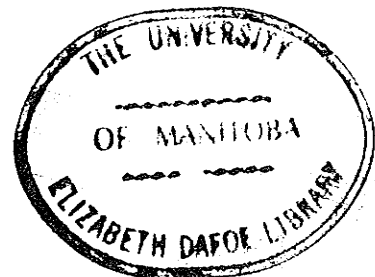


A STUDY OF SOME HAEMATOLOGICAL CHANGES IN THE
GOLDFISH (Carassius auratus)
FOLLOWING THERMAL ACCLIMATION
AND NON-LETHAL HEAT SHOCK

A Thesis
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ABSTRACT

The present investigation was undertaken in view of the conflicting reports in literature regarding the general haematology of fishes, and the relationship of haematological variations to temperature changes and thermal acclimation.

Because it was readily available, easily maintained, and because there exists a considerable body of information concerning its thermal relationships, the goldfish was used throughout as an experimental animal.

In fishes acclimated to 20°C. (control group) and also in fishes transferred from this temperature to 30°C. (experimental group), determinations were made of haematocrit, red cell concentration, blood iron content, and leukocyte concentration. Using the information obtained, mean corpuscular iron content and mean corpuscular volume were calculated. An electrophoretic study of changes in the relative abundancies of haemoglobin polymorphs was also carried out on fishes acclimated to temperatures of 5°, 12°, 20°, and 30°C.

The results of this study indicated that red cell concentration, haematocrit, and mean corpuscular volume remain relatively constant over a 240 hour period following transfer of the animals to 30°C. Under the same circumstances, white cell concentration showed a slight trend towards an increase, while total blood iron and mean corpuscular iron content exhibited a reverse trend of small magnitude.

In fishes acclimated to 5°C. two haemoglobin polymorphs were

apparent: (1) a cathodal fraction (C_1), (2) a anodal fraction of lesser abundance and greater mobility (A_2). In the 12°, 20°, and 30°C. acclimated animals a second anodal fraction appeared (A_1). This fraction was of lesser abundance and lesser mobility than the two previously mentioned fractions.

The data suggest that metabolic compensation to higher temperatures is associated with hormonally-induced changes in branchial blood flow and blood pressure rather than the metabolically more costly process of increased red cell production and haemoglobin synthesis.

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INTRODUCTION

The effect of temperature upon fish has long been the object of numerous investigations. As early as 1895 thermal acclimation was a recognized phenomenon (Davenport and Castle, 1895), but it was not until recent years that a distinct pattern could be ascribed to the various avenues of research. Brett (1959b), in his review of the related literature, classified studies regarding the effect of temperature on fishes into two distinct groups:

- (1) those in which temperature acted as a lethal factor;
- (2) those in which temperature acted as a controlling factor.

Fry (1947) initiated investigation regarding the effect of temperature as a lethal factor, and observed that temperature acted through metabolism by governing the relative rates of temperature demand. Thus, fishes subjected to increased environmental temperature showed increased oxygen demand and heightened metabolism. Such changes would lead one to expect haematological variations facilitating increased oxygen uptake.

Previous studies regarding the general haematological picture of fishes, although quite numerous, have tended to be restricted in scope. Investigations regarding the effect of temperature upon the blood of fishes are scanty and often contradictory. It is interesting to note that Bondar (1957) and Spoor (1951), in studies on Notropis blennioides and Carassius auratus respectively, observed an increase in

erythrocyte number with increased environmental temperature. Contrary to these authors, Anthony (1961) reported that the erythrocytes of the goldfish decreased in number with increased acclimation temperature.

In view of these facts, the present study was undertaken with the aim of: (1) describing the general haematological picture of the goldfish; (2) describing the immediate effects of thermal shock upon the blood, and adaptive responses of the blood to shock; (3) assessing the data obtained as possible criteria for determining rates of acclimation to temperature changes; (4) providing a basis for further haematological studies on the phenomena of thermal shock and acclimation in fishes.

Accordingly, determinations were made of the following: (1) haematocrit, (2) red cell concentration, (3) blood iron content, (4) white cell concentration. From these were calculated: (1) mean corpuscular iron content, (2) mean corpuscular volume. In addition to this, an electrophoretic study of the haemoglobin polymorphs was conducted to determine possible temperature-related changes in this protein.

LITERATURE REVIEW

1. Thermal Relationships of Fishes.

Prior to 1940, work done on the thermal relationships of fishes was of a fragmentary nature and difficult to draw into any generalized pattern (Brett, 1959). Brett (1956), in his review of the literature of that period, noted that upper and lower lethal temperatures were known to exist (Hathaway, 1927; Loeb and Wastenys, 1912), that acclimation was a recognized phenomenon (Davenport and Castle, 1895), and that deviations between the body temperature of the animals and the temperature of their external environment were small and transitory (Pearse and Hall, 1928; Neilson, 1938).

The movement towards a more systematic examination of the temperature relations of fishes was initiated by Doudoroff (1938). In his research on Girella nigricans (Ayres), Doudoroff studied temperature selection and the relationship of temperature selection to previous thermal history. In the same year, Sumner and Doudoroff (1938) carried out experiments on the relationship between oxygen consumption and temperature acclimation in Gillichthys mirabilis.

During the 1940's, much of the work on this general problem was centered around a description of the lethal effects of temperature, and the influence of thermal acclimation upon thermal tolerance. Among such investigations may be included those of Doudoroff (1938, 1942, 1945) on Girella nigricans, Fundulus paripinnis, and Atherinope affinis; of Sumner (1940, 1942), on a variety of species normally inhabiting warm

and cold springs; of Hart (1947), on various species of fish from the Toronto region; of Brett (1941, 1946), on the goldfish, Carassius auratus; and of Fry and his associates (Fry, Brett, and Clawson, 1942; Fry and Hart, 1946; Fry, Hart, and Walker, 1946), on Carassius auratus and Salvelinus fontinalis.

