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Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions

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Abstract

The anaerobic metabolism of the intertidal polychaete *Scoloplos armiger*, its recovery from anaerobiosis and the importance of anaerobic energy production during low tide in the field were investigated. Under anaerobic conditions *S. armiger* produces energy in the same manner as *Arenicola marina*, a prototype of an euryoxic invertebrate from the intertidal. Energy is produced from the phosphagen stores and from the breakdown of glycogen to volatile fatty acids, mainly propionate and to a lesser extend acetate. However, *S. armiger* cannot reduce its energy demand to the same degree as *A. marina*. This and the relatively small pool of glycogen may be the reason for its only moderate resistance to anoxia. The recovery from anaerobiosis proceeds in *S. armiger* significantly slower than in *A. marina*. *S. armiger* is able to maintain a fully aerobic metabolism down to a Pw_{O_2} of ca. 20 torr and even at a Pw_{O_2} of ≤ 10 torr a partly aerobic metabolism was retained. In the field during low tide *S. armiger* ascends into the oxidative layer, where it is able to maintain an aerobic metabolism even at parts without remaining puddels on the surface.

Introduction

In the sheltered tidal flats of the Wadden Sea only the first millimeters below the sediment surface contain oxygen, while the deeper layers are anoxic. Nevertheless, the first 20 to 30 cm of the sediment permanently harbour a rich diversity of invertebrates. The larger animals, the so called macrofauna, obtain oxygen from the oxygen saturated water above the sediment surface. Polychaetes such as *Arenicola marina* or *Nereis* species irrigate their burrows with this oxygenated water. Molluscs like *Mya arenaria* or *Scrobicularia plana* pump it down through their siphons. Meiofauna, which have no direct contact to the surface water, live preferentially in the upper centimeters or in deeper layers near the oxygenated burrows of the larger animals (Reise and Ax 1979). For all members of the infauna, oxygen supply becomes problematic at low tide, when the tidal flats are exposed. Under these conditions, no surface water can be pumped and the animals must obtain oxygen from the atmosphere, or produce energy by anaerobic metabolism. The first alternative is only possible for animals living near the surface, such as the mollusc *Cerastoderma edule* (Boyden 1972). So, it is not surprising that all animals from this habitat studied up to now are euryoxic, meaning they are able to exist for some time, usually several days, without oxygen.

The pathways involved in anaerobic energy production have been studied intensively during the past 15 yr, mainly on the mussel *Mytilus edulis* and the lugworm *Arenicola marina* (for reviews see Grieshaber 1982, de Zwaan 1983, de Zwaan and v. d. Thillart 1985, Zebe and Schöttler 1986). During prolonged anaerobiosis, these animals break down glycogen via malate to the volatile fatty acids propionate and acetate. Compared with anaerobic glycolysis these pathways are advantageous, because the energy yield is nearly doubled. The aim of the study presented here was to investigate to what extent the metabolic adaptations found in *A. marina* are also realized in *Scoloplos armiger*.

Scoloplos armiger is a thin, pale-red coloured polychaete worm, up to 12 cm long. It is a common inhabitant of sand sediments in tidal flats of the North Sea coast. *S. armiger* was chosen because: (1) it does not live in solid burrows (the worm only produces a transient cover of mucus, which it leaves after a short time), and (2) in contrast to *Arenicola marina*, it only lives in the upper 12 cm of the sediment.

Material and methods

Animals

Scoloplos armiger was sieved from a tidal flat in List/Sylt with a 1 mm mesh sieve and stored in well-aerated artificial,

circulating seawater (32‰ S) at 8 °C for several weeks in tanks containing a 2-cm layer of sand.

Experimental procedure

All experiments were performed at 12 °C. Prior to their use in the experiments the worms were adapted to this temperature in well-aerated artificial seawater (32‰ S) for 48 h. For the incubations 250-ml round flasks equipped with special fittings for gassing (Schöttler and Schroff 1976) were used. The flasks were filled with 100 ml of the seawater and gassed for 30 min with nitrogen. Thirty worms with an average weight of 70 ± 20 mg were added and gassing continued for further 30 min, after which the stop-cocks were closed.

Incubations at different Pw_{O_2} values

All gas mixtures were prepared from pure nitrogen and pure oxygen by means of a gas mixing pump (M 1007a, Wösthoff, Bochum, FRG)

Determination of oxygen uptake at different Pw_{O_2}

The oxygen uptake at different Pw_{O_2} was measured in a flow-through system. The animals were incubated in special chambers with a 5 cm layer of sterilized fine sand (125 to 250 µm grain diam.). The rate of oxygen consumption was measured continuously with an Orbisphere oxygen electrode (Model 2115 connected to an oxygen indicator Orbisphere 2609).

