

The effect of adaptation temperature on the metabolic level of the eel *Anguilla vulgaris* L.¹

HANS-DIETER JANKOWSKY

*Zoologisches Institut der Universität Kiel, Lehrstuhl für vergleichende
Physiologie und Tierpsychologie*

KURZFASSUNG: Der Einfluß der Adaptationstemperatur auf die Stoffwechselhöhe des Aales *Anguilla vulgaris* L. Beim Aal weisen der Grundstoffwechsel, gemessen am Sauerstoffverbrauch des Ganztieres, und die Atmung des Muskelgewebes in vitro eine partielle Kompensation auf. Die Höhe des Standardsauerstoffverbrauchs ist aber unabhängig von der Stoffwechselaktivität eines größeren Teiles der Skelettmuskulatur. Es wird über Messungen des Sauerstoffpartialdrucks in der Muskulatur und im venösen Blut unterschiedlich adaptierter Aale berichtet. Die niedrige Sauerstoffspannung im Gewebe und die starke Abhängigkeit des Sauerstoffpartialdrucks im venösen Blut von der Atmungsintensität sprechen dafür, daß ein Mechanismus, der den Standardsauerstoffverbrauch des adaptierenden Ganztieres steuert, in einer Regulation des Kreislaufs und der Atmung zu sehen ist.

With regard to temperature acclimation the eel shows in its metabolism, as measured by its oxygen consumption, a partial compensation like most other teleosts. Data from SCHULTZE (1965) are compiled in Table 1. The rates of respiration of eels adapted to 14° C for a period of ten days are significantly higher than rates of fish kept for the same time at the acclimation temperature of 25° C. At a test temperature of 18° C the difference due to adaptation is about 30 %. When the anterior end (approximately a third of the total length) was adapted to 14° C and the rest, that is the tail (equivalent to 60 % of the total muscle mass) to 25° C, the oxygen consumption of the eel was similar to that of animals which were kept at the cold temperature. When the temperatures are reversed, the decline in the metabolic rate of warm-acclimated eels persists even when the tail of the animal is adapted to 14° C. These experiments indicate that the metabolism of the intact eel depends on the temperature of the head.

When we investigate the oxygen uptake of skeletal muscles by standard Warburg manometry, we find also a compensation. Since there is a marked individual variation which makes a direct comparison of differently adapted eels difficult, relative values are given. These represent the percentage oxygen uptake of muscle

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samples taken from near the head, related to the oxygen uptake of muscle taken from the middle of the animal between anus and tip of the tail.

Oxygen consumption of the muscle from the tail is higher than that from the head. The latter only consumes 73 % of the amount that the former consumes. This difference does not change when the adaptation temperature is altered and is called

Table 1

Relative changes of metabolic functions of *Anguilla vulgaris* L. acclimated at different temperatures (modified and combined after SCHULTZE 1965 and PROSSER et al. 1965)

Conditions of acclimation	head at 14° C, tail at 25° C	14° C	25° C	head at 25° C, tail at 14° C	
Intact eels oxygen consumption at 18° C relative values	100 ± 5	100 ± 3	69 ± 5	69 ± 5	
Muscle tissue	Nitrogen content (tail/head) × 100	93 ± 9	94 ± 6	95 ± 12	87 ± 8
	O ₂ -uptake at 25° C (head/tail) × 100	95 ± 6	74 ± 4	73 ± 6	50 ± 5
	Temperature induced change	(95/73,5) × 100 = 129 ± 8 (50/73,5) × 100 = 68 ± 7			
Tonic electrical activity in muscle (head/tail) × 100	116 ± 6,2	75 ± 3,7	83 ± 14,5	—	

here "location-induced difference". But if the head of an eel is adapted to 14° C and the tail to the warm temperature, the oxygen uptake of the muscle tissue from the head increases to 95 % of that from the tail, so that the location-induced difference is reduced or almost disappears. When on the other hand the anterior end of an eel is kept at 25° C and the tail at 14° C, the in vitro metabolism of muscle from the head is lowered to 50 %.

To calculate the "temperature-induced change", we have fixed the location-induced difference at 100 % and referred the values of eels, the ends of which were at different temperatures, to this baseline. Thus the change due to altered adaptation temperature is about 30 %; this is in good agreement with the rate of respiration of those eels, in which the whole body was adapted to the different temperatures. It should be noticed that the nitrogen content in muscle tissue is not influenced by changing acclimation temperatures; therefore all values are calculated on a wet weight basis.

PROSSER et al. (1965) have measured the tonic electrical activity in the body muscles of eels maintained and adapted at similar conditions. The similarly calculated values are presented in the last line of Table 1.

In eels kept uniformly at 14° C, the number of spikes anteriorly averaged 75 % of those posteriorly, and for eels at the warm acclimation temperature, the percentage was almost the same. When the head of the eel was at 14° C and the tail at 25° C, the difference in electrical activity disappeared and even reversed. This striking corre-

spondence between tonic electrical activity and tissue oxygen consumption – with regard to the two ends of the fish – and the reduction of this difference when the head was cooled led to the suggestion that the nervous system can by its tonic discharge cause enzymatic changes which persist in isolated muscles.

