

Dirk FRITZSCHE

University of Rostock, Department of Marine Biology

***Marenzelleria* cf. *viridis*: Responses to salinity change and low oxygen partial pressure - A summary of information from resistance experiments and calorimetry**

Abstract

The responses of different development stages of *Marenzelleria* cf. *viridis* (Verrill 1873), an immigrant into Baltic coastal waters, to salinity changes and low oxygen partial pressure / anoxia were examined. The present study summarizes resistance experiments and data from direct, indirect and combusive calorimetry. The results were compared to those of the euryoecous common indigeneous polychaete *Nereis* (*Hediste*) *diversicolor* (O.F. Müller). The energetic turnover of adult individuals of both polychaetes was equal amounting to approximately 0,73 % daily, at a temperature of 10°C, indicating equal energetic prerequisites for matching stress. Adult *M. cf. viridis* showed equally high resistance to low salinities as *H. diversicolor*: $LC_{50} < 0.1$ PSU for both. The resistance to high salinities was lower for *M. cf. viridis* ($LC_{50}=29.8$ PSU at 10°C) than for *H. diversicolor* ($LC_{50} = 43.4$ PSU at 10°C) indicating a genetical adaptation of *M. cf. viridis* to brackish water conditions. Even larvae of *M. cf. viridis* were able to resist oxygen deficiency for a short time ($LT_{50} = 4.2$ h at 10°C). Resistance to oxygen deficiency increases for adult *M. cf. viridis* up to about 300 h depending on salinity and temperature. With that, *M. cf. viridis* reaches the tolerance of *H. diversicolor*. Measures of the metabolic activity revealed a more energy saving strategy at low oxygen partial pressures for *M. cf. viridis* than *H. diversicolor*. At anoxia both polychaetes gave equal metabolic activities. In summary, *M. cf. viridis* can be considered as well adapted to the Baltic coastal water levels of salinity and oxygen partial pressure as *H. diversicolor*.

Introduction

Marenzelleria cf. *viridis* (Verrill 1873) spread very successfully into coastal waters of the Baltic (cf. KUBE et al., 1996). Rate and extent of the polychaetes propagation were amazing because of the particular environmental conditions which are known to limit the macrozoobenthic diversity of these waters to only a few species.

The most important restricting factor in brackish waters like the Baltic is the low salinity (REMANE, 1958). A salinity range of 5 to 8 PSU, the Horohalinicum as named by KINNE, 1971, is wellknown to form a propagation boundary for most marine and freshwater organisms (REMANE, 1958). *M. cf. viridis* at present generally occurs at horohaline salinities and remarkable records were even given for salinities below 5 PSU (KUBE et al., 1996, ZETTLER, 1996). Moreover, the Baltic coastal waters are characterized by high trophic levels. Our main investigation site, the shallow estuary-like coastal inlet "Darß-Zingster-Boddenkette" (DZBK) is considered to be eutrophic to polytrophic (NAUSCH and SCHLUNGBAUM 1991). Problems of nutrient loaded aquatic biotopes like low and fluctuating oxygen partial pressures, oxygen deficiency and formation of hydrogen sulphide in the sediment, occur additionally and lead to a complex system of stressful conditions. Because of its success *M. cf. viridis* was believed to have remarkable adaptation strategies to be able to live at such an inhospitable habitat.

This study presents new information on the influence of potentially stressful environmental factors, specifically salinity and oxygen partial pressure, on resistance and energetic parameters of various development stages of *M. cf. viridis*. New findings and already published information are summarized to contribute to the description of the polychaetes ecological potency. The energetic parameters measured were energy content of adult individuals and metabolic activity (calorimetry and simultaneous respirometry) of different development stages. The results are compared with those of the polychaete *Nereis (Hediste) diversicolor* (O.F.Müller). *H. diversicolor* is highly suitable as a reference organism since it is wellknown. Its wide ecological tolerance (see KRISTENSEN, 1988) is highly qualified for a measure of the tolerance of *M. cf. viridis*. Moreover, *H. diversicolor* was the only macrobenthic polychaete species inhabiting regions of horohaline salinities with significant abundances before the arrival of *M. cf. viridis* (ARNDT, 1989).

Materials and methods

Organisms

Individuals of the polychaetes *M. cf. viridis* and *H. diversicolor* were sampled in the Southern Baltic coastal inlet Darß-Zingster Boddenkette (DZBK) between 1992 and 1994. For details of procedure and determination of biomass as ash free dry weight (AFDW) see FRITZSCHE and VON OERTZEN, 1995.

Resistance experiments

The polychaetes were acclimated to the experimental conditions for 1 week. The resistance to oxygen deficiency (as achieved by nitrogen bubbling of the experimental water) was determined at temperatures of 5, 10 and 20°C for adult individuals and at 10°C for larvae and juvenile polychaetes. Adult individuals were acclimated to

salinities of 10, 5, 2 and 0.5 PSU, larvae and juveniles to 5 PSU. The salinity of 5 PSU represents an average salinity of the sample site DZBK.

The resistance to salinity was measured with 5-PSU-adapted polychaetes (5 PSU = average habitat salinity) which were exposed to different salinity steps for 48 h (larvae) and 72 h (juveniles and adults). Adult polychaetes were kept at temperatures of 10 and 20°C, larvae and juveniles at 10°C.

The individuals of oxygen deficiency and salinity resistance experiments were exposed in groups comprising 10 specimens of adults and juveniles and 200 to 500 specimens of larvae for each temperature or salinity set. For details and more information about the resistance experiments see FRITZSCHE and VON OERTZEN, 1995 and BOCHERT et al., 1996.