Preparations of extracts

At the end of an incubation period the worms were rapidly blotted on paper tissue and freeze-clamped. The frozen animals were extracted with 3 Mol l^{-1} perchloric acids as described earlier (Schöttler 1978).

Determination of metabolites

L-alanine, D-alanine, aspartate, malate, succinate, ATP, adenosine diphosphate (ADP), AMP, creatine phosphate were estimated by standard enzymatic methods (Bergmeyer 1974). Glycocyaminephosphate was measured by a system corresponding to the phosphocreatine assay, using glycocyamine kinase, which was prepared from the body-wall musculature of *Nereis virens* (Schöttler 1982a). Strombine and alanopine were measured by HPLC (Siegmund and Grieshaber 1983). The volatile fatty acids propionate and acetate were measured by gas-liquid chromatography after steam distillation of the perchloric extracts (Kluytmans et al. 1975).

All results are presented as mean values ± SD. Significance was determined by Student's *t*-test $t_{0.05}$.

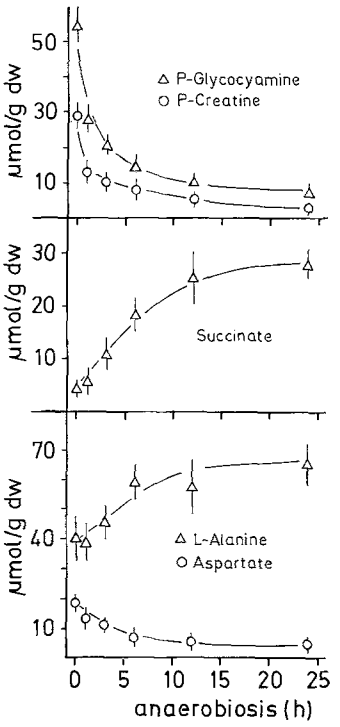

Fig. 1. *Scoloplos armiger*. Concentrations of phosphagens P-glycocyamine and P-creatine, of succinate and amino acids L-alanine and aspartate after different periods of anaerobiosis. (Mean values ± SD, $N=4$)

Enzyme assays

Ten worms were homogenized four times in a tenfold volume of 0.1 mol l^{-1} K-phosphate buffer (pH 7.4) in an Ultra-Turrax 10N homogenizer at full speed (total homogenizing time 1 min). The homogenate was centrifuged at 48 000 × g for 30 min, the supernatant was passed through a Sephadex G-25 column, the enzymes appearing in the void volume. All steps were performed at 0 to 4 °C and all enzymes measured within 5 h after homogenizing.

The activities of the following enzymes were measured at 25 °C:

Lactate dehydrogenase (E.C. 1.1.1.27) according to Schöttler (1978), Strombine dehydrogenase (E.C. 1.5.1.?) and Alanopine dehydrogenase (E.C. 1.5.1.?) according to Schöttler (1982b) and Octopine dehydrogenase according to Gäde and Carlson (1984).

Results

Experimental anoxia

Under anaerobic conditions at 12 °C *Scoloplos armiger* survived at the utmost for ca. 40 h. Time course experiments were therefore limited to 24 h. The results are shown in Figs. 1 and 2. In the first hours after onset of anaerobic conditions *S. armiger* mobilises its phosphagen stores, which consist of P-glycocyamine and P-creatine in an initial ratio

