

OXYGEN CONSUMPTION IN BRACHIOPODS AND THE POSSIBLE ROLE OF PUNCTAE

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Abstract: Oxygen consumption was monitored in four species of New Zealand brachiopods (*Terebratella* (*Waltonia*) *inconspicua* (Sowerby), *Neothyris lenticularis* (Deshayes), *Terebratella* (*Magasella*) *sanguinea* (Leach), and *Lingula bancrofti* (Johnston and Hirschfield)) under various experimental conditions. No significant differences were found between the three articulate species at 10°C and 33.5‰ salinity; however, *L. bancrofti* exhibits a much lower rate than the other three species. When exposed to declining oxygen tensions the species showed various degrees of oxygen independence (in order of increasing independence): *Neothyris lenticularis*, *Terebratella sanguinea*, *T. inconspicua*, *Lingula bancrofti*. *Terebratella inconspicua* continued to extract oxygen from the external medium during periods of shell valve closure at a rate equal to 22% of the rate in normal pumping animals. Evidence is presented to suggest that oxygen is entering the shell via punctae in the shell.

INTRODUCTION

While brachiopods are abundant and important fossils, living species are comparatively rare and it is probably for this reason that they have been virtually ignored by physiologists: brachiopod metabolism is known only by the work of Hammen and co-workers on inarticulates (Hammen *et al.*, 1962; Hammen, 1971, 1977). Other studies on live brachiopods have dealt mainly with behaviour and feeding (see Rudwick, 1970; McCammon, 1971; LaBarbera, 1977, 1978).

Brachiopods superficially resemble bivalve molluscs but have few characteristics in common with them. The two shell valves may be hinged (articulates) or not (inarticulates). The mantle cavity is large and contains a prominent organ known as the lophophore which was originally regarded as a respiratory organ since it superficially resembled the gills of many aquatic animals (Moore, 1965). It is now known to be primarily a feeding organ, but its large surface area may play an important role in respiration (Moore, 1965; Rudwick, 1970) as brachiopods have no specialized respiratory organ (Rudwick, 1970; Barnes, 1980).

The circulatory system in brachiopods consists of a series of long, tubular extensions of the main coelom which penetrate the connective tissue layers of the mantle and are known as mantle canals (Moore, 1965; Rudwick, 1970). In the

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articulates, these canals are narrow, paired, occur in different patterns and branch extensively towards the mantle edge or site of water entry. In the inarticulates, the mantle canals are more numerous and the canals themselves have a ciliary circulation in communication with the coelom (Chuang, 1964). This system is apparently open-ended. While its anatomy is poorly known, virtually nothing is known of its physiology. It would appear that gaseous exchange occurs over the general body surface, particularly through the lophophore and the mantle canals via the thin mantle wall. Moore (1965) stated that there is no respiratory pigment in brachiopods; however, it is well known that *Lingula* spp. possess haemerythrin (Manwell, 1960; Chuang, 1964). It is not known whether other species of brachiopods contain respiratory pigments, although the fluid drained from the mantle canals of *Terebratella inconspicua* appears pigmented (pers. obs.).

A unique characteristic of many articulate brachiopods is the presence of punctae, small blind ending perforations of the shell which bear extensions (caeca) of the outer mantle epithelium. They usually terminate just below the external surface of the shell, although a "brush" of extremely fine cytoplasmic threads extends from the head of the caeca through the very thick remaining part of the primary layer, thus providing a connection between the inner and outer surfaces of the shell (Bowen, 1968; Owen & Williams, 1969; Rudwick, 1970). The punctae are distributed uniformly over the surface of the shell (Kemezys, 1965) and their exact function is still uncertain, although their use has been a matter of discussion for some years. As long ago as 1883, Shipley considered punctae to be involved in oxygen uptake, but later abandoned this idea in favour of a function in the nourishment of the organic matrix of the shell (Shipley, 1895). Electron microscopy has demonstrated that the caeca exude mucopolysaccharides (Owen & Williams, 1969) which may serve to cement breaks inflicted on the organic exoskeleton of the shell, provide a deterrent to boring organisms, or serve as storage centres for chemical components circulating within the mantle.

New Zealand is an especially favourable place for studying living brachiopods in that at least 12 species inhabit the local waters. Of these, three can be collected intertidally and four others live in waters shallow enough to be dredged easily (Bowen, 1968), thus providing an ideal opportunity to study live specimens. In this paper I have compared the oxygen consumption of several species of brachiopods and investigated the possible role of the punctae in gas exchange.

