

## Comparative gill characteristics of *Munida quadrispina* (Decapoda, Galatheidae) from different habitat oxygen conditions

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The allometric (bilogarithmic) relationship between dry gill weight and organic body weight was compared for benthic galatheid crabs (*Munida quadrispina* Benedict, 1902) from a low-oxygen fjord and from a normal oxygen population. In the *M. quadrispina* from the low-oxygen fjord, the slope ( $b$ ) of the allometric function of gill weight versus body weight was 1.00. This  $b$  value was significantly higher (ANCOVA,  $p < 0.01$ ) than the corresponding slope for the same function in *M. quadrispina* from normoxic areas ( $b = 0.63$ ). However, only the largest crabs from the low-oxygen fjord were living consistently in low-oxygen ( $< 0.15$  mL/L) conditions; they also had significantly greater (twice as much) relative gill weight than their normoxic counterparts. This observation agrees with findings from previous studies that only the largest *M. quadrispina* are able to tolerate severe oxygen depletion. Small *M. quadrispina* from both the low-oxygen fjord and the normoxic area were always found in oxygen concentrations  $> 2.0$  mL/L. There were no significant differences between the relative gill sizes of the small crabs from different areas. It was concluded that gill development in *M. quadrispina* is affected by long-term habitat oxygen conditions. This factor could be important in comparisons of inter- and intra-specific allometric gill functions and in the study of weight-specific oxygen consumption rates of decapod crustaceans.

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La relation allométrique (bilogarithmique) entre la masse sèche des branchies et la masse organique du corps a été comparée chez des crabes benthiques *Munida quadrispina* Benedict, 1902 (Galatheidae) provenant d'un fjord peu oxygéné et des crabes d'une population en milieu normalement oxygéné. Chez les crabes du fjord peu oxygéné, la pente ( $b$ ) de la fonction allométrique branchies : corps est le 1,00. Cette valeur de  $b$  est significativement plus élevée (ANCOVA,  $p < 0,01$ ) que celle de la même fonction calculée chez les crabes du milieu normoxique ( $b = 0,63$ ). Cependant, dans le fjord hypoxique, seuls les crabes les plus gros vivent continuellement en milieu désoxygéné ( $< 0,15$  mL/L) et la masse relative de leurs branchies est significativement plus élevée (deux fois plus) que la masse des branchies des crabes du milieu normoxique. Ces résultats corroborent les conclusions d'études antérieures selon lesquelles seuls les *M. quadrispina* les plus gros peuvent tolérer des conditions anoxiques rigoureuses. Les petits crabes des deux milieux fréquentent toujours les régions où la concentration d'oxygène est supérieure à 2,0 mL/L. Il n'y a pas de variation significative de la taille relative des branchies chez les petits crabes des différents milieux. Le développement des branchies de *M. quadrispina* est tributaire des conditions à long terme d'oxygénation du milieu. Il s'agit là d'un phénomène important dont il faut tenir compte dans les comparaisons interspécifiques et intraspécifiques des courbes allométriques des branchies et dans l'étude des taux de consommation d'oxygène spécifiques à la masse chez les crustacés décapodes.

[Traduit par la revue]

### Introduction

Saanich Inlet is an intermittently anoxic, 236 m deep fjord located on the southeast side of Vancouver Island, British Columbia. Its water characteristics have been studied by a number of researchers (e.g., Herlinveaux 1962; Anderson and Devol 1973; Emerson *et al.* 1979). A shallow sill (70 m) at the mouth of the inlet prevents bottom water renewal for most of the year. Consequently, the deep water stagnates through winter, spring, and summer, resulting in deoxygenation and a buildup of metabolic by-products of anaerobic bacterial respiration (Emerson *et al.* 1979). In late summer, deep water with density greater than the bottom water of the inlet upwells off the coast of British Columbia, flows over the sill, and sinks to the bottom, forcing the deoxygenated water layer upwards to a midwater depth and, in some years, dispersing it completely. There is a low-oxygen layer (less than 0.5 mL/L) in Saanich Inlet throughout the year.