Energy content

Adult individuals of both species were dried for 24 h at a temperature of 60°C. They were then pulverized using a pestle. Pressed tablets of the powder were combusted at pure oxygen (35 at) inside a Parr 1425 Semimicro Bomb Calorimeter (Moline, USA).

Metabolic activity

The metabolic activity of the individuals was measured simultaneously by direct calorimetry and respirometry under steady state conditions. 5- and 25-ml-perfusion chambers within the Thermometric 2277 microcalorimeter (Thermal Activity Monitor, Järfälla, Sweden) were connected to oxygen sensors (2000-100 Eschweiler, Kiel, FRG and Orbisphere 2124, Neuenburg, Switzerland).

Measurements on adult individuals took place at temperatures of 10/20°C and at salinities of 5 PSU (10/20°C) and 0.5 PSU (20°C). Larvae and juveniles were measured at 10°C and 5 PSU. Each measurement started at normoxic conditions. The oxygen partial pressure was stepwise decreased maintaining a steady state of different oxygen partial pressures for certain periods until anoxia was reached.

For technical details and more information about procedure and evaluation see FRITZSCHE and VON OERTZEN, 1995a,b.

Results

Resistance to salinity stress

All examined development stages of *M. cf. viridis*, adapted to a temperature of 10°C and a salinity of 5 PSU, were able to tolerate very low salinities of < 1 PSU (Fig. 1). The resistance (as median lethal concentration of the medium: LC₅₀) in-

creased significantly with ongoing development from 0.77 PSU for larvae with 1-3 setigers up to 0.03 PSU for adult individuals (BOCHERT et al., 1996).

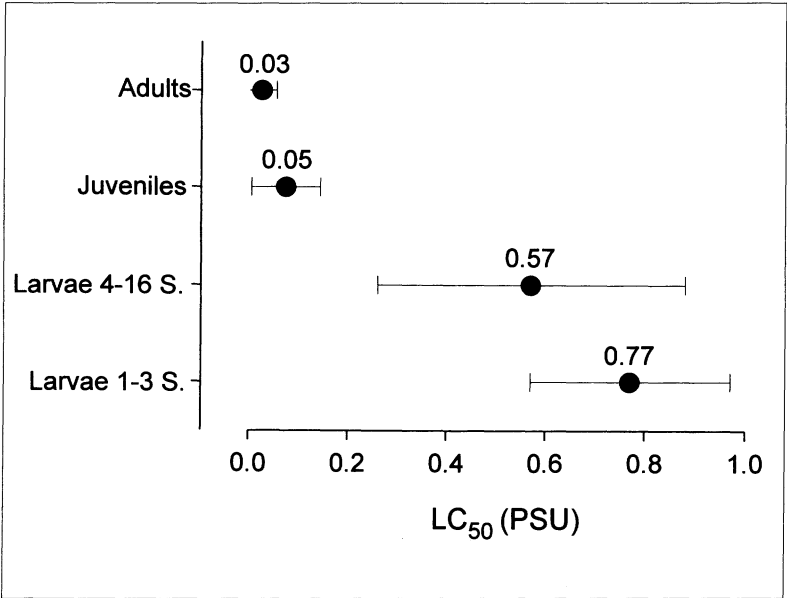


Fig. 1 *M. cf. viridis*: Resistances to low salinities (LC₅₀) and intervals of confidence (t_{0.05}) of various development stages at a temperature of 10°C and an adaptation salinity of 5 PSU, from BOCHERT et al., 1996.

With LC₅₀ of 0.03 and 0.09 PSU adult *M. cf. viridis* reached the similar resistance level to low salinity as adult *H. diversicolor* (0.02 and 0.02 PSU) at temperatures of 10°C and 20°C, respectively (Fig. 2).

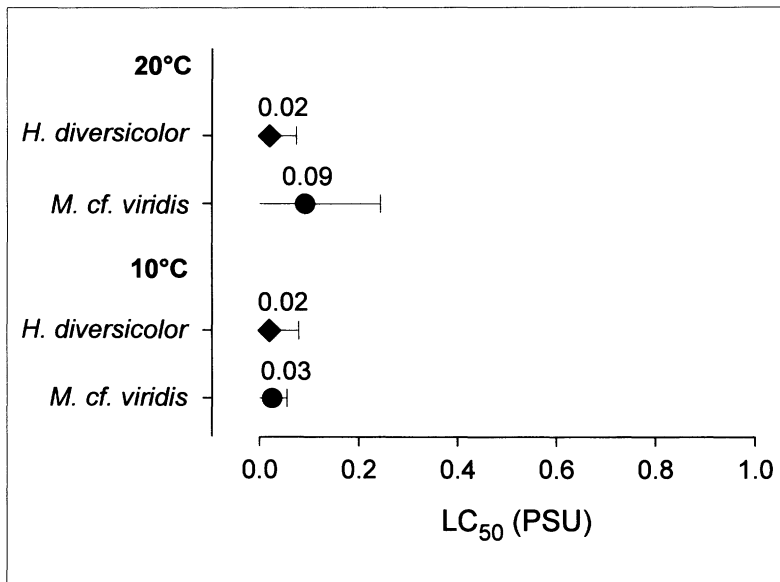


Fig. 2 *M. cf. viridis* and *H. diversicolor*. Resistances to low salinities (LC₅₀) and intervals of confidence (t_{0.05}) of adult individuals at a temperatures of 10°C and 20°C and at an adaptation salinity of 5 PSU.