MATERIALS AND METHODS

Specimens of *Terebratella* (*Waltonia*) *inconspicua* (Sowerby) were collected from the undersides of rocks along the low tide level at Quarantine Island and Aquarium Point in Otago Harbour. *Neothyris lenticularis* (Deshayes) and *Terebratella* (*Magasella*) *sanguinea* (Leach) were dredged on the outer continental shelf east of

Otago Peninsula (approximate position 170°40'E: 45°40'S) at a depth of ≈ 130 m. *Lingula bancrofti* Johnston and Hirschfield was collected at Amity Banks, Moreton Bay (27°26'S: 153°21'E), Australia, placed in plastic bags with sea water and flown to Dunedin. There was no mortality and none of the specimens had lost the pedicle. All animals were kept in tanks in running sea water from Otago Harbour at 10 to 12 °C and 33.5‰ salinity. Animals were maintained in the laboratory for at least 1 wk prior to use in experiments and no food was provided other than that available in the running sea water.

Shell and tissue dry weights were obtained by oven drying at 70 °C for 48 h. Shell heights were measured with vernier calipers accurate to 0.001 cm. Shell volume (internal) was determined by filling dried shells with plasticene and measuring water displacement of the plasticene in ml.

Oxygen consumption was monitored in individual animals using a Radiometer oxygen electrode connected via a Radiometer PHM 71 meter to a Smith's servo-scribe chart recorder. The closed system experimental procedure has been described previously by Taylor & Brand (1975) and Crisp *et al.* (1978). All experiments were carried out at 10 °C. Individual brachiopods were placed in experimental chambers for at least 1 h prior to measurements of oxygen uptake. The water in the experimental chambers was stirred continuously throughout the experiment.

In experiments to determine the effect of declining oxygen tension on oxygen consumption the brachiopods were allowed to deplete the oxygen supply in the experimental chamber (Taylor & Brand, 1975; Shumway, 1978). To minimize variations due to differences in weight between individuals, $\dot{V}_{O_2}/\dot{V}_{O_2 \text{ initial}}$ was plotted against P_{O_2} in torr. In addition, \dot{V}_{O_2} values were set equal to 1.0 and all subsequent values are expressed as fractions of 1.0.

One further series of experiments was carried out in which the shells of *Terebratella inconspicua* were covered with dental cement, care being taken not to seal the mantle edge shut. In this way, the animal could still open and close at will but punctae were isolated from the external medium.

It was noted early in the investigation that when disturbed, *T. inconspicua* would quickly clamp the valves shut and remain closed for some time. It was also noted that oxygen was still being consumed during these periods of closure which prompted the investigation of the possible role of the punctae in supplying the animal with oxygen. Both normal and cement-painted animals were prodded to induce shell valve closure and the oxygen uptake measured. As soon as an individual was seen to re-open, the experiment was terminated.

T. inconspicua is abundant on the undersides of rocks and is exposed in most locations at low tide. In the areas of collection the water is most always turbid. Rudwick (1962a) found that the animals continue to filter-feed in turbid water but that they are intolerant of siltation. This phenomenon was also observed in *T. sanguinea* and *Neothyris lenticularis*, which probably explains why they are usually found on the undersides of boulders. *Terebratella sanguinea* and *Neothyris lenti-*

cularis were both found in rather muddy environments; *Lingula bancrofti* were collected at low water neaps in a muddy sand habitat. Lingulids are generally the most muscular of the brachiopods but as pointed out by Chuang (1964) they are very sluggish in habit. They live in a sand burrow and at the least sign of danger the stalk is contracted violently and the body withdrawn to the upper portion of the burrow. This rapid retreat is followed by the collapse of the sand at the mouth of the burrow and all trace of the presence of the *Lingula* disappears (Shipley, 1895).

RESULTS

Terebratella inconspicua, more so than the other species studied, appeared to have rather irregular shaped shells caused by crowding, but the relationship between shell height and tissue dry weight is remarkably consistent (Fig. 1). Relative to several species of molluscs, the articulate brachiopods have a very low ratio of tissue to shell weight, leaving a considerable space available for sea-water storage during shell valve closure (Fig. 2, Table I). *Lingula*, the only inarticulate species studied, shows the highest ratio of tissue volume to shell weight (Table II); thus, this species does not have any excess space available for sea-water storage during shell closure.