From 1980 to 1984, the Canadian research submersible *Pisces IV* was used to examine the effects of dissolved oxygen on the ecology of the epibenthic galatheid crab *Munida quadrispina* Benedict, 1902 (methods in Burd and Brinkhurst 1984). Most of the adult population of *M. quadrispina* lived on substrates just above the anoxic or low-oxygen layer all year round (at levels from 0.1 to 0.2 mL/L). Only the largest crabs were

present in the lowest oxygen conditions and progressively smaller crabs were found at progressively higher oxygen levels. This relationship was found to be statistically significant at all locations and dates (Burd and Brinkhurst 1984). The size–depth distribution was not sex-related and was not evident in two other nonhypoxic fjords studied.

The crabs migrated vertically on the cliff in response to intolerably low oxygen conditions. Extensive field sampling and in situ observations suggested that the large crabs found at unusually high concentrations (compared with other fjords) in the low-oxygen areas of Saanich Inlet preferred this habitat because predation and competition from other species was nonexistent, and food availability was high (Burd 1983).

Burd (1985) showed that the relationship of  $P_c$  (critical oxygen concentration below which the rate of oxygen consumption declines) to crab size was not significantly different ( $p < 0.01$ ) from the relationship of habitat oxygen concentration to crab size (from Burd and Brinkhurst 1984). The large crabs were therefore able to survive low-oxygen conditions because of respiratory tolerance, whereas smaller crabs had to live in areas with progressively higher oxygen concentrations. No crabs were stressed at oxygen levels  $> 2$  mL/L. Die-offs of recently settled juveniles were noticed several times in areas that had recently been swept by upwelling low oxygen during

flushing (Burd 1983). Such die-offs served to reestablish the predominant size distribution each year.

*Munida quadrispina* living in low-oxygen areas of Saanich Inlet appeared to possess expanded gill chambers. The swelling was not due to parasitism and was not found in *M. quadrispina* from other fjords (Burd 1983). The swollen gills suggested that living in the low-oxygen habitat might cause the development of excessively large gills in these crabs.

In crustaceans and fish, gill surface area usually decreases relative to increasing body weight (Bergmiller and Bielawski 1970; Bock 1925; Gray 1957; Hughes 1966, 1983). The relationship can be represented by an allometric growth curve of the form:

$$\text{Gill surface area} = a(\text{body weight})^b$$

where  $a$  has traditionally been depicted by researchers as species specific and  $b$  is the slope of the function. Hughes (1983) indicated that  $b$  is usually about 0.8 for North American decapod crustaceans, although more active species and some British branchyuran crabs measured by Scammel (1971) are characterized by  $b$  values of about 1.0. Different authors have used different methods to measure gill surface area, thereby producing conflicting results for a given species (Hughes 1983).

In the few instances in which gill weight has been compared with body weight in decapods and other crustaceans, the allometric growth relationship is characterized by a slope,  $b$ , comparable to or less than that for gill surface area versus body weight (Hughes 1982, 1983). Assuming that gill shape is consistent within a species, gill weights could be used with greater accuracy and simplicity than gill surface area for comparing the relative gill sizes of different populations of the same species.

The present study tested the null hypothesis that the allometric relationship of gill weight versus organic body weight (metabolizing weight) in *M. quadrispina* of different sizes from Saanich Inlet was not significantly different from the relationship for *M. quadrispina* from an area outside Saanich Inlet where oxygen is consistently greater than 2.0 mL/L.

### Methods and materials

Fifty *Munida quadrispina* were obtained by trapping between 40 and 125 m depth from McCurdy and Elbow points in Saanich Inlet in 1980–1981 (48°33.6'N, 123°31.5'W) (for methods, see Burd and Brinkhurst 1984). Oxygen in the areas where the crabs were taken ranged between 0.1 and 2 mL/L. Water samples for Winkler titration analysis were taken within 2 ft. (1 ft. = 0.3048 m) of each trap through an external port in the submersible (oxygen results are presented in Burd and Brinkhurst 1984). Thirty-three of the crabs were preserved in 70% alcohol (group A) and 17 were kept alive for several months before the study in the University of Victoria aquarium at oxygen levels greater than 2 mL/L (group B).