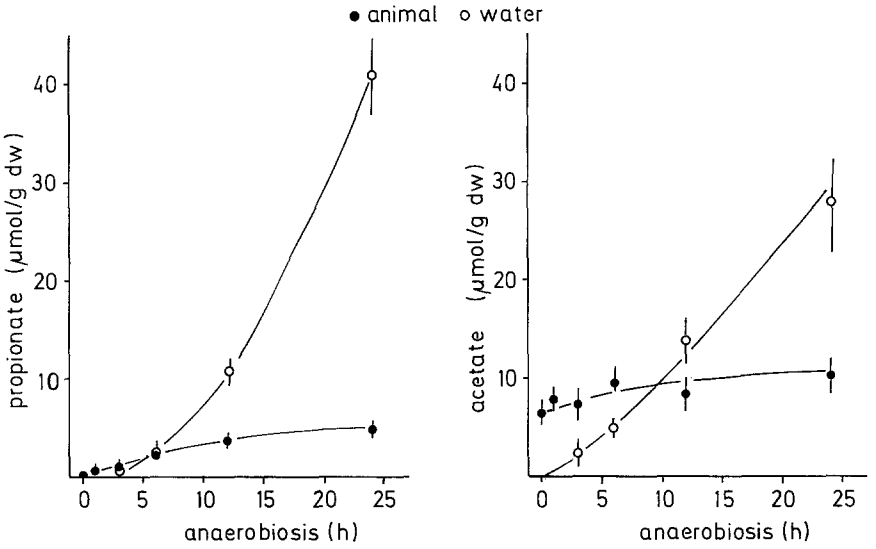

Fig. 2. *Scoloplos armiger*. Production of volatile fatty acids propionate and acetate after different periods of anaerobiosis. (Mean values ±SD, $N=4$)

Table 1. Activities of NADH-dependent pyruvate reductases. U g^{-1} fresh wt, 25 °C, mean values ± SD ($N=6$)

	U g fresh wt^{-1}
Lactate dehydrogenase	0.8± 0.4
Strombine dehydrogenase	96.7±13.6
Alanopine dehydrogenase	73.8± 9.1
Strombine dehydrogenase	–

Table 2. *Scoloplos armiger*. Concentrations of adenine nucleotide and calculated energy charge after different periods of anaerobiosis. (Mean values ± SD, $N=4$, 30 individuals per incubation vessel, µmoles g dry wt^{-1})

Control	ATP	ADP	AMP	Σ	Energy charge
	8.02±0.63	1.74±0.46	0.34±0.05	10.1	0.880
1 h N_2	6.60±0.81	2.58±0.26	0.64±0.14	9.82	0.803
3 h N_2	5.89±0.62	2.70±0.51	0.77±0.04	9.34	0.775
6 h N_2	6.51±1.19	2.71±0.48	0.82±0.13	10.04	0.783
12 h N_2	5.95±1.04	2.99±0.41	1.02±0.19	9.96	0.747
24 h N_2	5.07±0.57	3.05±0.41	1.42±0.21	9.54	0.691

Table 3. *Scoloplos armiger*. Glycogen content after anaerobic incubation (µmol glycosyl units g dry wt^{-1}). Mean value ± SD ($N=6$)

Incubation time (h)	Glycogen
0	121±19
12	81±23
24	67±15

of 2:1. In the first hour more than 40 µmoles g dry wt^{-1} are degraded, and after 6 h this store is nearly depleted. In contrast to the rapid mobilisation of phosphagens, energy production by glycolysis or the typical anaerobic pathways, leading to succinate and volatile fatty acids, is slow. After 1 h of anaerobiosis, neither succinate, alanine or an opine had accumulated significantly.

However, after anoxic periods of more than 6 h, energy is mainly produced by the pathways leading to succinate and volatile fatty acids. After 12 h only propionate and acetate were produced. Both acids were excreted nearly quantitatively (Fig. 2).

Between 1 and 6 h after onset of anaerobic conditions, some energy was also produced by glycolysis, with L-alanine as end product. D-alanine which is in *Arenicola marina* also an end product (Felbeck 1980) was detected only in traces. During the same time in which L-alanine was accumulated, aspartate was mobilized.

Although in *Scoloplos armiger* tissue contains high activities of alanopine and strombine dehydrogenase (Table 1), no significant accumulation of the corresponding end products was measured in this experiment. The energy charge declined during 24 h of anaerobiosis from 0.88 to 0.69, but the content of adenine nucleotides remained constant (Table 2). Nearly half of the glycogen stored was degraded within 24 h (Table 3).

Recovery after experimental anaerobiosis

Although anaerobiosis may be a necessary adaptation to the periodic hypoxia or even anoxia that occurs in tidal flats during low tide, it does nevertheless represent a stress, even to an euryoxic animal. So, the capability of recovering rapidly when oxygen returns during the rising tide is of great importance, too. The recovery of *Scoloplos armiger* after 20 h of experimental anaerobiosis was therefore investigated. The data presented in Fig. 3 show that the energy charge is re-established within 2 to 3 h. The stores of P-glycocyamine and P-creatine were replenished by more than 80% within 3 h. After 6 h the levels were not significantly different from the controls. The accumulated succinate (Fig. 4) disappeared significantly within 1 h after onset of aerobic conditions and ca. ½ was metabolized within 3 h. However, even after 12 h the succinate concentration was still significantly higher than in controls. Fig. 4 also