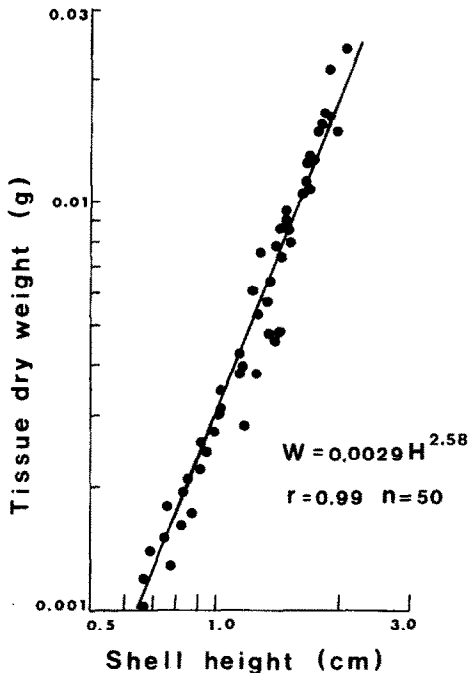


Fig. 1. Relationship between shell height (H) and tissue dry weight (W) for *Terebratella inconspicua*.

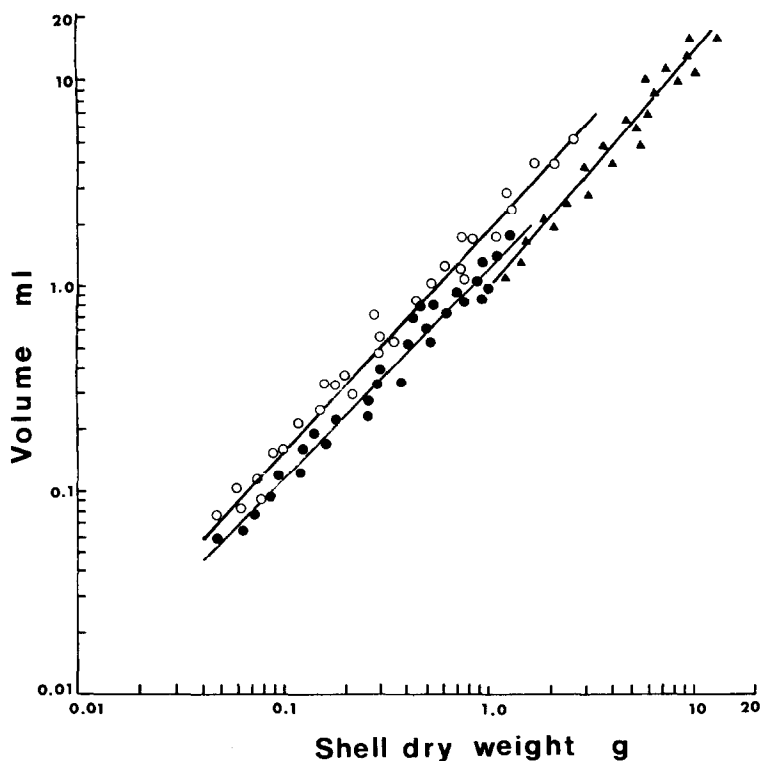


Fig. 2. Relationship between shell dry weight and shell volume in three species of articulate brachiopods: *Terebratella inconspicua* (●); *Terebratella sanguinea* (○); *Neothyris lenticularis* (▲); regression data are given in Table II.

TABLE I

Linear regression data for several species of New Zealand molluscs and brachiopods relating shell dry weight (S , g) to tissue dry weight (T , g); n , number of determinations; r , correlation coefficient; data were fitted to the equation $T = aS^b$; (B) and (M), brachiopod and mollusc species respectively.

| Species | a | b | n | r |
|--|-------|-------|-----|-------|
| <i>Cryptoconchus porosus</i> ^a | 0.678 | 0.960 | 17 | 0.997 |
| <i>Lingula bancrofti</i> (B) | 0.542 | 0.777 | 23 | 0.965 |
| <i>Sypharochiton pelliserpentis</i> ^a (M) | 0.429 | 0.780 | 23 | 0.981 |
| <i>Ischnochiton maorianus</i> ^a (M) | 0.385 | 1.190 | 11 | 0.994 |
| <i>Onithochiton neglectus</i> ^a (M) | 0.241 | 0.908 | 9 | 0.985 |
| <i>Chlamys delicatula</i> ^b (M) | 0.098 | 1.010 | 20 | 0.960 |
| <i>Amphibola crenata</i> ^c (M) | 0.098 | 0.870 | 80 | 0.989 |
| <i>Perna canaliculus</i> (M) | 0.059 | 1.060 | 30 | 0.983 |
| <i>Amphidesma australe</i> (M) | 0.040 | 1.080 | 18 | 0.998 |
| <i>Crassostrea glomerata</i> (M) | 0.040 | 0.780 | 18 | 0.961 |
| <i>Chione stutchburyi</i> (M) | 0.031 | 0.890 | 57 | 0.999 |
| <i>Neothyris lenticularis</i> (B) | 0.019 | 0.753 | 18 | 0.908 |
| <i>Terebratella inconspicua</i> (B) | 0.014 | 0.879 | 40 | 0.989 |
| <i>Terebratella sanguinea</i> (B) | 0.013 | 0.892 | 20 | 0.966 |

^a Data from Murdoch & Shumway (1980).

