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Bioenergetics of a highly adaptable brackish water polychaete [☆]

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Abstract

The metabolic activities of different developmental stages of the polychaete *Marenzelleria viridis* (Verrill 1873), which has successfully populated Baltic coastal waters since the 1980s, were determined under different temperatures, salinities and oxygen partial pressures by simultaneous calorimetry and respirometry. Larvae of *M. viridis* maintained their metabolic activity and met this fully aerobically down to severe hypoxia. Adult individuals gradually reduced their metabolic activity with decreasing oxygen partial pressures. An additional hyposmotic stress of 0.5‰ salinity, referring to low salinities in the biotope, led to an approach of the response of *M. viridis* to the oxyconformer model. The results for adults were compared to those of the common indigenous polychaete *Nereis (Hediste) diversicolor* (O.F. Müller), which responded with maintained metabolic activities to hypoxia. The ecological efficiency of the different adaptation strategies to hypoxia are discussed.

Keywords: Anoxia; Bioenergetics; Calorimetry; *Hediste*; Hypoxia; *Marenzelleria*; *Nereis*; Polychaete; Respirometry

1. Introduction

A new species, the spionide polychaete *Marenzelleria viridis* (Verrill 1873), appeared in European coastal waters in the 1980's. Until then the species was only

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known in North American Atlantic estuaries [1]. After appearances in the North Sea, the first specimen in a Baltic coastal inlet was found in 1985 [2]. Since then the polychaete has proliferated and propagated very successfully. Baltic coastal waters are characterized by a range of stressful living conditions. Due to the effects of eutrophication, large oxygen amplitudes may occur, with oxygen deficiency in the sediment and formation of sulphide. Salinities may be decreased noticeably in several estuarine-like regions. Such decreased salinities, especially around the critical range of the Horohalinicum (5‰–8‰) form a propagation border for many marine and freshwater organisms [3]. Species-poor biotopes with high abundances of a few species result. Because *M. viridis* is able to propagate below horohaline regions, it is believed to have remarkable adaptation strategies enabling it to live under such inhospitable conditions.

To discover the nature of the energetic adaptations of *M. viridis*, we investigated the metabolic activity of different developmental stages of *M. viridis* by simultaneously measuring its metabolic heat dissipation and oxygen consumption under varying temperature, oxygen and salinity conditions. The results were compared to those of the common indigenous polychaete *Nereis* (*Hediste*) *diversicolor* (O.F. Müller), whose habitats, however, are considered to be restricted to salinities >5‰ [4].

2. Materials and methods

Measurements of metabolic heat dissipation were carried out with the Thermometric 2277 microcalorimeter (Thermal Activity Monitor, Järfälla, Sweden). Perfusion chambers of 25 and 4 ml were used for adult and juvenile organisms. In each case a second perfusion chamber served as a reference system for calorimetric as well as for oxygen consumption measurements [5]. Oxygen consumption was measured by thermostated polarographic oxygen sensors (2000-100 Eschweiler, Kiel, Germany) placed at the outflow of the calorimetric perfusion chambers. By comparing the oxygen partial pressure of the sample system with the reference system, the major fraction of bacterial oxygen consumption in the chambers and tubes is considered as an automatic baseline correction. Nevertheless, baselines for at least 12 h before and after each experiments were recorded in order to evaluate a minor bacterial fraction in the sample system and to provide a proper appraisal of the measurement system.

The chambers were filled with a layer of ashed (450°C) and washed sediment for experiments with juvenile and adult polychaetes. Single adult specimens were placed in the 25 ml chambers. Groups of juveniles (60 for the first benthic stage, 5 for the second benthic stage) were inserted in 4-ml chambers. Groups of approx. 200 planktonic larvae were placed in 4-ml chambers without sediment. Membrane-filtered water (0.45 μm) was pumped from a stirred reservoir by a peristaltic pump (IPN4 Ismatec, Glattbrugg-Zürich, Switzerland) placed at the end of the measuring system with flow rates of 28 and 19 ml h^{-1} for the 25-ml and 4-ml systems.

Different oxygen partial pressures were generated by a combined oxygen-sensor–valve-gear unit (Oxyguard 1, Birkerød, Denmark). Two valves controlled the supply of air and nitrogen to the reservoir water.

