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The haemoglobin of the herring, *Clupea harengus*

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mainly occur in estuarine waters, where ambient oxygen tensions may be low and temperatures high.

Summarizing, the data reveal the following differentiation in function of herring haemoglobin components. The cathodal components (fraction I) have a low oxygen affinity, no Bohr effect and a moderately low temperature sensitivity of the oxygenation reaction. Fraction II, however, has a high oxygen affinity, a normal or large Bohr effect and a temperature sensitivity changing during development. The anodal fraction III appears to be intermediate in its function between fractions I and II.

Differentiation of the oxygen binding properties of the haemoglobin components will ensure an adequate oxygen supply and transport to the tissues under various environmental conditions. Moreover, the diverse properties of the haemoglobin components and a shift in the relative concentrations of the individual components, may be the basis for adaptive changes of the blood, so that the individual fish can adapt to changing environmental circumstances. In this respect interesting differences appeared to occur between the juvenile and adult stages. The first juvenile stages, which are rather passively transported and living in coastal or estuarine areas, have a relatively high proportion of the anodal, pH sensitive haemoglobin fraction. The adults on the contrary, which swim great distances on their way to and from the spawning areas and have higher metabolic rates that could reduce blood pH, have a relatively high proportion of the cathodal, pH insensitive fraction, which will provide a continued oxygen uptake from the water when the pH of the blood drops by muscular exertion. Also differentiation in temperature sensitivity of the oxygenation reaction of the haemoglobin components, will be of importance since the temperature insensitive haemoglobin ensures oxygen binding (and thus oxygen transport) when increasing temperature hinders the loading of the temperature sensitive components in the gill.

VIII. SUMMARY

This study deals with the haematological and oxygen binding properties of blood of a marine teleost, the herring, *Clupea harengus*, and the change of these properties during ontogenetic development. It traces the influences of physical and chemical factors like pH, temperature and the erythrocytic cofactor adenosine triphosphate, ATP, on oxygen binding properties at the level of the whole blood, the isolated erythrocytes, the "stripped" (cofactor-free) haemolysates, as well as the isolated haemoglobin components that are present within individual fish. The data on haemoglobin multiplicity are compared with parallel measurements made on the sprat, *Sprattus sprattus*.

The haematocrit of herring obtained during different seasons is positively correlated with body length and temperature. Higher temperatures induce higher haematocrits, resulting in a steeper slope of the haematocrit-size relation. Males have higher haematocrits than females. The haemoglobin concentration of the blood shows a similar positive correlation with body length and temperature. While the mean corpuscular haemoglobin concentration appears to increase during the first year of development, it is constant for the rest of life.

The mean blood pH is about 7.6 (at 15° C) and does not change appreciably during growth. ATP concentrations increase from about 1.0 mmol.l⁻¹ in juvenile herring to about 1.7 mmol.l⁻¹ in adults. The ATP-Hb molar ratio, however, remains fairly constant (about 0.9) during growth. The spectral properties of herring haemoglobin and some of its derivatives show similarity with those of other fish and those of mammals.

Herring haemoglobins show a high degree of intra-individual multiplicity (heterogeneity). Within the species distinct polymorphs appear to be present in adults, which coincide with North Sea autumn spawners and coastal spring spawners. In both types of herring an increase in the number of haemoglobin components during growth is demonstrated. Herring haemoglobin demonstrates a reversible loss in oxygen binding capacity, with decreasing pH (Root effect). In the presence of the erythrocytic cofactor for oxygen binding, ATP, the Root effect occurs at higher pH than in absence of ATP. The effect is greater in adults than in juveniles. The maximum loss of oxygen binding capacity at low pH is, however, greater in juveniles than in adults.

Blood of juvenile and adult North Sea herring has a moderately low oxygen affinity (p_{50} 15 to 18 mm Hg at pH 7.6 and 15° C), a distinct Bohr effect and a Hill cooperativity coefficient varying between 1.0 and 2.0. Stripping the haemoglobin of organic phosphates results in increased oxygen affinities and decreased Bohr effect. The haemoglobin of adult herring, in erythrocytes as well as in "stripped" (cofactor-free) haemolysates, has a lower Bohr factor than that of juveniles. The organic phosphate ATP, strongly decreases the oxygen affinity of the haemoglobin; the effect is more pronounced in juveniles than in adults. The haemoglobin, both in erythrocytes and in stripped haemolysates from all developmental stages studied, show an almost equal temperature sensitivity of the oxygenation reaction. Corresponding data on oxygen affinity, Bohr effect and temperature sensitivity of the oxygenation reaction are presented for haemoglobin from coastal herring, and the results are comparatively discussed.

Determination of the oxygen binding properties of isolated haemoglobin fractions, revealed that the cathodal haemoglobin fraction (I)

shows the lower temperature sensitivity of the haemoglobin fraction (I) and the highest oxygen affinity (stage). The positive correlation between those

The haematocrit is discussed in relation to body length in relation to sex and blood oxygen tension. The oxygen transport properties of herring reveals that the haemoglobin fraction (I) has a lower oxygen binding

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shows the lowest oxygen affinity, no Bohr effect and a relatively low temperature sensitivity of the oxygenation reaction. The next haemoglobin fraction (II) has the highest oxygen affinity, a large Bohr effect and the highest temperature sensitivity (except in the early juvenile stage). The properties of the anodal fraction (III) are intermediate between those of the other fractions (I and II).

The haematological data and oxygen binding properties are discussed in relation to their possible physiological functions, particularly in relation to swimbladder function, metabolic oxygen demand and blood oxygen transport under different conditions. Comparison of the oxygen transport system in the different developmental stages of herring reveals adaptive differences both in the intrinsic properties of the haemoglobins and in the intraerythrocytic factors that modulate oxygen binding.

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