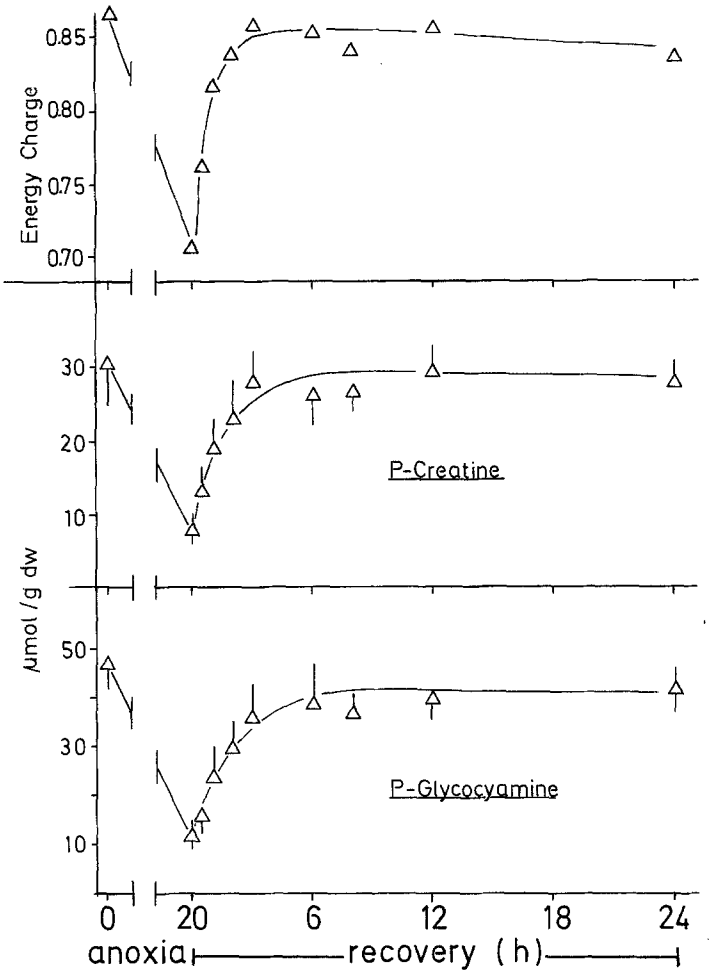

Fig. 3. *Scoloplos armiger*. Concentrations of phosphagens P-glycocyamine and P-creatine and calculated energy charge during recovery after 20 h of anaerobiosis. (Mean values ± SD, $N=4$)

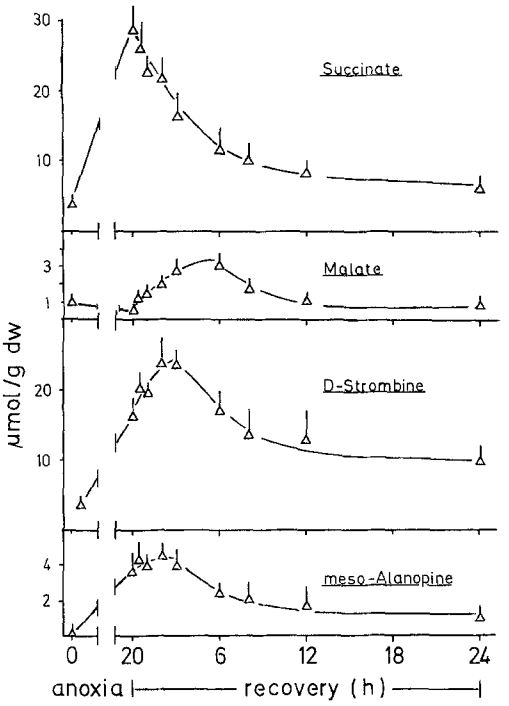

Fig. 4. *Scoloplos armiger*. Concentrations of succinate, malate, D-strombine and meso-alanopine during recovery after 20 h of anaerobiosis. (Mean values ± SD, $N=4$)