Resistance to high salinities was > 24 PSU for all development stages of *M. cf. viridis* at a temperature of 10°C and with an adaptation salinity of 5 PSU. LC₅₀ increased from 26.0 PSU for larvae with 1-3 setigers to 29.8 PSU for adult individuals without a significant difference (Fig. 3).

For both temperatures (10°C and 20°C, respectively) adult *M. cf. viridis* showed with LC₅₀ of 29.8 and 25.9 PSU a significant lower resistance to high salinities as adult *H. diversicolor* (43.4 and 36.2 PSU) (Fig. 4).

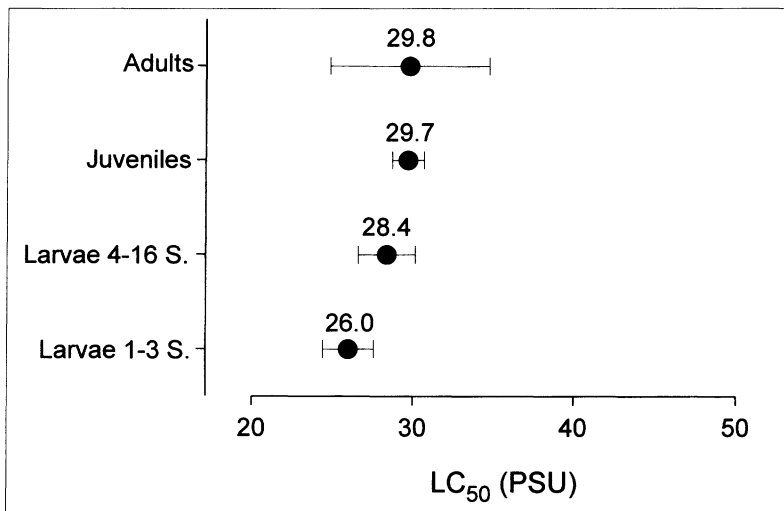


Fig. 3 *M. cf. viridis*: Resistances to high salinities (LC₅₀) and intervals of confidence ($t_{0,05}$) of various development stages at a temperature of 10°C and an adaptation salinity of 5 PSU.

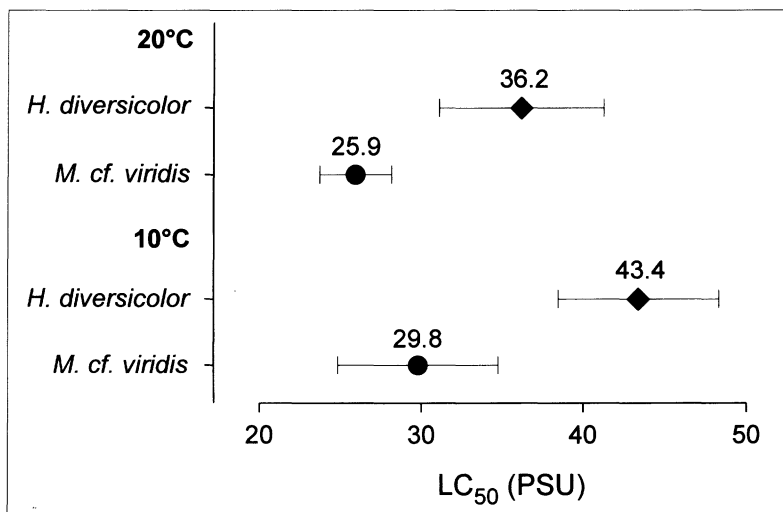


Fig. 4 *M. cf. viridis* and *H. diversicolor*: Resistances to high salinities (LC₅₀) and intervals of confidence ($t_{0,05}$) of adult individuals at a temperatures of 10°C and 20°C and at an adaptation salinity of 5 PSU.

Resistance to oxygen deficiency

At a temperature of 10°C and an adaptation salinity of 5 PSU, all development stages of *M. cf. viridis* were able to survive oxygen deficiency (Fig. 5). The resistance (as median lethal time: LT_{50}) increased exponentially and significantly with the development of the polychaete. Larvae with 1-3 setigers survived anoxia for only 4.2 h whereas adult individuals were able to survive oxygen deficiency for 186 h (more than 1 week).

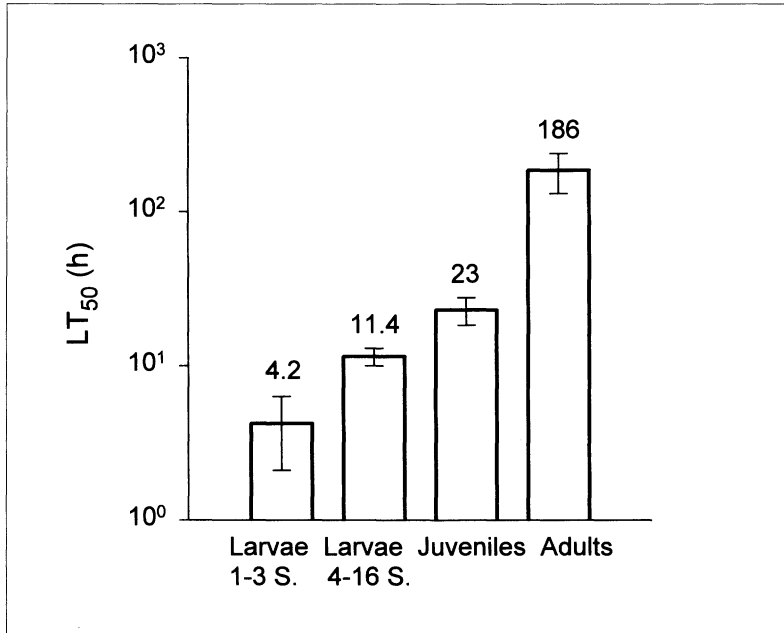


Fig. 5 *M. cf. viridis*: Resistances to oxygen deficiency (LT_{50}) and intervals of confidence ($t_{0.05}$) of various development stages at a temperature of 10°C and an adaptation salinity of 5 PSU.