Twenty-one crabs of all sizes were obtained from traps set outside the sill (at the mouth) of Saanich Inlet (48°34.0'N, 123°49.0'W), where oxygen levels are consistently greater than 2.0 mL/L (University of Victoria and Department of Fisheries and Oceans, unpublished oceanographic data). The 21 crabs were all preserved in 70% alcohol (group C).

All crabs analysed (total of groups A–C = 71) in the study were in intermolt condition (i.e., hard-bodied). The crabs were processed in the following manner. Gills were analysed by counting the total number of gill filaments with a dissecting microscope, and then obtaining dry weights. The bodies (without gills) and half of the gills of the specimens were freeze-dried separately for 24 h, ground with pestle and mortar, and freeze-dried for another 24 h to ensure that no mois-

TABLE 1. Data for preserved *Munida quadrispina* from Saanich Inlet (group A)

Carapace length	Sex	Organic wt. (g)	Half of gill wt. (g)
	F	0.0350	0.0003
	M	0.0360	0.0005
	F	0.0460	0.0006
14 mm	M	0.0420	0.0007
	M	0.0570	0.0005
	F	0.0610	0.0006
15 mm	F	0.0460	0.0006
	M	0.0790	0.0008
16 mm	M	0.1170	0.0007
	F	0.0780	0.0008
	M	0.0900	0.0016
17 mm	M	0.1440	0.0011
19 mm	M	0.1540	0.0006
	M	0.1570	0.0014
22 mm	F	0.3390	0.0041
	F	0.4110	0.0051
	M	0.3350	0.0017
23 mm	M	0.4170	0.0043
	M	0.3010	0.0031
24 mm	F	0.2470	0.0024
26 mm	F	0.3670	0.0036
27 mm	F	0.6820	0.0083
	M	0.6720	0.0068
28 mm	F	0.5400	0.0071
30 mm	M	1.0350	0.0186
	M	1.2100	0.0131
31 mm	F	0.6560	0.0062
32 mm	F	0.7840	0.0077
	F	0.4770	0.0096
33 mm	F	0.7020	0.0106
	M	0.9590	0.0110
37 mm	M	0.9690	0.0147

ture remained. The freeze-dried gills and bodies of each animal were weighed separately with a Sartorius analytical balance to the nearest 0.0001 g. Bodies were then ashed at 450° for 8 h and reweighed. Ash-free dry weight was considered to represent the weight of metabolizing tissue (organic fraction). The use of organic instead of dry weight eliminated the potentially complicating factor of variable calcification in animals of different sizes. The additional organic fraction of the gills was not added to the organic weight of the body since it was negligible in comparison. Ash fraction of the gills was not measured because of problems in handling and in accuracy of measurement associated with such small tissue quantities, but was considered to be the same proportion of the total dry gill weight as was found in the body (e.g., Belman and Childress 1976). The use of dry gill weight was considered adequate to compare relative differences in gill sizes between animals. The hypothesis that gill weight was not related to body weight was tested by correlation for the three groups (A–C) of crabs.

### Results

*Munida quadrispina* have phyllobranch gills consistent in structure with those of other galatheids (Gurney 1960). Tables 1–3 contain analysis data for all of the crabs studied. Only the largest crabs from the inlet were found at oxygen levels as low as 0.1 mL/L and could be expected to be adapted to low oxygen. The smallest crabs examined were living in oxygen conditions comparable to those of the crabs from outside the inlet (Group C).

la superficie de las branquias se comparó entre poblaciones

TABLE 2. Data for live *Munida quadrispina* from Saanich Inlet (group B)

Carapace length	Sex	Organic wt. (g)	Half of gill wt. (g)
	F	0.0100	0.0003
	M	0.0160	0.0003
	F	0.0840	0.0007
	M	0.1750	0.0011
	M	0.2790	0.0019
	M	0.2000	0.0018
	F	0.3320	0.0032
	M	0.3520	0.0023
23 mm	F	0.1390	0.0010
24 mm	F	0.4760	0.0054
	M	0.5140	0.0062
25 mm	M	0.6080	0.0080
26 mm	F	0.8200	0.0153
27 mm	M	0.8540	0.0153
30 mm	F	0.8225	0.0180
	M	1.1780	0.0154
32 mm	M	0.9800	0.0090