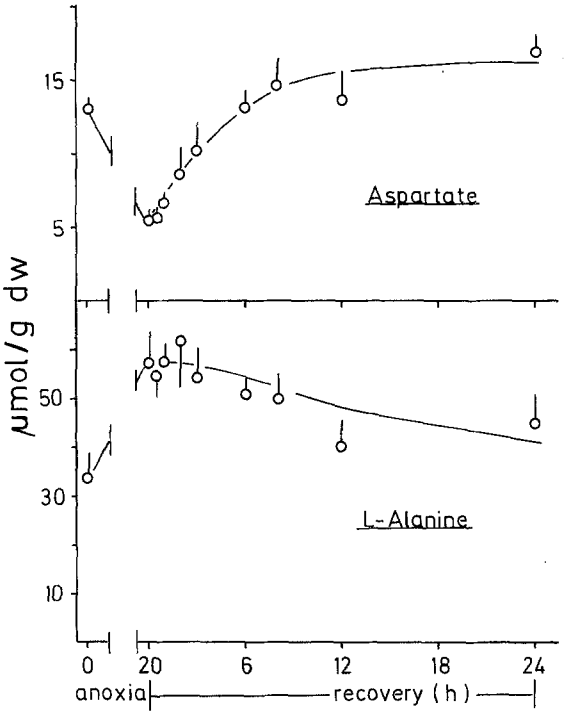

Fig. 5. *Scoloplos armiger*. Concentrations of L-alanine and aspartate during recovery after 20 h of anaerobiosis (Mean values ± SD, $N=4$)

shows that after returning to aerobic conditions the content of malate increased from 1 µmol g dry wt^{-1} to more than 3 µmoles within 6 h. Thereafter it decreased and 12 h after onset of aerobic conditions the level of the controls was reached again. In contrast to the first experiments in this series, D-strombine and to a lesser extent alanopine were accumulated significantly under anaerobic conditions. During recovery the concentration of alanopine remained constant for 3 h, then decreased after 6 h and returned to the level of the control after 24 h. Contrary to all other endproducts of anaerobic metabolism, D-strombine was accumulated even further in the first 2 to 3 h of recovery. A first decrease was measured after 6 h, but even after 24 h concentrations were significantly higher than in controls. The control level of aspartate was restored after 6 h, whereas the degradation of alanine, due to great individual variations, was not significant until 12 h after recovery begin (Fig. 5).

Metabolite levels during low tide

In this series we investigated whether or not anaerobiosis occurs in the natural habitat. As shown in Table 4, the concentrations of the individual adenine nucleotides remained unchanged during the 6 h of ebbing tide. Hence the energy charge was constant at 0.79. The concentrations of P-glycocyamine and P-creatine seemed to be unaffected in the first 3 h (Table 5). After 6 h a small but significant decrease was established. The concentrations of other me-

tabolites, which are known to change in a characteristic manner during anoxia, were not affected.

Anaerobic metabolism at different oxygen tensions

Since we could detect no real indications for an anaerobic energy metabolism in the natural habitat, we investigated the lowest Pw_{O_2} at which *Scoloplos armiger* is able to maintain an aerobic metabolism. The worms were exposed for 24 h to different Pw_{O_2} levels, which are maintained by continuously gassing the incubation vessels with O_2/N_2 mixtures.

As shown in Fig. 6, the energy charge and the contents of the phosphagens remained constant down to a Pw_{O_2} of 30 torr. At a Pw_{O_2} of 22 torr a slight decrease was recorded, but it was only significant at a Pw_{O_2} below ca. 16 Torr. At a Pw_{O_2} of 8 Torr the phosphagen stores were degraded nearly to the same degree as under anoxic conditions, but the energy charge was higher (0.72 vs 0.68).

The production of succinate and the volatile fatty acids propionate and acetate was first measured at a Pw_{O_2} of 16 Torr (Fig. 7). At 8 torr the accumulation of succinate was in the same range as under anaerobic conditions, whereas the production of propionate and acetate was quite lower. Due to great individual variations no significant changes in the contents of L-alanine and aspartate could be detected until a Pw_{O_2} of 8 Torr (Fig. 8).

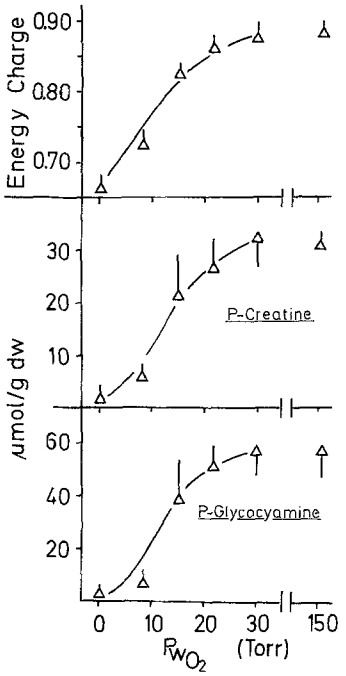

Fig. 6. *Scoloplos armiger*. Calculated energy charge and concentrations of phosphagens P-glycocyamine and P-creatine after 24 h of incubation at different Pw_{O_2}. (Mean values ±SD, $N=4$)