Adult *M. cf. viridis* reached nearly the same survival times at anoxia as adult *H. diversicolor* (Fig. 6). There was no significant difference between the two species at all temperature-salinity-combinations (FRITZSCHE and VON OERTZEN, 1995b). Highest survival times were determined at a temperature of 5°C and a salinity of 5 PSU: 296 h for *M. cf. viridis* and 312 h for *H. diversicolor*. The resistance to oxygen deficiency decreased for both species with increasing temperature. The difference became significant between 5°C and 20°C and between 10°C and 20°C, respectively. The lowest resistances were registered at a temperature of 20°C and a salinity of 0.5

PSU: 22 h for both *M. cf. viridis* and *H. diversicolor*. Very low salinities also led to a decrease in the survival times. The survival times below a salinity of 5 PSU were significantly different from salinities ≥ 5 PSU at the temperatures of 5°C and 10°C, respectively. At a high temperature of 20°C, the difference became insignificant.

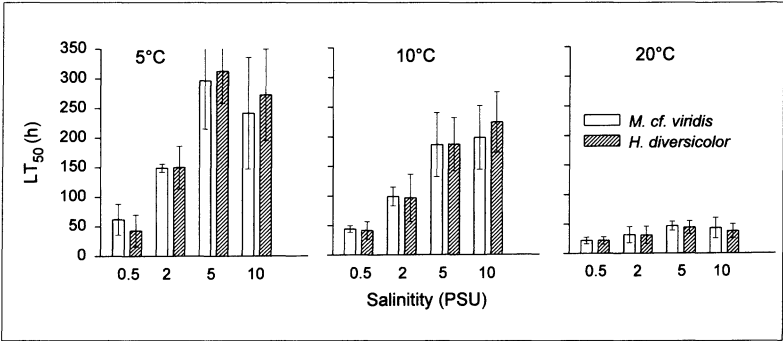


Fig. 6 *M. cf. viridis* and *H. diversicolor*: Resistances to oxygen deficiency (LT₅₀) and intervals of confidence (t_{0,05}) of adult individuals at temperatures of 5, 10 and 20°C and at adaptation salinities of 0.5, 2, 5 and 10 PSU.

Energy content

There was no significant difference between the energy content of adult individuals of both species: 23.02 ± 0.73 J/mgAFDW for *M. cf. viridis* and 22.20 ± 1.10 J/mgAFDW for *H. diversicolor*.

Metabolic activity at normoxia

The biomass related metabolic activity of the different development stages of *M. cf. viridis* at routine activity, measured as heat dissipation at a temperature of 10°C and a salinity of 5 PSU, decreased with the increase of biomass (Fig 7) following a power equation:

$$Q_{BM} = 10.655 \cdot m^{-0.2507} \qquad r^2 = 0.893$$

Q_{BM} : biomass related heat dissipation rate (mJ·h⁻¹·mg⁻¹AFDW)

m : biomass (mgAFDW).

$\dot{Q}_{BM}$ decreased from 28-51 $\text{mJ}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}\text{AFDW}$ for larvae to 2.7-8.9 $\text{mJ}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}\text{AFDW}$ for adult individuals.

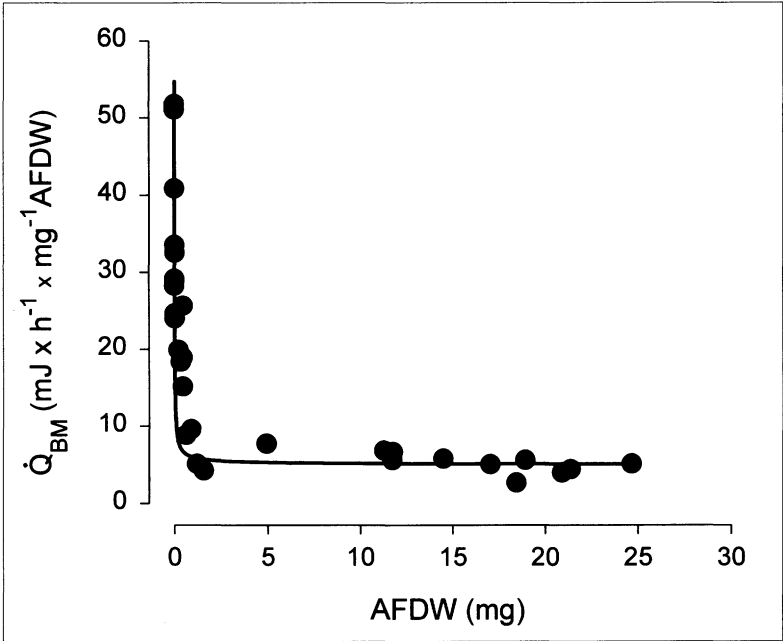


Fig. 7 *M. cf. viridis*: Relationship between biomass and biomass specific rates of metabolic heat dissipation of different development stages at a temperature of 10°C and a salinity of 5 PSU.