Measurements took place at a temperature of 10°C and a salinity of 5‰. The temperature of 10°C refers to temperatures occuring in autumn and spring. The salinity of 5‰ was used to represent an average biotope salinity for some estuarine-like biotopes. In addition, a salinity of 0.5‰ was applied to adult individuals at a temperature of 20°C which represents the highest biotope temperature in summer, when oxygen defficiency occurs more frequently. The 0.5‰ salinity represents an extreme hyposmotic stress.

The metabolic activity became stable 12–24 h after inserting animals into the measurement system and they were then considered to be acclimated. The first measurements were then undertaken. Each measurement period was at least 6 h in order to record a wide range of routine activity and to neglect the time constant of both the calorimetric and respirometric measurements (10 min for both). After changing the oxygen partial pressure, the animals were allowed to adapt to the new conditions for at least 6 h.

The signals of heat dissipation and oxygen partial pressure were recorded by an analogue–digital converter and analysed by computer (integration of the measurement period, recording and analysing program: Baumbach, Berlin, Germany).

The metabolic activities with decreasing oxygen partial pressures were plotted as standardized values (normalized to the heat and oxygen flux at normoxia). We assumed a fully aerobic metabolism at normoxia, supported by the experimental oxycaloric coefficients (within the range 431–483(±8–34) kJ per mol O_2, see Table 1) which were in accordance with the theoretical range of the oxycaloric equivalent for aerobic metabolism (445–478 kJ per mol O_2 [6]). Therefore the rates of heat dissipation and oxygen consumption at normoxia were set equal to 100%. A graph consists of 3–6 measurements with different animals. Each data point results from

Table 1
Experimental oxycaloric coefficients (ratio of heat production to oxygen consumption, *C/R* ratio) of *Marenzelleria viridis* (adults, larvae and juveniles) and *Hediste diversicolor* (adults) at normoxia: temperatures/salinities (°C/‰), *C/R* ratio (kJ per mol O_2), *n* = number of measurements

Conditions	*M. viridis* (adults)		*H. divirsicolor* (adults)	
	C/R	*n*	*C/R*	*n*
10°C/5‰	452 ± 8	4	454 ± 25	4
20°C/0.5‰	440 ± 11	2	431 ± 20	3
	M. viridis (larvae)		*M. viridis* (juven. 20–25 segments)	
	C/R	*n*	*C/R*	*n*
10°C/5‰	454 ± 13	3	483 ± 30	3

a 6 h integral of the metabolic activity. Function plots were made with a regression analysis using saturation function equations.

3. Results

M. viridis reduced its metabolic activity gradually with declining oxygen partial pressure at a temperature of 10°C and at the average biotope salinity of 5‰ (Fig. 1). But this depression was not proportional to the reduction of oxygen partial pressure. *M. virdis* regulated its metabolic activity to a certain degree. The oxygen consumption equalled the metabolic heat dissipation even at very low oxygen, indicating aerobic metabolism down to severe hypoxia.

Comparing the curves of the metabolic heat dissipation of *M. viridis* and *H. diversicolor* (Fig. 2), the greater regulation ability of *H. diversicolor* at the same conditions becomes obvious. *H. diversicolor* was also able to meet its metabolism aerobically down to very low oxygen levels. Extreme hyposmotic conditions of 0.5‰ salinity at summer temperatures of 20°C led to a more clear distinction between the responses of the two polychaetes to hypoxia (Fig. 3). Whereas the invader *M. viridis* further reduced its metabolic heat dissipation with decreasing oxygen, *H. diversicolor* maintained high metabolic heat dissipation down to severe hypoxia. But in contrast to *M. viridis*, which was able to meet its metabolism aerobically down to very low oxygen levels, the oxygen consumption of *H. diversicolor* dropped markedly, even under oxygen partial pressures below 10 kPa (Fig. 4). Its ability to regulate oxygen consumption decreased rapidly with increasing hypoxia. This indicated a significant anaerobic energy production below 10 kPa oxygen.

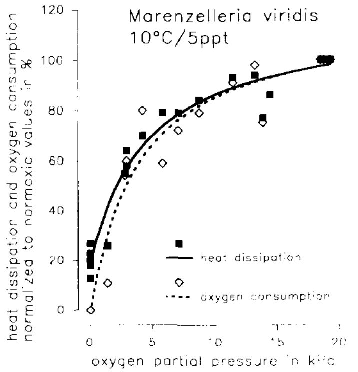


Fig. 1. Heat dissipation and oxygen consumption rates of adult *Marenzelleria viridis* in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 10°C and a salinity of 5‰.