Table 4. *Scoloplos armiger*. Concentrations of adenine nucleotides during a low tide in May 1986 (mean values ± SD, $N=6$, µmoles g dry wt^{-1})

Time of exposure (h)	ATP	ADP	AMP	Σ	Energy charge
0	4.51±0.89	1.58±0.23	0.54±0.07	6.63	0.799
1	4.97±0.87	1.82±0.36	0.61±0.10	7.40	0.795
3	5.56±1.12	1.84±0.54	0.64±0.21	8.04	0.806
6	4.51±0.83	1.80±0.72	0.58±0.22	6.89	0.785

Aerobic metabolism at different oxygen tensions

The oxygen consumption at different oxygen tensions was examined in two series, the first in April 1986 and the second

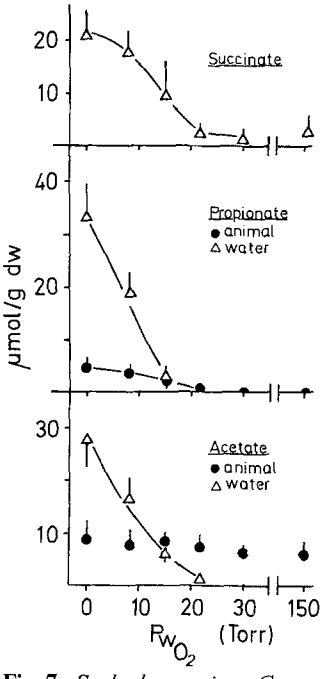

Fig. 7. *Scoloplos armiger*. Concentrations of succinate, propionate and acetate after 24 h of incubation at different Pw_{O_2}. (Mean values ±SD, $N=4$)

Table 5. *Scoloplos armiger*. Concentrations of phosphagens and of succinate, L-alanine and aspartate during a low tide in May 1986 (mean values ± SD, $N=6$, µmoles g dry wt^{-1})

Time of exposure (h)	P-Creatine	P-Glycocyamine	Succinate	L-Alalanine	Aspartate
0	24.93±5.42	43.73±6.28	0.98±0.34	12.56±3.84	15.62±3.21
1	21.62±4.62	37.88±5.71	0.58±0.29	10.02±1.59	12.16±2.58
3	20.78±6.12	39.44±8.23	1.24±0.68	13.03±3.61	14.24±2.53
6	17.76±3.43	35.20±4.29	1.55±0.53	14.97±2.36	12.09±2.56

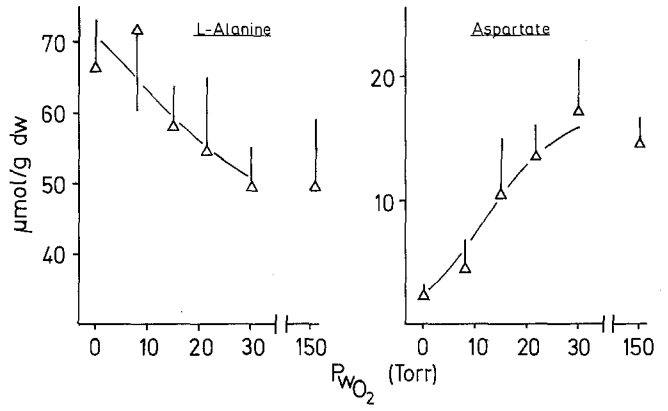

Fig. 8. *Scoloplos armiger*. Concentrations of L-alanine and aspartate after 24 h of incubation at different Pw_{O_2}. (Mean values ±SD, $N=4$)

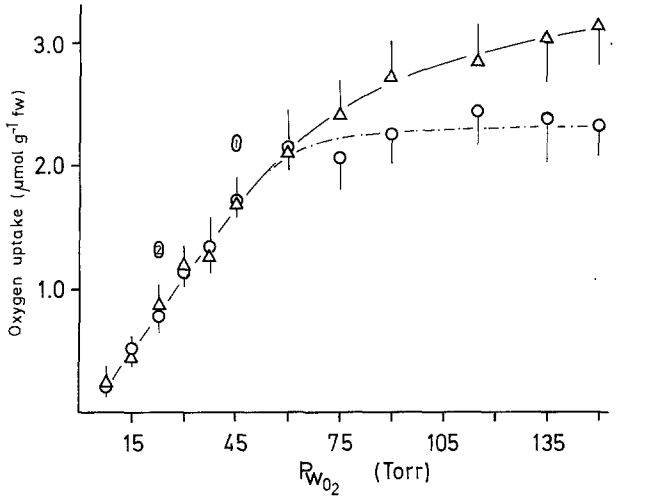

Fig. 9. *Scoloplos armiger*. Oxygen consumption at different Pw_{O_2}. —: data from April, –·–·: data from June