^b Data from Mackay & Shumway (1980).

^c Data from Shumway (1981).

Fig. 3 and Table III show the relationship between body size and oxygen uptake in the four species. There is no significant difference in the oxygen consumption rates of animals of the same body size belonging to the three articulate species; however, the inarticulate *L. bancrofti* exhibits a much lower rate of oxygen uptake than any of the others.

Fig. 4 and Table IV describe the effect of declining oxygen tension on the rate of oxygen consumption in the four species. Mangum & Van Winkle (1973) showed that the quadratic polynomial equation provides the best fit to data relating oxygen

TABLE II

Regression data for three species of articulate brachiopods relating shell dry weight (S , g) to shell volume (V , ml); n , number of determinations; r , correlation coefficient; data were fitted to the equation: $V = aS^b$.

| Species | a | b | n | r |
|---------------------------------|------|------|-----|-------|
| <i>Neothyris lenticularis</i> | 1.82 | 1.07 | 22 | 0.986 |
| <i>Terebratella inconspicua</i> | 1.22 | 1.03 | 30 | 0.972 |
| <i>Terebratella sanguinea</i> | 0.80 | 1.26 | 30 | 0.966 |

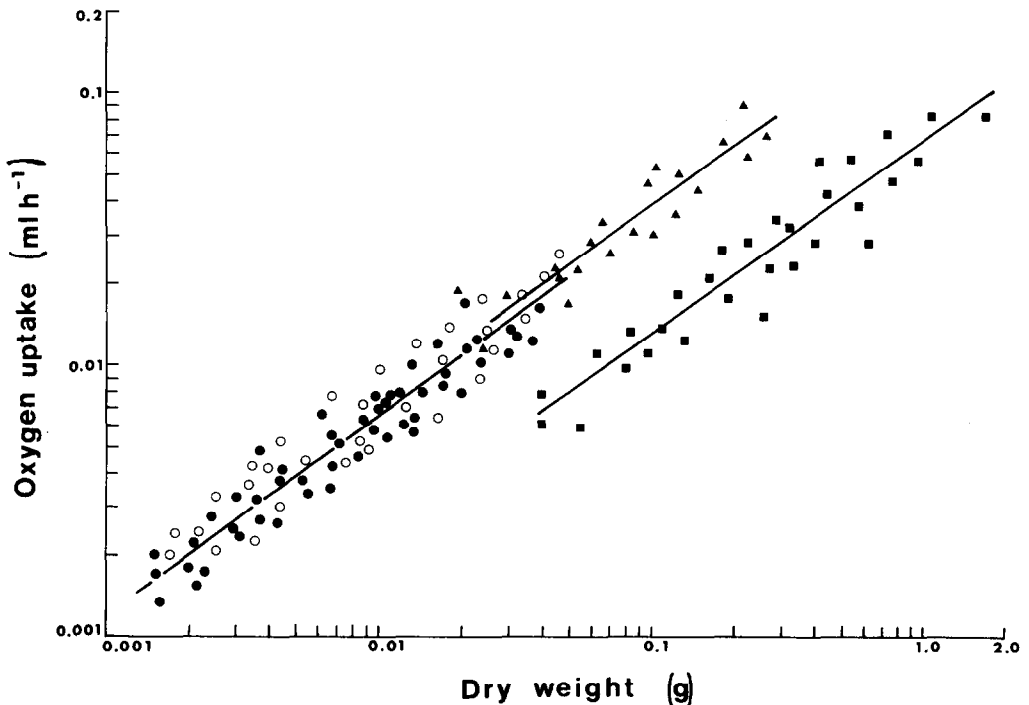


Fig. 3. Oxygen consumption in four species of brachiopods: *Terebratella inconspicua* (●); *Terebratella sanguinea* (○); *Neothyris lenticularis* (▲); *Lingula bancrofti* (■); regression data are given in Table III.

