1%	reject
Aug. 1982	738	CL = 0.10D + 7.9**	0.1%	reject
Sept. 1982	192	CL = 0.52D−17.3	0.1%	reject
Station 3				
Nov. 1980	254	CL = 0.24D − 7.7	0.1%	reject
Apr. 1983	76	CL = 0.20D − 2.0	0.1%	reject
Station 6				
Mar. 1981	25	CL = 0.009D + 13	5%	accept
Station 8				
Feb. 1981	233	CL = 0.004D + 11	5%	accept
Sept. 1981	70	CL = 0.003D + 12	5%	accept
Nov. 1982	153	CL = 0.003D + 11	5%	reject

carcasses remained where these juveniles had settled. Concurrent with this disappearance, oxygen levels decreased to < 0.2 ml/l at both stations. It appears that some juveniles settling in fall 1981 survived at Station 2 until August, only to be killed by upwelling low oxygen water in September.

The larger group of juveniles above the low oxygen layer settled from 100–30 m in spring 1981 and 1983 in oxygen levels > 0.2 ml/l. Since major benthic recruitment and reproduction both occur in spring (Burd, 1983) most juveniles are ≈ 1 yr of age at settlement.

BEHAVIOURAL OBSERVATIONS

Some important aspects of field and laboratory behaviour of *M. quadrispina* were observed but not quantified during this study. One hour spent in *Pisces IV* observing

M. quadrispina at 85 m 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. *M. quadrispina* in laboratory tanks have, however, been kept alive for 6 months or more with only sediment from a closed running sea-water system for food.

Observations made over the entire sampling period indicate that *M. quadrispina* living in low oxygen conditions (0.1–0.15 ml/l) were sedentary, even when so crowded that they overlapped (Fig. 8). These *M. quadrispina* did not display any observable territoriality or aggression such as defending a space or crevice. In sharp contrast, *M. quadrispina* living at higher oxygen concentrations (i.e. 85 m) 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. This suggests that *M. quadrispina* are normally aggressive, except in low oxygen areas. On the four occasions that a large number of trapped *M. quadrispina* were put 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 was observed as seen in the field at 85 m. Once the spacing pattern was established, individual *M. quadrispina* remained stationary for long periods.

DISCUSSION

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

The change in population density–depth distribution of *M. quadrispina* in response to oxygen concentration, without any concurrent change in overall population size, indicates that most adults of this species will migrate vertically to avoid suffocation during upwelling deoxygenation. Observations of dead young-of-the-year during upwelling in August 1982 show that not all animals escape the rapidly changing oxygen conditions. Such changes in oxygen are probably more of a problem for young crabs than for the large adults usually observed in these areas. This is especially true since respiration demands increase substantially during moulting in crustaceans (Thompson & Pritchard, 1969; Laird & Haefner, 1976) due to a burst of activity and increase of permeability of the exoskeleton which necessitates metabolic input into internal regulation. A 2.5-fold increase in respiration has been recorded during ecdysis in *Crangon vulgaris* (Hagerman, 1976). This makes frequently moulting animals such as newly settled juveniles more sensitive to changes in environmental oxygen conditions than adults (Hagerman, 1976).

The high density of adult *Munida quadrispina* in low oxygen areas of Saanich Inlet suggests that this is an optimum habitat. Adults probably migrate downward after the low oxygen layer moves deeper, in order to follow the large food source from planktonic and detrital material in the scattering layer. This layer was always at about the same depth as the depth limit of the adult population.

The decline in total *M. quadrispina* adults in Saanich Inlet in spring 1981 and 1983 occurred in the deepest and, therefore, largest animals. Since juvenile recruitment coincided with this event, it may be that the total population size remains stable, and that the decline in large adults is due to a natural mortality of older animals. Those animals lost in spring may have reached the limit of their life span, since two related species of galatheids, *M. gregaria* (Williams, 1971) and *Pleuroncodes planipes* (Boyd, 1967) reach about the same maximum size (70 mm total length) as *Munida quadrispina*. Further studies, however, would be necessary to prove this hypothesis.