Further it was concluded that the metabolic compensation of muscles during temperature acclimation may be influenced indirectly from adaptive changes in the spinal cord. But more recent unpublished investigations of MALESSA on partially spinalectomized eels show that even denervated muscles are able to maintain different metabolic levels when the acclimation temperature is changed.

There are a number of factors that can influence the results obtained from *in vitro* studies on tissue metabolism. In an attempt to throw light on the question about how high the oxygen consumption of muscle tissue is *in vivo* we have used Beckman

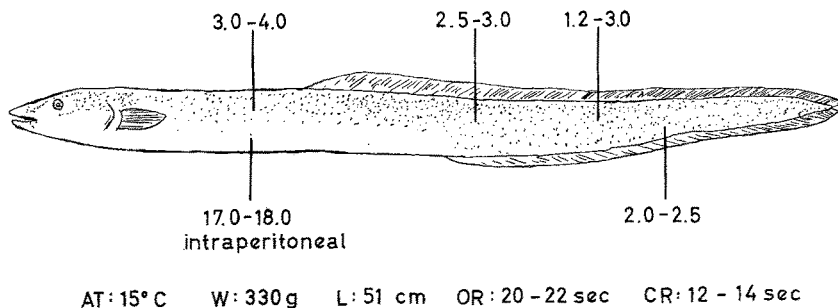


Fig. 1: Oxygen tension in the muscle tissue of an eel (in mm Hg). The eel was acclimated at 15° C (AT). The test temperature was 21° C. Arrows mark the position of the electrode, which was inserted at a depth of 5 or 8 mm. W: weight; L: length; OR: time for 10 breathing movements; CR: time for 10 cardiac beats. All values represent the average of the recordings which lasted at least 30 minutes

micro polarographic oxygen electrodes to measure the local oxygen pressure in the muscles and in the venous blood. The level of the oxygen depends mainly on the following factors: the external respiration, the circulation of blood, and the metabolic consumption of oxygen.

The results of an experiment in which the oxygen pressure was measured are given in Figure 1.

The oxygen tension in the muscles of the tail is very low; when the electrodes were inserted more anteriorly, the values show a slight increase. In the body cavity we could measure a noticeable increase of oxygen tension. In such intraperitoneal measurements it is very difficult to distinguish between changes which are directly induced by alterations in the oxygen pressure of tissues of the digestive tract and experimental artifacts, caused by an entrance of air or water in the body cavity.

Recordings of the oxygen pressure in the muscle of warm acclimated eels do not differ significantly from those of cold-adapted fish. We have the impression that there may exist a slightly higher tension, but the relative errors prevent definite conclusions.

The oxygen tension in the venous blood was determined by fastening plastic

catheters into the large caudal vein. To do this the eel was placed in an eel-holder and the caudal vein exposed by cutting off a small piece of muscle and opening the hemal arches about 5 cm posteriorly to the anus. The free ends of the catheters were connected with a T-shaped canula of plastic, which was fitted to the tip of the

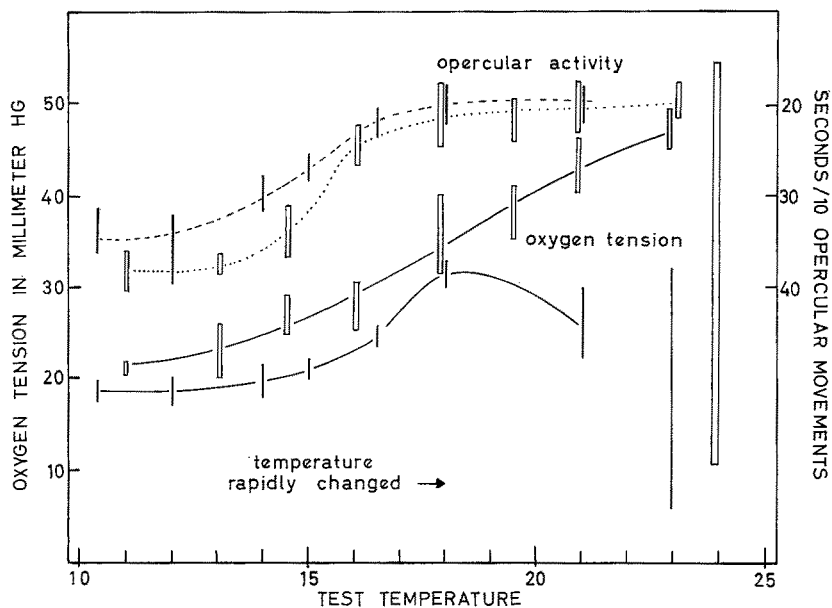


Fig. 2: Oxygen tension of venous blood and opercular rate of differently adapted eels at various temperatures. The oxygen tension is plotted in the lower curves. Each vertical line represents the range in which the pressure changes, the recordings lasted for at least 20 min for each test. The upper curves represent the rate of opercular activity; the ordinate on the right side of the diagram shows the time for 10 movements. Single bars on the right side represent oxygen tension at artificial respiration. Solid bars: eel acclimated at 8° C (W: 354 g). Open bars: eel acclimated at 22° C (W: 420 g).

electrode. The oxygen tension in the bloodstream was recorded for periods of several hours while the eel was submerged in well aerated water, the temperature of which could be controlled and changed by a heating and cooling device.