TABLE III

Regression data for the four species of brachiopods relating oxygen consumption (\dot{V}_{O_2} , ml · h⁻¹) to tissue dry weight (W , g); n , number of determinations; r , correlation coefficient; regressions were fitted by the method of least squares to the equation: $\dot{V}_{O_2} = aW^b$.

| Species | a | b | n | r |
|---------------------------------|-------|-------|-----|-------|
| <i>Lingula bancrofti</i> | 0.068 | 0.710 | 31 | 0.921 |
| <i>Neothyris lenticularis</i> | 0.201 | 0.731 | 22 | 0.889 |
| <i>Terebratella inconspicua</i> | 0.196 | 0.741 | 50 | 0.938 |
| <i>Terebratella sanguinea</i> | 0.194 | 0.720 | 31 | 0.929 |

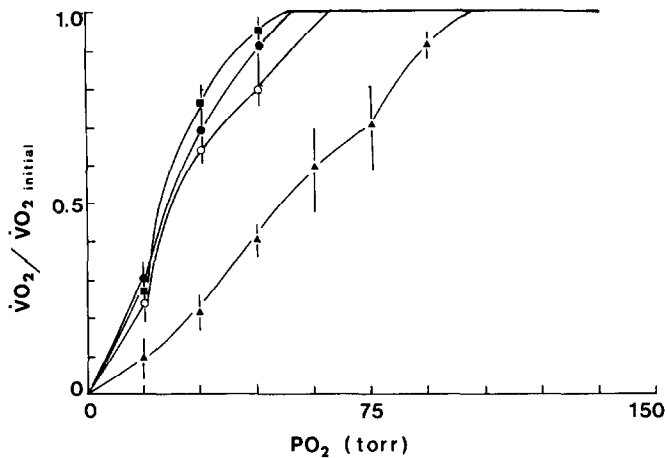


Fig. 4. The effect of declining oxygen tension on oxygen consumption in four species of brachiopods: *Terebratella inconspicua* (●, $n = 15$); *Terebratella sanguinea* (○, $n = 5$); *Neothyris lenticularis* (▲, $n = 5$); *Lingula bancrofti* (■, $n = 6$); initial \dot{V}_{O_2} (ml $O_2 \cdot h^{-1} \cdot g^{-1}$) values were set equal to 1.0 and all subsequent values are expressed as fractions of 1.0; points on each line represent the mean \pm 95% confidence limits; experimental conditions: 10 °C, 33.5‰ salinity.

TABLE IV

Quadratic coefficients [$B_2 (\times 10^3)$] for four species of brachiopods exposed to declining oxygen tensions; n values are the same as in Fig. 5.

| Species | $B_2 (\times 10^3)$ | r | Degree of regulation ^a |
|---------------------------------|---------------------|-------|-----------------------------------|
| <i>Neothyris lenticularis</i> | -0.052 | 0.942 | E |
| <i>Terebratella sanguinea</i> | -0.075 | 0.911 | C |
| <i>Terebratella inconspicua</i> | -0.084 | 0.899 | B |
| <i>Lingula bancrofti</i> | -0.089 | 0.919 | B |

^a Based on a comparison of the experimental curves with a series of hypothetical curves calculated by Mangum & Van Winkle (1973) ranging from A = near perfect regulation to H = complete conformity of oxygen uptake to oxygen tension.

consumption to oxygen tension. They proposed that the quadratic coefficient (B_2) could be used to indicate the extent of regulation of oxygen uptake in that B_2 will become increasingly negative as the degree of independence of oxygen consumption increases.

When each of 20 specimens of *Terebratella inconspicua* was induced by prodding to close its valves, the animals continued to extract oxygen from the external medium at a rate equal to $\approx 22\%$ of that of normal, pumping animals. Covering the shells with dental cement and prodding the mantle to induce shell valve closure resulted in total cessation of oxygen removal from the external medium.