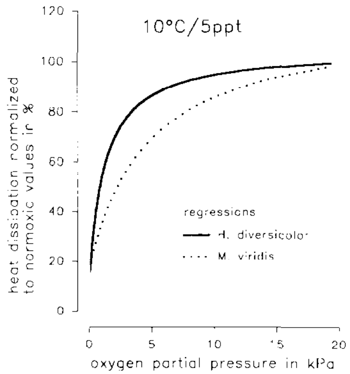
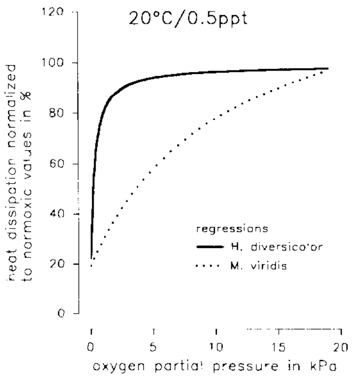


Fig. 2. Regressions for the heat dissipation of adult *Marenzelleria viridis* and *Hediste diversicolor* in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 10°C and a salinity of 5‰.



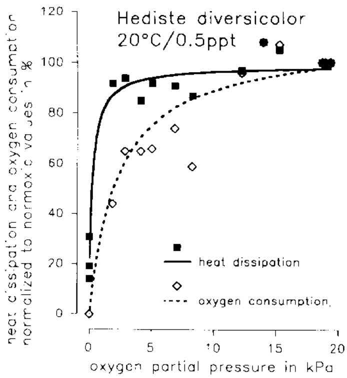


Fig. 3. Regressions for the heat dissipation of adult *Marenzelleria viridis* and *Hediste diversicolor* in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 20°C and a salinity of 0.5‰ (additional hyposmotic stress).

Fig. 4. Heat dissipation and oxygen consumption rates of adult *Hediste diversicolor* in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 20°C and a salinity of 0.5‰ (additional hyposmotic stress).

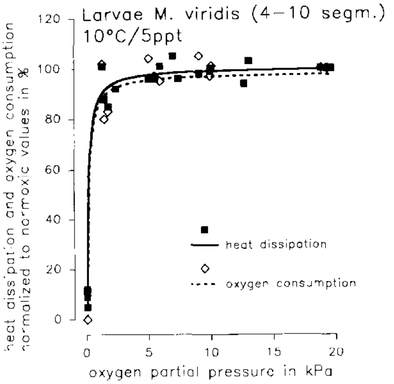
Under anoxia both polychaetes (adults) reduced their metabolic heat dissipation down to approximately 20% of the normoxic rates at all temperature and salinity conditions (Table 2).

In contrast to adult individuals, larvae of *M. viridis* were able to maintain their metabolic activity down to very low oxygen (Fig. 5). The oxygen consumption equalled the heat dissipation down to severe hypoxia indicating fully aerobic metabolism. Under anoxic conditions, larvae of *M. viridis* reduced their heat dissipation to 10% of the normoxic rates (Table 2).

Table 2

Anaerobic metabolic heat dissipation of *Marenzelleria viridis* (adults, larvae and juveniles) and *Hediste diversicolor* (adults), normalized to normoxic heat dissipation: temperatures/salinities (°C/‰); *Q*, relative metabolic heat dissipation (%); *n*, = number of measurements

Conditions	*M. viridis* (adults)		*H. diversicolor*	
	Q	*n*	*Q*	*n*
10°C/5‰	20.2 ± 8.4	5	18.0 ± 4.1	4
20°C/0.5‰	19.0 ± 6.0	4	21.3 ± 8.7	3
	M. viridis (larvae)		*M. viridis* (juven. 20–25 segments)	
	Q	*n*	*Q*	*n*
10°C/5‰	10.0 ± 1.4	5	14.0 ± 3.7	5



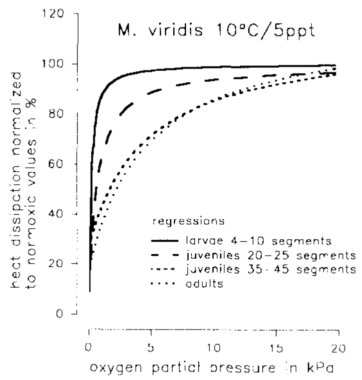


Fig. 5. Heat dissipation and oxygen consumption rates of larvae of *Marenzelleria viridis* in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 10°C and a salinity of 5‰.