Some typical values of the oxygen tension in the venous blood are given in Figure 2; experiments were selected showing similar breathing rates to keep this parameter comparable. The cold-acclimated eel shows a lower oxygen tension than the warm-adapted fish, especially at higher test temperatures. This difference is significant; at a test temperature of 21° C the oxygen tension of venous blood was in at 22° C acclimated fish 59 ± 4.1 mm Hg (7 eels), in at 14° C acclimated fish 38 ± 3.6 mm Hg (10 eels).

The oxygen tension increases when the breathing goes up and decreases when it drops. In apnoe, when breathing stops, it has been observed repeatedly that the oxygen tension is lowered to zero within some minutes; on the other hand artificial respiration

raises the oxygen level to higher values, as the vertical bars indicate on the right side of Figure 2.

When the test temperature is rapidly increased, the oxygen tension increases at a lower rate than the breathing movements. The conspicuously high value in the curve of the cold-adapted fish probably reflects a transitory state in which the oxygen supply is higher than the usual demand, due to an initial overshoot of respiration. If the temperature remains the same for a longer period, a slow decrease of oxygen tension takes place, caused by an increased metabolic consumption at higher temperatures.

The presented data leave several questions unanswered. How is it possible that the temperature-induced change in metabolic activity of the predominant tissue, the muscle, does not alter the oxygen uptake of the whole animal? The medium which SCHULTZE (1965) has used for his Warburg-tests was a mixture of glucose and sodium succinate; thus he has measured the activity of succinic dehydrogenase only. But measurements of the oxygen uptake by muscle tissue of another fish species – the golden orfe, *Idus idus* – show that the degree of adaptation of the isolated muscle which only utilizes endogenous substrate is similar to that which exists if exogenous substrates are provided. In addition, evidence was obtained that most mitochondrial enzymes show changes in their activity parallel to the oxygen consumption of muscle, in regard to altered acclimation temperature.

The above mentioned extreme low oxygen tension in the muscle suggests that this tissue of the eel generally lives in a hypoxic state, thus depressing the overall metabolic activity of the oxydative Krebs-cycle, even if the enzyme activities of the latter may be increased by cold-acclimation.

The relatively high oxygen values of the blood in the caudal vein are in contrast to the low oxygen tension in the muscles. Since the eels in our experiments were kept in a resting state we may assume that the capillaries in the tail muscles were shunted to a great extent, because the blood volume of the eel is very low (only 2.9% of the body weight as compared with 6% or more in mammals). Therefore the resting eel probably uses most of the blood for supplying the capillary systems of brain, liver or kidney. Further cardiovascular alterations, as blood pressure and blood flow, may exist in fishes adapted to different temperatures. These problems have to be investigated.

In this context it should be mentioned that the arterial blood from resting eels has a comparatively low oxygen tension, while the arterial blood from mammals is always about 95% saturated. Eels responded to exercise by increasing the arterial oxygen saturation while the venous oxygen tension remained unchanged, as STEEN & KRUYSSÉ (1964) reported. There is evidence that at high temperatures the raised breathing frequency will increase the arterial oxygen saturation, which improves the supply to the metabolizing tissues.

As the breathing rate is governed by the central nervous system and this rate shows an adaptation according to a partial compensation, we suggest that the adaptation of the oxygen uptake of the intact eels is based to a great extent on an adaptive response of the central nervous system to different temperatures, even when direct effects of acclimation temperature in tissues are to be seen. Temperature acclimation

in the central nervous system of fish has been reported by ROOTS & PROSSER (1962), ROBERTS (1964, 1966), and KONISHI & HICKMAN (1964).

SUMMARY

1. The present paper reviews some investigations on the problem of temperature adaptation of the eel. The experiments were made in order to find out why the metabolic rate of muscle in vitro does not reflect the capacity adaptation of the intact eel.
2. Oxygen tension in the muscle tissue and in the venous blood has been measured by inserting micro oxygen electrodes. Oxygen tension in the muscle of the tail is very low; tension in the large caudal vein is more than ten times higher.
3. Oxygen tension in the muscle is not altered by changing the adaptation temperature. The cold-acclimated eel shows a lower oxygen tension in the venous blood than the warm-adapted fish.
4. Oxygen tension in the caudal vein depends largely on the breathing rate; this can be seen when the experimental temperature is changed and differently adapted individuals are tested. Therefore we suggest that the metabolic rate is certainly influenced by adaptive changes in the nervous system.

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