DISCUSSION

The articulate brachiopods have a very low tissue to shell ratio, while the inarticulate *Lingula bancrofti* has one of the highest ratios. Comparing the rates of oxygen consumption by these species (Fig. 3, Table III), we find that, while the articulates have the least tissue, they have the higher metabolic rate. Hammen *et al.* (1962) studied oxidative metabolism in *Lingula reevi* and compared it with two species of bivalve molluscs, *Modiolus demissus* and *Crassostrea virginica*. Unfortunately, they presented their results for oxygen consumption based on whole body weight (including shell) and tissue wet weight. In addition, their determinations on *Lingula reevi* were made on animals which had lost the pedicle muscle or just started to regenerate one. It was found in the present study that the pedicle muscle, i.e., the muscle held within the pedicle sheath, accounted for a substantial portion of the respiring tissue ($21.09\% \pm 2.78$ SD). Thus, although Hammen *et al.* (1962) reported that *L. reevi* had a low rate of oxygen uptake, their estimate is probably too low. In addition, when they compared the oxygen uptake of *L. reevi* with that of the two bivalves, they found that *L. reevi* had a lower rate than either of the two bivalves despite the fact the brachiopods had a higher tissue to shell ratio. Table V compares \dot{V}_{O_2} values for several species of molluscs and brachiopods; it can be seen that, with the exception of *Crassostrea virginica*, all of the bivalves studied have a higher weight specific metabolism than the brachiopods and that, amongst the brachiopods, the inarticulate *Lingula bancrofti* has the lowest rate. It is interesting to note from Table I that *Crassostrea virginica* shows one of the lowest tissue to shell ratios for any of the bivalves, pointing out the absurdity of relating oxygen uptake to total animal weight.

Two factors which affect the oxygen uptake rate are the amount of water that an animal is able to pump per unit time and the amount of oxygen it can extract from the pumped water. A major difference between brachiopod and bivalve pumping mechanisms is that in brachiopods the lophophore filaments are not fused to each other or to other structures as are bivalve gill filaments. Therefore, since the partition across the mantle cavity is only maintained by the strength of the

filaments themselves, the pressure difference at which the pumping system can operate is limited. This means that the rate at which the animal can pump water is restricted (Rudwick, 1970). Rudwick (1962b) also pointed out that, if brachiopods are observed alongside lamellibranchs of the same size and living in the same habitat, the brachiopods ventilate at a much lower rate than the lamellibranchs as evidenced by the velocities of the water currents.

Doherty (1976) related the pumping rate of *Terebratella inconspicua* to tissue dry weight as $P = 0.048 W^{0.55} \text{ l} \cdot \text{h}^{-1}$ (W , mg). From the present study, a typical animal

TABLE V

Oxygen consumption rates for a 0.01 g (dry tissue weight) specimen of several species of molluscs and brachiopods; (M), mollusc; (B), brachiopod; \dot{V}_{O_2} data taken from indicated sources.

| Species | \dot{V}_{O_2} ($\text{ml} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$) | References |
|-------------------------------------|---|----------------------------|
| <i>Mytilus perna</i> (M) | 1.920 | Bayne (1967) |
| <i>Mytilus edulis</i> (M) | 1.550 | Bayne <i>et al.</i> (1973) |
| <i>Chlamys delicatula</i> (M) | 1.390 | Mackay & Shumway (1980) |
| <i>Modiolus demissus</i> (M) | 1.350 | Shumway & Youngson (1979) |
| <i>Cardium edule</i> (M) | 1.070 | Vahl (1972) |
| <i>Terebratella sanguinea</i> (B) | 0.704 | Present study |
| <i>Neothyris lenticularis</i> (B) | 0.694 | Present study |
| <i>Terebratella inconspicua</i> (B) | 0.646 | Present study |
| <i>Crassostrea virginica</i> (M) | 0.582 | Dame (1972) |
| <i>Lingula bancroftii</i> (B) | 0.258 | Present study |

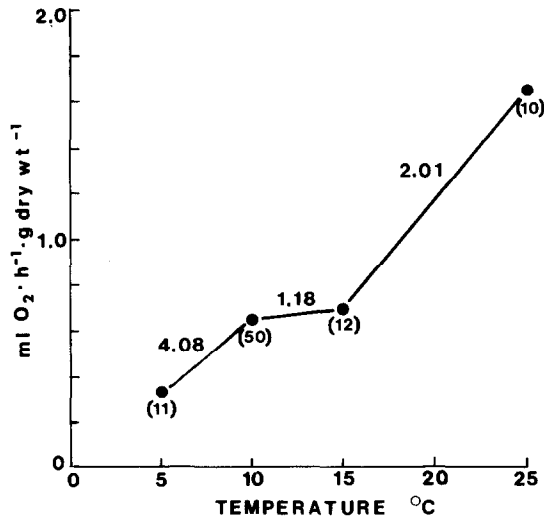


Fig. 5. The acute rate: temperature curve for *Terebratella inconspicua* corrected to value for an animal of 0.01 g dry tissue weight; experimental conditions: $P_{\text{O}_2} = 140$ torr; salinity = 33.5‰, n indicated in parentheses for each temperature.