The biomass related rates of metabolic activity of adult *M. cf. viridis* were not significantly different from those of *H. diversicolor* for temperatures of 10°C and 20°C, respectively (FRITZSCHE and VON OERTZEN, 1995b).

Metabolic activity at hypoxia

Different development stages of *M. cf. viridis* responded in different ways to declining oxygen partial pressures. At a temperature of 10°C and a salinity of 5 PSU larvae of *M. cf. viridis* were able to maintain their aerobic metabolic activity of a normoxic level down to oxygen partial pressures of below 2 kPa. With ongoing development the pattern of oxygen regulation approached that of the adults, which showed a nonproportional decrease of metabolic activity at declining oxygen partial

pressure including a certain regulation ability (for all see FRITZSCHE and VON OERTZEN, 1995a).

However, adult *H. diversicolor* showed a little more regulating ability at a salinity of 5 PSU compared to *M. cf. viridis*. At an additional low salinity of 0.5 PSU *M. cf. viridis* further reduced its metabolic activity with declining oxygen partial pressure. Its regulation pattern nearly reached that of an oxyconformer. But *M. cf. viridis* was able to meet that further reduced metabolism fully aerobically whereas the measures for *H. diversicolor* had a gap between a further increased heat dissipation and an decreased oxygen consumption, even below an oxygen partial pressure of 10 kPa. These findings indicated an anaerobic metabolic compensation for the energy expenditure of *H. diversicolor* below 10 kPa at the very low salinity of

0.5 PSU (for all findings see FRITZSCHE and VON OERTZEN, 1995b).

Metabolic activity at anoxia

The anaerobic metabolic heat dissipation related to the heat dissipation at normoxia at a temperature of 10°C and a salinity of 5 PSU significantly increased with the development of *M. cf. viridis* from 10.0 % for larvae to 14.0 % for juveniles and 20.2 % for adult individuals (FRITZSCHE and VON OERTZEN, 1995a).

Adult *M. cf. viridis* gave nearly the same anaerobic heat dissipation rates as adult *H. diversicolor* without a significant species difference: about 20 % of the normoxic heat dissipation rates for the following temperature/salinity-combinations: 10°C/5PSU, 20°C/5PSU and 20°C/0.5PSU, respectively (FRITZSCHE and VON OERTZEN, 1995b).

Discussion

Stressful environmental conditions may be described as those which lead to elevated demands on the animal's metabolism (see BAYNE, 1980 and 1985). A balanced relation between energy reserves, metabolic gain and metabolic loss of energy that can buffer additional energy demands due to metabolic responses to stressful conditions is an energetic prerequisite for the survival under stressful conditions. The energetic turnover of an organism can partly describe this. It provides the relation between the daily metabolic loss of energy and the total energy available to the organism.

The energetic turnover can be calculated on the base of the total energy content measured by combustive calorimetry and the rate of metabolic loss measured by heat dissipation. Nearly equal energy contents were measured for the invader *M. cf. viridis* as for *H. diversicolor*, 23.02 and 22.20 J·mg⁻¹AFDW, respectively. These values correspond to a general range of 22.6 - 23.9 J·mg⁻¹AFDW for benthic invertebrates given by WACASEY and ATKINSON, 1987. Nearly the same metabolic activities were measured for both, *M. cf. viridis* and *H. diversicolor*. This results in an equal energetic turnover: An adult polychaete with a biomass of 10 mgAFDW and a bio-

mass related energy content of about 23 J/mgAFDW possesses an absolute energy content of 230 J. On the base of a median routine metabolic heat dissipation rate of $7 \text{ mJ} \cdot \text{h}^{-1} \cdot \text{mg}^{-1} \text{AFDW}$ at a temperature of 10°C (for *M. cf. viridis* see Fig. 7, for both species see FRITZSCHE and VON OERTZEN, 1995b) a heat of 1.68 J within 24 h will be dissipated. This amounts to a daily turnover of 0.73 % of the total energy content of one of these polychaetes.

The daily energetic turnover of 0.73 % for *M. cf. viridis* and *H. diversicolor* is low compared to the available data of two completely different organisms, 48.3 % for the ciliate *Paramecium calicinski* (SCHARF, 1979) and 3.8 % for the mysid *Neomysis integer* (with a biomass of 2-4 mg AFDW, calculated from data in ARNDT and JANSEN, 1986 at a temperature of 20°C). The big difference between the examined polychaetes and the ciliate is clearly caused by the much higher biomass related metabolic activities of small animals as also found for the larvae of *M. cf. viridis* (Fig. 7). But correcting the value of the more equivalent *Neomysis integer* for biomass and for temperature, an equivalent weighting *M. cf. viridis* or *H. diversicolor* would give only half of the energetic turnover of *Neomysis integer*. This is caused by a twofold higher metabolic activity of *Neomysis integer* compared to the polychaetes, which could result from the different mode of living of *Neomysis integer*. The mysid lives on the benthic-pelagic boundary and exhibits higher swimming activities compared to the examined polychaete species.

The relatively low energetic turnover of *M. cf. viridis* and *H. diversicolor* could be a general advantage for surviving energetically stressful conditions since energy reserves would not be depleted so quickly. Exhibiting nearly equal energetic turnover rates, *M. cf. viridis* possesses the same range of energetic prerequisites to match stress as *H. diversicolor*.