*Gills of M. quadrispina from Saanich Inlet (groups A and B)*

Saanich Inlet *M. quadrispina* (see Table 1) ranged in size from 0.015 to 1.16 g organic weight and had a mean ash content of  $47.9 \pm 0.2\%$  (SE) of dry weight. The correlations and best-fit allometric growth equations were initially calculated separately for preserved ( $n = 33$ , group A) and fresh ( $n = 17$ , group B) *M. quadrispina*. The results were as follows:

- [1] Group A:  
(preserved) gill wt. =  $0.023$  (organic body wt.)<sup>1.04</sup>  
( $r = 0.96$ )
- [2] Group B: (fresh) gill wt. =  $0.021$  (organic body wt.)<sup>0.94</sup>  
( $r = 0.94$ )

The hypothesis that total gill weight was not related to organic body weight was rejected ( $p < 0.01$ ) in both cases. The slopes and elevations of the two functions were not significantly different (ANCOVA,  $p < 0.01$ ). Therefore it was concluded that no significant shrinkage occurred as a result of preservation, and that 6 months in higher oxygen conditions did not affect the gill size of the 17 crabs in group B. The data were combined to produce the following best-fit equation for the relationship of gill weight to organic body weight in Saanich Inlet *M. quadrispina* ( $n = 72$ , Fig. 1, curve A):

- [3] Group A + B: gill wt. =  $0.022$  (organic body wt.)<sup>1.00</sup>  
( $r = 0.94$ ;  $p < 0.01$ )

*Gills of M. quadrispina from outside Saanich Inlet sill*

*Munida quadrispina* from outside the sill of Saanich Inlet were all from areas with oxygen concentrations greater than 2.0 mL/L. The 21 crabs ranged in size from 0.02 to 1.03 g organic body weight, with a mean ash content of  $50.4 \pm 0.1\%$  (SE) of dry weight. The best-fit line of the correlation of gill weight with organic body weight (Fig. 1, curve B) was as follows:

- [4] Group C: gill wt. =  $0.010$  (organic body wt.)<sup>0.68</sup>  
( $r = 0.94$ ;  $p < 0.01$ )

The slope and elevation of eq. 4 were significantly different

TABLE 3. Data for preserved *Munida quadrispina* from outside Saanich Inlet (group C)

Carapace length	Sex	Organic wt. (g)	Half of gill wt. (g)
	F	0.0230	0.0004
	F	0.0340	0.0004
12 mm	F	0.0680	0.0007
14 mm	F	0.0870	0.0009
16 mm	M	0.0430	0.0011
	M	0.0370	0.0013
	M	0.0560	0.0012
	M	0.0470	0.0015
	M	0.0900	0.0011
17 mm	M	0.1020	0.0016
18 mm	M	0.0530	0.0008
	F	0.1300	0.0008
	M	0.1370	0.0016
20 mm	F	0.1830	0.0020
21 mm	F	0.1820	0.0012
22 mm	M	0.1490	0.0017
23 mm	M	0.3550	0.0033
25 mm	M	0.4620	0.0033
	M	0.3910	0.0030
	M	0.5330	0.0028
30 mm	F	0.5240	0.0044
31 mm	M	0.7730	0.0056
32 mm	F	0.7190	0.0065
	M	1.0200	0.0049

(ANCOVA) from those of eq. 3 ( $p < 0.01$ ). The greatest difference in relative gill size between Saanich Inlet crabs and those from outside the sill occurred in the largest specimens. For example, the gill weight of a hypothetical 1-g Saanich Inlet crab (0.022 g) would be more than twice that of a 1-g group C crab (0.01 g) (Fig. 1, no overlap in 95% confidence intervals). However, a small Saanich Inlet crab of 0.015 g organic weight would have slightly smaller gills (0.0004 g vs. 0.0005 g) than a crab of similar size from outside the sill, although the overlap in 95% confidence intervals indicates that the difference would not be significant.

### Discussion

Lamellar counts in crabs of different sizes indicated that increasing gill weight was related to an increase in the number of lamellae on the filaments (Burd 1983).