Table 6. *Scoloplos armiger*. Distribution of the worms in sediment at end of high and low tide

Distribution of worms	Only in oxygenated layer (*N*)	Only in anoxic layer (*N*)	Anterior part in anoxic posterior part in oygenated layer (*N*)
At end of high tide	49	19	82
At end of low tide	98	8	44

in June 1986. In April the oxygen consumption at a Pw_{O_2} of 150 torr amounted to nearly 3.2 µmol O_2 h^{-1} g^{-1} fresh wt. With increasing hypoxia down to a Pw_{O_2} of around 60 Torr the oxygen consumption fell linearly to nearly 2 µmol h^{-1} g^{-1} fresh wt. At lower Pw_{O_2} values the decline in oxygen consumption was more pronounced (Fig. 9).

The experiments in June lead to quite different results. At oxygen saturation the oxygen consumption was lower than in April (2.3 µmol h^{-1} g^{-1} fresh wt), but it remained constant down to a Pw_{O_2} value of 60 to 70 Torr. Thereafter the oxygen consumption decreased linearly with falling Pw_{O_2}.

In both series we observed that at a Pw_{O_2} of around 40 torr the first worms began to leave the sand and crawl to the surface, where they remained nearly motionless. At a Pw_{O_2} of 25 torr all animals had appeared at the surface and 90% of the individuals had crawled to the inlet opening of the incubation vessel. They did not move around, but a slow peristaltic movement of the body wall was observed.

These last observations induced us, to look for the position of the worms during high and low tide. *Scoloplos armiger* feeds on bacteria (Reise 1979), mostly in the anoxic sediment. At high tide the majority of the animals are found down to 15 cm in the anoxic layer, but usually only the anterior parts of the worms. The posterior ends, which are rich in gills, remain in the oxygenated layer. Since *Scoloplos armiger* does not built permanent tubes through which oxygen-saturated water from the surface can be pumped, it seems that this behaviour guarantees a sufficient oxygen supply. As shown in Table 6, during prolonged low tide most individuals withdraw into the upper, oxic layer (in the area of investigation ca. 5 cm).

Discussion

For an animal which permanently lives in the sediments of the intertidal the resistance of *Scoloplos armiger* to anoxia is relatively low. At 12 °C this species does not tolerate more than 24 h without greater mortality. Only in particular cases did single individuals survive more than 40 h. This is only moderate compared with other polychaetes from the same habitat. Under identical conditions *Nereis diversicolor* and *N. virens* survive for more than 5 d and *Arenicola marina* up to 5 d. However, the reason for this lower resistance is not that the degradation of glycogen under anaerobic conditions is less effective in *Scoloplos armiger* than (for example) in *Arenicola marina*. This is clearly indicated by the results presented in this study. As in *A. marina*, under anaerobic conditions *S. armiger* produces mainly the volatile fatty acids propionate and acetate, thereby utilizing glycogen as effectively as other euryoxic invertebrates, typified by *A. marina* (Zebe and Schöttler 1986). (The degradation of glycogen to propionate leads to twice the gain in energy, compared to anaerobic glycolysis with the same substrate.)

There are, however, some distinct differences between *Scoloplos armiger* and *Arenicola marina*:

(1) During the initial phase of anaerobiosis, the so-called transition period (Schöttler et al. 1984b), *Scoloplos armiger* gains most of its energy from the mobilisation of its very large phosphagen stores. In contrast to *Arenicola marina*, the Embden-Meyerhof-Pathway is of little importance for anaerobic energy production in this phase (Table 7).