Fig. 6. Regression for the heat dissipation of *Marenzelleria viridis* (larvae, juveniles and adults) in response to declining oxygen partial pressure, relative to normoxic values at a temperature of 10°C and a salinity of 5‰.

The regulation pattern of the metabolic activity of juvenile *M. viridis* approached that of adult individuals during the early development (Fig. 6). Juveniles of 35 to 45 segments had already reached the response pattern of adults.

4. Discussion

The invader *M. viridis* responded to hypoxic conditions at average biotope salinity (5‰) with gradually reduced metabolic activities (Fig. 1). Its response was identical neither to the model of an ideal oxygen conformer nor to that of an ideal oxygen regulator (see Refs. [7,8]). This result of a more or less oxygen-dependent metabolism coincides with results published by other authors for polychaetes [9–12]. The approach to the model of an oxyconformer with the additional stress of extremely low salinity (0.5‰) illustrates the reduction of metabolic activity as an adaptation strategy of *M. viridis* to hypoxic conditions (Fig. 3).

Comparing the response of *M. viridis* to that of *H. diversicolor* which tends to maintained metabolic activity at reduced oxygen (Figs. 2 and 3), raises the question whether the concept of regulated metabolic activity at hypoxia or that of depressed metabolic activity is ecologically more efficient. To maintain metabolic activity and to do so fully aerobically as shown for *H. diversicolor* at a salinity of 5‰ may be advantageous for life under hypoxic conditions. If the maintained metabolic activity is not caused by increased ventilation activities alone, it could indicate the realization of normal routine activity including movement and feeding. However, the reduced metabolic activities of *M. viridis* indicate an energy-saving strategy in response to hypoxia. The diminished consumption of energy and substrates does not need high activities for to provide this. The two approaches may be successful for surviving periods of hypoxia.

Considering the additional stress of extreme hyposmotic conditions to both species the advantage of the strategy of *M. viridis* becomes clear. The reduced metabolic activities enables it to meet metabolism fully aerobically down to very low oxygen levels. In *H. diversivolor*, however, the supply of oxygen does not meet all the energy-demanding processes below 10 kPa oxygen. The polychaete is forced to compensate the reduction of aerobic metabolic rates by anaerobic processes. Because anaerobic pathways are energetically less efficient because of the higher substrate demand and lower ATP yield compared to aerobic pathways [13], the flux throughout the anaerobic processes increases considerably. Therefore the strategy of *H. diversicolor* leads to a rapid depletion of substrate stores while maintaining high activity. The energy-saving strategy of the invader *M. viridis* may be more advantageous for surviving periods of prolonged hypoxia at hyposmotic conditions.

At anoxia, adults of both polychaetes reduced their metabolic heat dissipation to approx. 20% of normoxic rates. The heat dissipation per unit ATP turnover in anoxic metabolism may decrease to 50% compared to aerobic catabolism [13]. Therefore the anaerobic metabolic rates, represented in terms of ATP turnover, could be twice as high as those reflected in the measured heat dissipation. Nevertheless both polychaetes reduced their metabolism. Thus, the substrate-demanding anaerobic pathways will be restricted to conserve substrate stores. The same reduction of metabolic rates in both polychaetes indicates equal efficiency for surviving periods of anoxia.

Like adult individuals larvae of *M. viridis* were also able to survive hypoxic and anoxic conditions. They responded to hypoxia with maintained and fully aerobic metabolic activities down to very low oxygen levels, behaving as an ideal oxygen regulator (Fig. 5). Larvae of other euryoxic invertebrates were also found to maintain energy metabolism at reduced oxygen levels [14,15]. But these maintained metabolic rates cannot be interpreted as a true regulation of oxygen consumption. They are more likely to be a function of the high surface-area-to-volume-ratio and the lower limitation of oxygen diffusion in small animals [16]. Nevertheless, the oxygen-independent metabolic rates may reflect the maintenance of feeding and larval growth [15] and as such provide larval development even under hypoxic conditions. The approach of regulation pattern to that of the adults within the early development (Fig. 6) reflects the rapid decrease of the surface-area-to-volume-ratio and therefore the increase of oxygen diffusion limitation.