The results of this study suggest that some functional relationship exists between gill development and long-term habitat oxygen levels in *M. quadrispina*. Small specimens from Saanich Inlet live at oxygen levels of about 2 mL/L or more, and have gills similar in size to those of small crabs from areas with similar oxygen conditions outside Saanich Inlet. Large Saanich Inlet specimens that live in low-oxygen conditions have significantly larger gills than do crabs of similar size from areas with oxygen levels greater than 2 mL/L. A similar example of gill development was recorded for *Gnathophausia ingens* (Dohrn, 1870), a hypoxia-tolerant mysid which had proportionately more gill surface area in large animals than in small ones (Belman and Childress 1976).

The allometric growth curve for gills of *M. quadrispina* is dependent on habitat oxygen conditions. Therefore there is no species-specific function for gills in this decapod. Other deca-

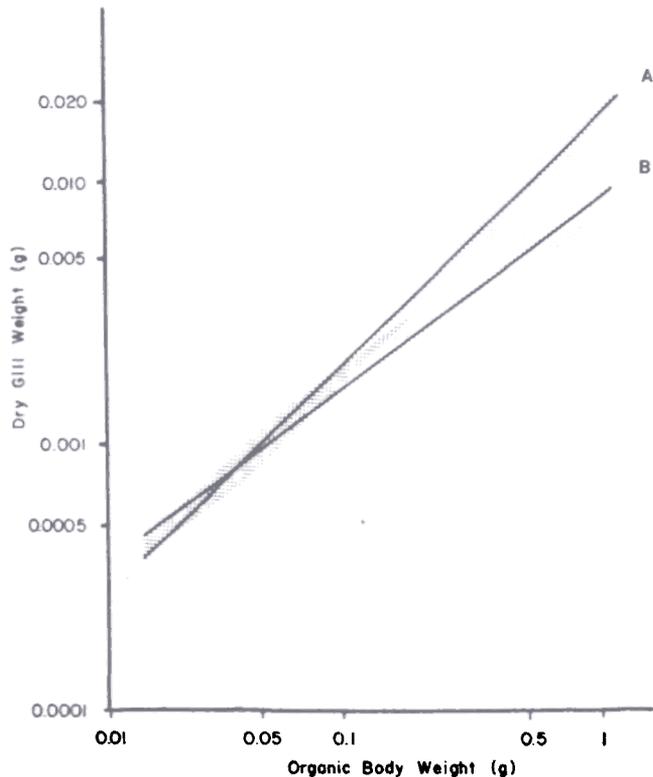


FIG. 1. Allometric relationship of total dry gill weight (g) to organic body weight (g), shown on log/log scale for (A) *M. quadrispina* from low-oxygen areas and (B) *M. quadrispina* from normoxic areas. The 95% confidence intervals for the regression lines are illustrated by the shaded areas.

pod crustaceans that are tolerant of low oxygen or change their habitat and activity levels during their life cycle might exhibit similar gill development. For example, in the galatheid crab, *Pleuroncodes planipes* Stimpson, 1860, the largest benthic individuals have been found at oxygen levels of less than 0.5 mL/L (Boyd 1967), whereas in the pelagic stage specimens have been found at oxygen levels as low as 0.1 mL/L (Childress 1975). This species, and *Pleuroncodes monodon* Milne Edwards, 1837, which is found at oxygen levels as low as 0.5 mL/L off the coast of Chile (Bahamonde *et al.* 1985), may have more than one allometric function describing gill development. Therefore some caution should be exercised in comparing allometric gill functions of different species. Habitat differences may also partly account for some of the conflicting results presented by different authors (Hughes 1983) for gill surface areas of decapod crustacean species.

If relative gill size varies within a species, functions describing weight-specific respiration rates may also vary depending on the habitat oxygen conditions. Therefore, the functions describing oxygen consumption rates and (or)  $P_c$  versus body weight measured for *M. quadrispina* from Saanich Inlet (Burd 1985) or for *Pleuroncodes planipes* from the oxygen minimum layer off California (Childress 1975) could be considerably different in individuals from normal oxygen habitats.

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