With a LC_{50} of < 1 PSU (Fig. 1) all examined development stages of *M. cf. viridis* were highly resistant to very low salinities. Adult *M. cf. viridis* with $\text{LC}_{50} < 0.1$ PSU showed nearly the same resistance to low salinities as *H. diversicolor* (Fig. 2). Compared to other data of marine and brackish water polychaetes such high resistances were only given yet for *H. diversicolor*: 0 PSU by HOHENDORF, 1963 and THEEDE et al., 1973. *H. diversicolor* has been characterized as an euryhaline species by different authors (HOHENDORF, 1963, THEEDE et al., 1973, KRISTENSEN, 1988). Other polychaetes which also have high resistances to low salinities were discussed to be genuine brackish water species (ARNDT, 1989, MICHAELIS et al., 1992 and REMANE, 1958): *Alkmaria romijni* with a LC_{50} of 0.3-0.7 PSU (ARNDT, 1973) and *Streblospio shrubsoli* with a LC_{50} of 0.4-0.6 PSU (NAUSCH, 1982). Compared to the other polychaetes *M. viridis* can be described as highly tolerant to very low salinities. Nevertheless there is a critical salinity of 5 PSU below which the development of *M. cf. viridis* cannot be completed (BOCHERT et al., 1996). Field investigations confirmed this critical salinity as a lower boundary for larval settlement (KUBE et al., 1996). But even larvae with more than 4 setigers can finish development at salinities of only 3.5 PSU (BOCHERT et al., 1996). Nevertheless the high short time tolerance of even larvae enables them to match transient periods of very low salinities. That can be an important advantage for colonizing oligohaline waters.

The high-salinity resistance of *M. cf. viridis* of > 24 PSU for all development stages is sufficient to survive salinity shifts as they could occur in the Baltic. But it was very low compared to the resistance of *H. diversicolor* (Fig. 4) and to data of other polychaetes. Even the polychaetes *Alkmaria romijni* and *Streblospio shrubsoli*, considered to be genuine brackish water species, were able to resist to higher salinities: 36.3-40.6 PSU (ARNDT, 1973) and 45.6-57.0 PSU (NAUSCH, 1982), respectively. This finding supports the hypothesis that *M. cf. viridis* is probably genetically adapted to brackish water conditions. This is also reflected in the Baltic habitats of *M. cf. viridis* showing highest abundances at low Baltic salinities between 5 and 8 PSU (Zettler et al., 1995, KUBE et al., 1996).

All examined development stages of *M. cf. viridis* were able to survive anoxic conditions (Fig. 5). WIDDOWS et al., 1989 and WANG and WIDDOWS, 1991, also described the ability of even larvae of the euryoxic mussels *Crassostrea virginica* and *Mytilus edulis* to resist to oxygen deficiency for a short time. It shows that anaerobic capacity can be evolved early during individual development of euryoxic species. The resistance to oxygen deficiency increased exponentially with the development of *M. cf. viridis*. There are two main reasons for that: 1. The biomass related metabolic activity decreases potentially with the increase of biomass (Fig. 7). The exponent of the power equation of -0.2507 coincided with the values around -0.3, summarized by NEWELL, 1970. Substrate storages for that relation will be depleted more slowly in bigger individuals. 2. Biomass related energy storages grow as the individuals grow (for the glycogen content of juvenile *Arenicola marina*: SCHIEDEK and SCHÖTTLER, 1990). Substrate storages, therefore, can supply sufficient fuel for a longer time.

The resistances to oxygen deficiency of adult individuals of *M. cf. viridis* and *H. diversicolor* of around 300 h (Fig. 6) are among the longest recorded for marine and brackish water polychaetes until now. Most other euryoxic polychaetes exhibit lower resistances (LT₅₀ and temperature): < 120 h at 12°C for *Arenicola marina* (SCHÖTTLER and GRIESHABER, 1988), 132 h at 10°C for *Nephtys ciliata* (DRIES and THEEDE, 1974), 240 h at 12°C for *Cirriformia tentaculata* (BESTWICK et al., 1989). Both, *M. cf. viridis* and *H. diversicolor* reach the level of resistance of euryoxic mussels (see DRIES and THEEDE, 1974). *M. cf. viridis*, therefore, can be considered as highly adapted to oxygen deficiency related habitats.

Temperature significantly influenced the survival times at anoxia (Fig. 6). High temperatures led to very low survival times. Resistance is at its lowest in summer, just when oxygen deficiency is more likely to occur. But even at a temperature of 20°C both species were able to survive anoxia for nearly 2 days at moderate salinities. This ability should be sufficient for surviving in shallow coastal waters, since a complete absence of pelagic oxygen for longer than diurnal periods is improbable.

Very low salinities significantly decreased the resistance to oxygen deficiency in both *M. cf. viridis* and *H. diversicolor*. The influence became significant below a salinity of 5 PSU. This is a further indication for a critical salinity of approximately 5 PSU (see above) that could act selectively. Demands on osmoregulation increase at very low salinities. There are indications of a breakdown of osmoregulation as the main cause of death during anoxia at very low salinities (see FRITZSCHE and VON

OERTZEN, 1995b). Nevertheless survival times reached nearly one day at a very low salinity of 0.5 PSU, even related to the rate of catabolized substrates a lower me-

In contrast to adult individuals, larvae of *M. cf. viridis* were shown to maintain metabolic activity completely oxygen independent down to severe hypoxia (FRITZSCHE and VON OERTZEN, 1995a). Similar findings were given for larvae of other species (WIDDOWS et al., 1989, for *Crassostrea virginica* and WANG and WIDDOWS, 1991, for *Mytilus edulis*) or for other very small animals (GNAIGER, 1993, for *Cyclops abyssorum*). The relation between the oxygen partial pressure and the metabolic activity of an animal depends on the ability to extract and transport oxygen since the critical oxygen partial pressure for saturation of the oxidative capacity of mitochondria is < 0.03 kPa (see PÖRTNER and GRIESHABER, 1993). Small animals are less oxygen diffusion limited than big animals (see HERREID, 1980 and GRAHAM, 1990). Therefore, the high metabolic activities of larvae at very low oxygen cannot be interpreted as active regulation of oxygen consumption. Nevertheless, they could provide energy for the maintenance of normal life functions like feeding and growth as it was shown for larvae of *Crassostrea virginica* and *Mytilus edulis* (WIDDOWS et al., 1989 and WANG and WIDDOWS, 1991). Very low oxygen partial pressures, therefore, seem to have no restrictive influence on the larval development.