Larvae of *M. viridis* reduced their metabolic heat dissipation to 10% of the normoxic rates (Table 2) compared to 20% in adults. Substrate storages in larvae are believed to be quite small. The diminished supply of substrates to anaerobic pathways may be a reason for the decreased anaerobic heat dissipation. But it could also be interpreted as conserving the small substrate storages.

5. Conclusions

All investigated developmental stages of the invader *M. viridis* were able to survive hypoxic and anoxic conditions. But the responses to hypoxia were different.

Larvae maintained the metabolic rates and met them fully aerobically whereas juveniles and adults responded with decreased metabolic rates to increasing hypoxic conditions. By comparing the response of adult *M. viridis* to those of adult *H. diversicolor* with an additional hyposmotic stress, the advantage of the reduction of metabolic rates while meeting an additional stressor has been shown. This may be an ecophysiological part of the explanation of the invaders success in their propagation in Baltic coastal waters.

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References

[1] E.M. Dauer, R.M. Ewing, G.H. Tourtellotte and H.R. Baker, Jr., Nocturnal swimming of *Scolecolepides viridis* (Polychaeta: Spionidae), Estuaries, 3 (1980) 148–149.

[2] A. Bick and R. Burckhardt, Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee, Mitt. Zool. Mus. Berlin, 65/2 (1989) 237–247.

[3] O. Kinne, 4. Salinity, 4.3. Animals, 4.3.1. Invertebrates, in O. Kinne (Ed.), Marine Ecology, Vol 1., Environmental Factors, Wiley, London, 1971, pp. 821–995.

[4] E.A. Arndt, Ecological, physiological and historical aspects of brackish water fauna distribution, in J.S. Ryland and P.A. Tyler (Eds.), Proc. 23rd Eur. Mar. Biol. Symp., Swansea UK, Olsen & Olsen, Fredensborg, 1989, pp. 327–338.

[5] J. Widdows, Application of calorimetric methods in ecological studies, in A.M. James (Ed.), Thermal and Energetic Studies of Cellular Biological Systems, Wright, Bristol, 1987, pp. 182–215.

[6] E. Gnaiger, Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, in E. Gnaiger and H. Forstner (Eds.), Polarographic Oxygen Sensors, Springer-Verlag, Berlin 1983, pp. 337–345.

[7] E. Gnaiger, Animal energetics at very low oxygen: information from calorimetry and respirometry, in R. Woakes, M. Grieshaber and C.R. Bridges (Eds.), Strategies for Gas Exchange and Metabolism, Soc. Exp. Biol. Seminar Ser. 44, Cambridge University Press, London 1991, pp. 149–171.

[8] H.O. Pötner and M.K. Grieshaber, Critical P_{O_2} (s) oxyconforming and oxyregulating animals: gas exchange, metabolic rate and the mode of energy production, in: J. Eduardo and P.W. Bicudo (Eds.), The Vertebrate Gas Transport Cascade — Adaptations to Environment and Mode of Life, CRC Press, Boca Raton, 1993, pp. 330–357.

[9] C.P. Mangum and W. van Winkle, Responses of aquatic invertebrates to declining oxygen conditions, Am. Zool., 13 (1973) 529–541.

[10] S.E. Shumway, The effects of body size, oxygen tension and mode of life on the oxygen uptake rates of polychaetes, Comp. Biochem. Physiol., 64A (1979) 273–278.

[11] A. Toulmond and C. Tchernigovtzeff, Ventilation and respiratory gas exchange of the lugworm *Arenicola marina* (L.) as functions of ambient P_{O_2} (20–700 torr), Respir. Physiol., 57 (1984) 349–363.

[12] T.F. Pedersen, Metabolic adaptations to hypoxia of two species of polychaeta, *Nephtys ciliata* and *Nephtys hombergii*, J. Comp. Physiol. B, 161 (1991) 213–215.

[13] E. Gnaiger, Heat dissipation and energetic efficiency in animal anoxibiosis: economy contra power, J. Exp. Zool., 228 (1983) 471-490.

[14] J. Widdows, Calorimetric and energetic studies of marine bivalves, in W. Wieser and E. Gnaiger (Eds.), Energy Transformations in Cells and Organisms, Georg Thieme, Verlag, Stuttgart, 1989, pp. 145-154.

[15] W.X. Wang and J. Widdows, Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia, Mar. Ecol. Progr. Ser., 70 (1991) 223-236.

[16] C.F. Herreid, Hypoxia in invertebrates, Comp. Biochem. Physiol., 67A (1980) 311-320.