(2) Although *Scoloplos armiger* produces more energy per time interval than *Arenicola marina*, its energy charge decreases much more sharply [from 0.89 to 0.69 in *S. armi-*

Table 7. Energy production at different times of anaerobiosis. A comparison between *Scoloplos armiger* and *Arenicola marina*. (μmoles g dry wt^{-1})

Time (h)	Σ ATP	ATP/h	% Share in energy production		
			Phos-phagens	EMW	Suc, Prop, Ace
Scoloplos armiger					
0– 3	78	26	69	13	18
3–12	145	16	10	12	78
12–24	169	14	4	6	90
Arenicola marina					
0– 3	114	38	23	59	18
3–12	96	11	6	21	73
12–24	110	9	–	–	100

ger as opposed to 0.89 to 0.75 in *A. marina* (Schöttler et al. 1984b)]. This clearly indicates that the energy supply is not sufficient. Compared to *A. marina, S. armiger* is much less able to reduce its metabolic rate under anaerobic conditions.

(3) Furthermore, it is conspicuous that, compared to the anaerobic energy expenditure, the glycogen reserve in *Scoloplos armiger* is relatively low. [In those individuals, which survived more than 40 h of anoxia, glycogen was nearly depleted (Schöttler unpublished data)].

In addition to the resistance to anoxia, the ability to recover quickly from previous hypoxia or anoxia is an important factor for survival. Infaunal animals must be able to recover from the consequences of anaerobiosis (ineffective energy production and a reduced metabolism, the accumulation of acid endproducts, a decrease in energy reserves) as quickly as possible when the tide begins to rise again. Only during high tide is the oxygen supply sufficient to enable normal growth and production of gametes.

With the return of oxygen, *Scoloplos armiger* immediately switches to the aerobic mode of energy production, as is evident from the rapid normalisation of the energy charge and the replenishment of phosphagen stores. In this phase the flux through the Embden-Meyerhof-Pathway exceeds the aerobic capacity of the animals, so that strombine, an endproduct of anaerobic glycolysis (de Zwaan and Zurburg 1981, Siegmund and Grieshaber 1983), is accumulated. However, complete restitution of the phosphagenes is not reached before 6 h. The concentrations of anaerobic endproducts are still after 8 h of recovery significantly higher than in controls. This shows that *S. armiger* requires more time for complete recovery than *Arenicola marina* (Pörtner et al. 1979).

However, in contrast to *Arenicola marina* (Pionetti and Toulmond 1980, Schöttler et al. 1984a), on sandy flats *Scoloplos armiger* is not dependent on anaerobic energy production at low tide, even in areas, in which the sediment surface dries out for several hours. The species rather is able to utilize oxygen even under extremely hypoxic conditions. Energy is not produced anaerobically, until the Pw_{O_2} drops below 15 torr; at a Pw_{O_2} as low as 8 torr a partially aerobic metabolism is still maintained.

The question remains why *Scoloplos armiger*, with its pronounced ability to use oxygen at very low Pw_{O_2}, is not found in the upper intertidal. The sediment composition, i.e., the particle size distribution, usually differs from that of the middle and lower intertidal, but cannot be of much importance, since *S. armiger* is found in comparable sediments in the sublittoral. Predation, too, cannot be a reason, because the main predators, epibenthic crustacea (Alphei 1987), occur in lower abundance in the upper intertidal. Possibly the determining factor for the absence of *S. armiger* in this area is, that the oxidation layer consists only of the first few millimeters of the sediment surface. During low tide this thin layer can dry out completely. One could assume that under these conditions *S. armiger* would switch to anaerobic energy production and that the short period of water cover during high tide would be insufficient in the long term for complete recovery.

Conclusion

Earlier studies (Pionetti and Toulmond 1980; Schöttler et al. 1984a) showed that at low tide *arenicola marina* must produce energy anaerobically in sediments that had dried out on the surface. Our data for *Scoloplos armiger* clearly indicate that the results for *A. marina* cannot be generalized. This investigation and, in addition, studies on *Anaitides mucosa* (Schöttler unpublished data), clearly shows that at low tide, even at locations which dry out on the surface, smaller and mobile polychaetes can produce energy by aerobic mechanisms. A special adaptation was observed in the behaviour of *S. armiger*, where a withdrawal into the upper oxidized layer occurred during low tide. It seems that this behaviour guarantees an avoidance of anaerobic situations.

It ought to be mentioned that the investigations in the field were not yet done under extreme conditions, for instance, on a hot summer day with offshore winds. Moreover, different seasons could lead to different metabolic responses. The variation in reactions of *Scoloplos armiger* to hypoxic conditions supports this hypothesis. In April most worms had just spawned, but in June there was no such stressful situation. The variation in the formation of strombine in the separate anaerobiosis/recovery experiments also leads to the conclusion that the metabolic answer to hypoxic or anoxic conditions may vary in details depending on the time of year.

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