Adult *M. cf. viridis* were shown to reduce their metabolic activities with declining oxygen partial pressures but also sustaining a certain regulating ability. An additional low salinity led to a further reduction of metabolic activity at hypoxia, whereas *H. diversicolor* increased its metabolic activity on the help of anaerobic metabolism (FRITZSCHE and VON OERTZEN, 1995b). The strategy of reduction of the metabolic activity of *M. cf. viridis* could be more energy saving than that of *H. diversicolor*. But a higher metabolic activity could also be advantageous when met fully aerobically as for *H. diversicolor* at reduced oxygen partial pressures on a moderate salinity of 5 PSU. Thus, *H. diversicolor* is probably not forced to reduce normal life functions like feeding or locomotory movement. But the strategy of the maintenance of high metabolic activities becomes disadvantageous when depending on a partly anaerobic metabolism as for *H. diversicolor* at hypoxia at a very low salinity of 0.5 PSU. The substrate flux during such high activities increases manyfold, since anaerobic pathways are energetically less efficient compared to aerobic pathways (for relation to calorimetric measures see GNAIGER, 1980). This, consequently, leads to a more rapid depletion of energy reserves. Thus, the energy saving strategy of reduced metabolism by *M. cf. viridis* becomes energetically and ecologically more efficient.

Adult individuals of both, *M. cf. viridis* and *H. diversicolor* reduced their metabolic heat dissipation at anoxia to about 20 % of the normoxic level whereas larvae and juveniles of *M. cf. viridis* exhibited a lower heat dissipation (FRITZSCHE and VON OERTZEN, 1995b). When related to the rate of catabolized substrates a lower metabolic activity should lead to higher resistances to anoxia since substrate reserves will be depleted less quickly. But larvae and juvenile *M. cf. viridis* were not as able to resist oxygen deficiency as adults (Fig. 5). The lower rates of metabolic heat dissipation, therefore, could be related to a lower ability to anaerobiosis and to the much higher biomass related metabolic activity of larvae (Fig. 7). The equal anaerobic rates for adults of *M. cf. viridis* and *H. diversicolor* are reflected in nearly equal resi-

stances to oxygen deficiency (Fig. 6). This indicates equally efficient anaerobic pathways for *M. cf. viridis* and *H. diversicolor*, respectively.

Conclusions

M. cf. viridis revealed at least equally potent responses to the stressful environmental conditions of low salinity and low oxygen partial pressures / anoxia compared to the euryoicous *H. diversicolor*. Even the larvae of *M. cf. viridis* were shown to be highly tolerant. The Baltic coastal waters range of salinity and oxygen partial pressure gives suitable conditions for *M. cf. viridis*. There is a critical salinity below 5 PSU which acts selectively in combination with oxygen deficiency. There are indications for a genetic adaptation to brackish waters for *M. cf. viridis*.

Acknowledgements

I wish to thank Dr. J.-A. von Oertzen for his critical and helpful supports and discussions of my works. This study was supported by the BMBF, FRG, FKZ: 03F0031A.

References

- ARNDT, E.A., (1989). Ecological, physiological and historical aspects of brackish water fauna distribution. In: Ryland, J.S., Tyler, P.A. (eds.) Proc. 23rd Eur. Mar. Biol. Symp. Swansea UK, Olsen & Olsen, Fredensborg: 327-338.
- ARNDT, E.A. and JANSEN, W., (1986). *Neomysis integer* (Leach) in the chain of Boddens south of Darss / Zingst (Western Baltic) - Ecophysiology and population dynamics. Ophelia suppl. 4: 1-15.
- ARNDT, E.A., (1973). Ecophysiological and adaptational problems confronting animals living in brackish water. Oikos suppl. 15: 239-245.
- BAYNE, B., (1980). Physiological measurement of stress. Rapp. P. V. Réun. Cons. Int. Explor. Mer. 179: 56-61.
- BAYNE, B., (1985). Responses to environmental stress: Tolerance, resistance and adaptation. In Gray J.S., Christiansen M.E. (eds.): Marine biology of Polar regions and effects of stress on marine organisms. London.
- BESTWICK, B.W., ROBBINS, I.J., WARREN, L.M., (1989). Metabolic adaptations of the intertidal polychaete *Cirriiformia tentaculata* to the life in an oxygen-sink environment. J. Exp. Mar. Biol. Ecol. 125: 193-202.
- BOCHERT, R., FRITZSCHE, D., BURCKHARDT, R. (1996). Influence of salinity and temperature on growth and survival of the planctonic larvae of *Marenzelleria viridis* (Polychaeta, Spionidae). J. Plankt. Res. 18 no.7: 1239-1251.
- DRIES, R.R. and THEEDE, H., (1974). Sauerstoffmangelresistenz mariner Bodenevertebraten aus der westlichen Ostsee. Mar. Biol. 25: 327-333.
- FRITZSCHE, D. and VON OERTZEN, J.A., (1995a). Bioenergetics of a highly, adaptable brackish water polychaete, *Thermochimica Acta* 251: 1-9.
- FRITZSCHE, D. and VON OERTZEN, J.A., (1995b). Metabolic responses to changing environmental conditions in the brackish water polychaetes *Marenzelleria viridis* and *Hediste diversicolor*. Mar. Biol. 121: 693-699.
- GNAIGER, E., (1980). Das kalorische Äquivalent des ATP-Umsatzes im aeroben und anoxischen Metabolismus. *Thermochimica Acta* 40: 195-223.
- GNAIGER, E. (1993). Adaptation to winter hypoxia in a shallow alpine lake. Ecophysiological energetics of *Cyclops abyssorum* and rainbow trout. Verh. Dtsch. Zool. Ges. 86.2: 43-65.