The uncharacteristic lack of aggression or territorial behaviour of *M. quadrispina* in low oxygen areas could be related to a lack of stimulus to hide from predators. Another possibility is that suppressed aggression in high density areas is a result of accumulated catabolites from excretion. This was suggested by Vannini (1981) who found that water from large concentrations of *Carcinus mediterraneus* decreased intraspecific aggressive encounters. A general decrease in aggressive interactions upon crowding has also been noted in pagurid crabs by Hazlett (1968) and Courchesne & Barlow (1971), and in lobsters by Dunham (1972). These studies suggest that high density alone could reduce intraspecific aggression in *Munida quadrispina* living in low oxygen areas of Saanich Inlet.

Low aggression of *M. quadrispina* in these areas might also be a result of lower metabolic and consequently activity levels, to conserve oxygen during long term deoxygenation. A related species, *M. bamffica* has been shown to have high blood magnesium levels (R. Uglow, pers. comm.) indicative of low activity in crustaceans (Wolvekamp & Waterman, 1960). This suggests that *Munida* may be a sedentary genus, a useful characteristic for survival in low oxygen conditions. When oxygen levels, however, get too low in Saanich Inlet, inactivity is probably not sufficient to conserve oxygen. The crabs may then be stimulated to emigrate away from the area, producing the population shift in density–depth distribution observed during upwelling anoxia.

Settlement of some juvenile *M. quadrispina* below the low oxygen layer during flushing provides an effective mechanism for recolonization of previously anoxic cliff areas. This was noted in Howe Sound after anoxic recovery in 1977 (Levings, 1980). In years that anoxia does not re-develop after flushing, juvenile *M. quadrispina* would remain as the primary colonizers in the dead areas. The long pelagic juvenile phase increases the opportunity for such recolonization.

Recruitment temporarily upsets the size distribution of *M. quadrispina* in Saanich Inlet. This is not evident in size gradient results since these juveniles are too small to be measured in photographs. The oxygen conditions at the time of settlement dictate where these juveniles will settle, whereas later oxygen conditions determine their survival. In spring 1980 and 1981 it was observed that juveniles did not settle as deep as the largest adults, probably because the low oxygen layer was shallow and extensive. Favourable oxygen conditions throughout 1982 (following flushing in fall 1981) could, however, explain the continued presence of young-of-the-year below the adults until 25 August, 1982, and the consequent reduction in the size gradient normally observed at Station 2. At Station 1, previous dives indicate that small *M. quadrispina* were still present deeper than large adults until mid-August (Tunnicliffe, pers. comm.), although they were not present by 25 August. By 10 September upwelling of low oxygen water had killed most of these juveniles, re-establishing a steep size gradient.

Size gradients with depth have also been observed in other deep sea crabs. The galatheid *Pleuroncodes planipes* has been found in the benthos on the continental shelf-slope off Baja California from 75 to 300 m in depth (Boyd, 1967). Boyd noted that the deepest crabs had a significantly greater carapace length than shallower ones. Only the largest crabs were observed in oxygen concentrations <0.5 ml/l. Somerton (1981) observed similar size gradients in some deep sea king crabs but did not determine a reason. Depth–size gradients in intertidal invertebrates can be caused by food availability, competition, and predation (Bertness, 1977; McQuaid, 1981), all of which could affect the distribution of *Munida quadrispina* in Saanich Inlet. As noted, large *M. quadrispina* probably migrate to areas of high food concentration, where survival is enhanced by low competition and predation, but are limited in further migration by low oxygen levels. It is, therefore, not surprising that large numbers of *M. quadrispina* collect in these areas. It is also important to note that high densities and size gradients did not occur in the other sampling areas tested, where oxygen was not limiting.

Smaller *M. quadrispina* in shallow areas are exposed to potential predators and competing species, but do not move into the low oxygen areas where food is more abundant. It is, therefore, likely that smaller *M. quadrispina* cannot tolerate conditions in low oxygen areas. A physiological explanation for this size gradient is that metabolism increases as animals decrease in size (Zeuthen, 1953; Bayne, 1971; Leffler, 1973; Taylor & Brand, 1975), which means that large animals consume less oxygen per unit weight than small animals. It follows that large animals can tolerate lower oxygen levels over time than small animals. This possibility will be tested in a later study.

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