of 0.014 g dry tissue weight respire at a rate of $0.009 \text{ ml} \cdot \text{h}^{-1}$ and, from Doherty's equation, the same animal would pump $\approx 205 \text{ ml h}^{-1}$. Assuming a salinity of $\approx 33\%$ and a temperature of 15°C (experimental conditions of both studies) the animal has available an oxygen concentration in the external medium of $5.8 \text{ ml} \cdot \text{l}^{-1}$. This means that the animal has available $1.189 \text{ ml O}_2 \cdot \text{h}^{-1}$ and is only extracting $0.009 \text{ ml} \cdot \text{h}^{-1}$ or 0.76% . This is a very low rate of extraction when compared with bivalves such as *Modiolus demissus* (8 to 9% extracted; Booth & Mangum, 1978), *Mya arenaria* (5 to 10%; Van Dam, 1938), *Mytilus edulis* (3 to 15%; Rotthauwe, 1958), and *Mytilus perna* (4 to 7%; Bayne, 1967).

Several species of articulate brachiopods overcome part of the problem associated with low pumping ability by actively orienting themselves to the ambient water movements such that the anterior-posterior axis of the shell is perpendicular to the direction of ambient flow. LaBarbera (1978) showed that *Lagueus californianus*, *Terebratulina unguicula*, and *Hemithyris psittacea* actively reorient to water currents and that other species, such as *Terabratalia transverse*, do not reorient but instead are oriented in nature with the anterior-posterior axis of the shell perpendicular to the prevailing currents (LaBarbera, 1977). It is not known whether *Terebratella inconspicua* actively reorients to the water currents or whether it is oriented in nature. Although Rudwick (1962b) stated that the shells do not appear to have any preferred orientation relative to the horizontal, orientation to currents was not studied.

Hammen *et al.* (1962) found that *Lingula reevi* showed unusually high levels of succinic dehydrogenase activity suggesting that the animal is capable of a high level of oxidative activity. They also found that *Lingula* exhibited equal or greater activities of the enzymes studied than two bivalves and concluded that the low rate of metabolism is the result of control mechanisms rather than any enzyme deficiency. While no data are presently available for pumping rates in the lingulids, it is possible that, in addition to their sluggish sedentary habit, one of the factors leading to their depressed metabolic rate is that they are not able to orient to enhance water movement through the mantle cavity.

When exposed to declining oxygen tensions, all four species showed some degree of oxygen independence, with *L. bancrofti* and *Terebratella inconspicua* having the highest degree. *Lingula* is also most likely to experience conditions of declining oxygen in its natural muddy infaunal habitat. It is possible, though not probable, that *Terebratella inconspicua* could be exposed to low oxygen conditions due to crowding and it is highly unlikely that the sub-tidal species *T. sanguinea* and *Neothyris lenticularis* would ever encounter low oxygen in their natural environment.

It is known that several species of articulate brachiopods close their valves for long periods, sometimes spontaneously but usually in response to such phenomena as physical disturbance or heavy siltation (Savage, 1972). While it has been shown that some species are capable of anaerobic metabolism (Hammen, 1977) the present

investigation indicates that conversion to anaerobic pathways may not always be necessary. Let us consider an average *Terebratella inconspicua* of 1 g dry shell weight, or a tissue dry weight of 0.014 g and a shell volume of <1.22 ml (a slight overestimate of volume since the space occupied by the animal is ignored). The animal respire at a rate of 0.008 ml · h⁻¹. Since 1 ml of saturated sea water at 33.5% and 10 °C has ≈ 6.4 μl of O₂, the water contained within a shell of 1 g will contain 7.808 μl of oxygen when closed. The animal within this shell consumes 8 μl O₂ · h⁻¹ and will therefore consume 7.808 μl (the total amount available) in 0.976 h. The animal only consumes oxygen at the rate of 8 μl · h⁻¹ when the P_{O₂} is ≥ 45 torr or 30% saturation, however. At 30% saturation the water within the shell contains ≈ 2.342 μl of oxygen. Thus, the animal consumes 5.466 μl of oxygen in reducing fully oxygenated sea water within the shell, to ≈ 30% saturated sea water. At that rate, 5.466 μl of oxygen will last the animal ≈ 0.683 h or 41 min. It would appear then, that at least in the short term, there would be no need for these animals to revert to the more inefficient anaerobic pathways during shell closure. It is also unlikely that they would be exposed for any longer than 41 min during any tidal cycle.

Perhaps the more interesting results reported here are those for *T. inconspicua* which continued to respire despite shell valve closure, but only if the shell was not painted with dental cement. This result strongly suggests that oxygen is entering the shell through the punctae.