- GRAHAM, J.B., (1990). Ecological, evolutionary and physical factors influencing aquatic animal respiration. *Amer. Zool.* 30: 137-146.
- HERREID, C.F., (1980). Hypoxia in invertebrates. *Comp. Biochem. Physiol.* 67A: 311-320.
- HOHENDORF, K., (1963). Der Einfluß der Temperatur auf die Salzgehaltstoleranz und Osmoregulation von *Nereis diversicolor* O.F. Muell. *Kieler Meeresforschungen* XIX: 196-218
- KINNE, O., (1971). 4 Salinity, 4.3 Animals, 4.31 Invertebrates. In: Kinne, O. (ed.) *Marine Ecology*, Vol 1, Part 2, London: 821-995.
- KRISTENSEN, E., (1988). Factors influencing the distribution of nereid polychaetes in Danish coastal waters. *Ophelia* 29: 127-140.
- KUBE, J., ZETTLER, M.L., GOSSELCK, F., OSSIG, S., POWILLEIT, M. (1996). Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the southwestern Baltic Sea in 1993/94 - ten years after introduction. *Sarsia* 81: 131-142.
- MICHAELIS, H., FOCK, H., GROTHJAHN, M., POST, D. (1992). The status of the intertidal zoobenthic brackish-water species in estuaries of the German Bight. *Neth. J. Sea Res.* 30: 201-207
- NAUSCH, G. and SCHLUNGBAUM, G. (1991). Eutrophication and restoration measures in the Darß-Zingst bodden chain. *Int. Revue Ges. Hydrobiol.* 76: 451-463.
- NAUSCH, M. (1982). Experimentell-ökologische Untersuchungen an Polychaeten der Darß-Zingster Boddenengewässer. PhD-thesis, Wilhelm-Pieck-Universität, Rostock: 1-128.
- NEWELL, R.C. (1970). *Biology of intertidal Animals*. London.
- PÖRTNER, H.O. and GRIESHABER, M.K. (1993). Critical PO_2 (s) in oxyconforming and oxyregulating animals: gas exchange, metabolic rate and the mode of energy production. In: Eduardo J., Bicu-do P.W. (eds.): *The vertebrate gas transport cascade - adaptations to environment and mode of life*. CRC Press, Boca Raton: 330-357.
- REMANE, A. (1958). Ökologie des Brackwassers. in Thienemann, A. (ed.): *Die Biologie des Brackwassers*. Stuttgart, 1-213.
- SCHARF, E.M. (1979). Die Bedeutung benthischer heterotropher Protozoen (Ciliaten) im Stoffkreislauf und Energiefluß eines mesohalinen Brackgewässers (Barther Bodden). PhD-thesis, Wilhelm-Pieck-Universität, Rostock: 1-145.
- SCHIEDEK, D. and SCHÖTTLER, U., (1990). The energy production of juvenile *Arenicola marina* (Polychaeta) under anoxic and hypoxic conditions. *Helgoländer Meeresuntersuchungen* 44: 135-145
- SCHÖTTLER, U. and GRIESHABER, M.K. (1988). Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. *Mar. Biol.* 99: 215-222.
- THEEDE, H., SCHAUDINN, J., SAFFÉ, F., (1973). Ecophysiological studies on four *Nereis* species of the Kiel Bay. *Oikos Suppl.* 15: 246-252.
- WACASEY, J.W. and ATKINSON, E.G., (1987). Energy values of marine benthic invertebrates from the Canadian Arctic. *Mar. Ecol. Prog. Ser.* 39: 243-250.
- WANG, W.X. and WIDDOWS, J., (1991). Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia. *Mar. Ecol. Progr. Ser.* 70: 223-236.
- WIDDOWS, J., NEWELL, R.I.E., MANN, R., (1989). Effects of hypoxia and anoxia on survival, energy metabolism and feeding of oyster larvae (*Crassostrea virginica*, Gmelin). *Biol. Bull. mar. biol. Lab. Woods Hole* 177: 154-166.
- ZETTLER, M.L., (1996). Successful establishment of the spionid polychaete, *Marenzelleria viridis* (Verrill, 1873), in the Darß-Zingst estuary (southern Baltic) and its influence on the indigenous macrozoobenthos. *Arch. Fish. Mar. Res.* 43(3): 273-284.
- ZETTLER, M.L., BICK, A., BOCHERT, R., (1995). Distribution and population dynamics of *Marenzelleria viridis* (Polychaeta, Spionidae) in a coastal water of the southern Baltic. *Arch. Fish. Mar. Res.* 42(3): 209-224

Author

Dr. Dirk Fritzsche
Rheingasse 4
D-78462 Konstanz

Fax: ++49 7531 914246