Using the following form of the Fick equation (Piiper *et al.*, 1971), it is possible to calculate the rate of movement of oxygen through the punctae of *T. inconspicua*:

$$M_x = A_p L^{-1} D_x \beta_g \Delta P_x,$$

where: M_x = net flow of gas x across the punctae (ml · s⁻¹); D_x = diffusion coefficient for gas x = 1.54 × 10⁻⁵ cm² · s⁻¹ (Horne, 1969); A_p = total pore area (cm²); L = length of diffusion path (cm); ΔP_x = partial pressure difference (torr); β_g = $\Delta C_x / \Delta P_x$ = capacitance coefficient = 1/RT; R = gas constant 2.785 cm³ · torr · (°K)⁻¹ · cm⁻³ therefore, β_g at 10 °C = 0.0013 cm³ · cm⁻³ · torr⁻¹.

A typical specimen of *T. inconspicua* has the following characteristics: 1 g total dry shell weight, 0.014 g dry tissue, 2 cm shell height, 1.22 ml shell volume, ≈ 700 mm² surface area and ≈ 1 mm shell thickness. If we assume the puncta to be a hollow tube (which it is not, therefore the estimate will be high) 1 mm in height and ≈ 25 μm in diameter (Owen & Williams, 1969), the total area of one puncta or pore will be 4.91 × 10⁻⁶ cm². There are ≈ 150 punctae · mm⁻² in *T. inconspicua* (Kemezys, 1965; Bowen, 1968) or, for our typical animal 1.05 × 10⁵ punctae. Therefore $A_p L^{-1}$ will be equal to 9.515 cm.

To calculate ΔP_x one must know the P_{O₂} on both sides of the shell. We know the external P_{O₂} to be ≈ 150 torr. The internal P_{O₂} was not measured, but for this discussion we can use the estimate of 50 torr based on values available for bivalve molluscs (Booth & Mangum, 1978). These figures will give a value for M_x of

$3.71 \times 10^{-3} \text{ ml} \cdot \text{h}^{-1}$ which is most likely an overestimate since as pointed out previously the punctae are not hollow. This value of M_x also represents the best possible conditions when the animal is exposed to fully oxygenated sea water.

From the experimental data, a closed *T. inconspicua* can respire at a rate equal to $\approx 20\%$ of its normal rate or at a rate of $1.87 \times 10^{-3} \text{ ml} \cdot \text{h}^{-1}$. Since M_x , the theoretical amount of oxygen which could diffuse through the shell is much larger than the amount of oxygen actually used, $1.87 \times 10^{-3} \text{ ml} \cdot \text{h}^{-1}$, it would appear at least feasible that the animals can acquire adequate oxygen through the punctae to maintain this depressed rate of oxygen uptake during periods of shell closure. These values are calculated for the best possible conditions and re-calculating M_x when the external P_{O_2} has dropped to 30 torr and assuming an internal drop in P_{O_2} to ≈ 10 torr the amount of oxygen available will be $7.42 \times 10^{-4} \text{ ml} \cdot \text{h}^{-1}$. It is also known that at a P_{O_2} of 30 torr the animal will be respiring at a rate equal to about half of its normal rate, that is 50% of 20%, and will use $8.3 \times 10^{-4} \text{ ml} \cdot \text{h}^{-1}$. It can be seen that M_x under these conditions could still be sufficient to supply the necessary oxygen.

Even though these estimates are high, it appears sufficiently high to compensate for the tissue within the puncta and would seem to indicate that the brachiopod is acquiring oxygen through the shell during periods of shell closure. Kemezys (1965) showed that the distance between punctae in *T. inconspicua* and indeed in many terebratuloids, spiriferoids, and dalmanelloids is similar. He pointed out that the only readily apparent environmental factor which has the same order of magnitude is the dividing line commonly operative in nature for the behaviour of sedimentary material or the silt/sand dividing line. Since it is known that several of these species can withstand turbidity but not siltation (Rudwick, 1970), it appears possible that when exposed to sedimentation there may be some advantage in having the punctae spaced at this critical distance. It is proposed that this spacing will allow the animals to close their shell valves to avoid "clogging" of the lophophore while at the same time continuing to respire aerobically even though at a depressed rate, via the punctae.

It appears that, at least in *T. inconspicua*, there are two separate mechanisms working to aid the animal in withstanding adverse environmental conditions. One, they may continue to respire at a normal rate for about 41 min after shell closure after which they may continue to respire at a lower rate (20% of normal) via the punctae. In addition, the punctae appear to be spaced at a critical distance which may aid this process. It is not known, however, how long the animals could continue to function at this depressed metabolic rate although one would assume a considerable length of time.

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