The work of Fry and his associates, referred to above, has been of particular significance in the description of thermal relationships in fishes. These studies, in general, followed the pattern established by Hathaway (1927). Fry, Brett and Clawson (1942), for example, on the basis of intensive studies made on the goldfish, determined upper and lower lethal temperatures (LD₅₀) for this species at a series of acclimation temperatures. Using these data they defined the limits of a thermal polygon. This polygon included all combinations of existing temperatures and acclimation temperatures in which temperature, acting alone, was not lethal to the animals. In later studies these concepts were extended to a variety of species (e.g., Fry, Hart and Walker, 1946).

On the basis of earlier studies, Fry (1947) presented a general review of the physiological effects of environmental variation upon animal activity. This study proved to be of great significance in the determination of lines of endeavour followed by later investigators. In this work a new approach to the organism-environment relationship was introduced, with environmental actions upon the organism being categorized as lethal, controlling, limiting, masking, accessory, and directive in nature. This classification provided clarity to the investigations followed by previous and succeeding researchers. Of prime importance

was the introduction of a tendency to pursue the topics of thermal acclimation and thermal tolerance in terms of metabolic functions and temperature-dependent activities.

Any discussion of the various avenues of research that have been followed would be unnecessarily repetitive as these have been admirably reviewed by several authors (e.g., Brett, 1956, 1959b; Bullock, 1955; Fry, 1958). Of considerably greater significance to the present study are the investigations directly pertaining to the effect of temperature on metabolism.

The extreme diversity of the various metabolic studies that have been carried out prohibits any strict classification of the research, but broad classification is possible under the following headings: (a) respiratory studies; (b) studies on fat metabolism; (c) endocrine studies; (d) studies on tissue metabolism; (e) haematological studies.

a. Respiratory Studies. One of the earlier experiments concerned with the relationship between temperature and respiration in fish was that of Edge and Krogh (1914), who studied temperature and respiratory exchange in fishes. Later research on thermal acclimation as related to oxygen consumption were undertaken by Fry and his associates (Fry, Hart and Walker, 1946; Fry and Hart, 1948) on the effect of environmental temperature and body temperature on oxygen consumption in Carassius auratus, and by Scholander (1953) on the oxygen consumption of tropical and arctic fishes at the temperature of their normal habitats and at various higher and lower experimental temperatures.

Other investigators have studied the effects of various oxygen and carbon dioxide tensions on thermal acclimation in fishes. Representative of this group were Fry (1947), who conducted studies on the relationship between temperature and various tensions of oxygen and carbon dioxide with respect to the asphyxiation of goldfish; Graham (1949), on the effects of oxygen tension and temperature on the metabolism of Salvelinus fontinalis; Downing and Merkins (1957), on the effect of low oxygen and temperature on the survival of several species of fish; and Shepard (1955), on the acclimation of Salvelinus fontinalis to low oxygen tensions. Kanungo and Prosser (1959), in their investigation of the physiological and biochemical adaptations of goldfish to various temperatures, measured the standard and active oxygen consumption of this animal while exposed to different acclimation temperatures.

b. Studies on Fat Metabolism. Another field of investigation has centered around fat metabolism and its association with temperature resistance and thermal acclimation. Of importance in this area of study was the work of Hoar and his associates (Hoar and Dorchester, 1949; Hoar and Cottle, 1952; Irvine, 1954; and Irvine, Newman and Hoar, 1957). Thus, Hoar and Dorchester (1949), and Hoar and Cottle (1952) investigated the relationship between dietary fats and thermal resistance in Carassius auratus. Irvine (1954) conducted research into cold resistance and the effect of various lipid diets on the same species. Irvine, Newman and Hoar (1957) extended these studies with an investigation on the effects of dietary phospholipids and cholesterol on temperature resistance in the goldfish.

c. Endocrine Studies. Endocrinological studies pertaining to thermal resistance and thermal acclimation have been a subject of considerable interest. Of particular note are investigations conducted by Hoar (1946, 1958), Hoar, Keenlyside and Goodall (1957), and Hoar and Robertson (1959) on the goldfish and Pacific salmon. This work was mainly concerned with the influence of photoperiod on thryoidal, gonadal, and adrenocortical activity, and the resultant effect on thermal acclimation and thermal resistance. Similar studies have been pursued by Northcote (1958), and Evans, Purdie and Hickman (1962), on the rainbow trout, Salmo gairdneri.

d. Studies on Tissue Metabolism. Recently, an increasing amount of attention has been devoted to the study of tissue metabolism and its relationship to thermal tolerance and thermal acclimation. Initially, interest was centered upon the respiratory metabolism of excised tissues (e.g., Battle, 1929; Peiss and Field, 1950; Exberg, 1957, 1958), but there has been an ever-increasing trend towards chemical analysis of the tissues, for example, the work of Hoar and Cottle (1952) on the relationship of the melting points of lipids to thermal resistance.

e. Haematological Studies. Studies of the cellular phenomena related to thermal tolerance and thermal acclimation have, to a large extent, been neglected until recent years. Of the relatively few investigations that have been reported, the majority have been confined to analysis of the blood. Spoor (1951) studied the erythrocyte counts of three

groups of goldfish acclimated to different temperatures, and Bondar (1957) conducted similar experiments on the River Shiner, Notropis blennius. Anthony (1956, 1960, 1961) carried out extensive research into the effects of the thermal environment upon the blood of Carassius auratus. The effects of cold shock upon the leucocytes of fishes have been pursued by Slicher and her associates (e.g., Slicher, Pickford and Ball, 1962).

2. Thermal Adaptation.

Fisher (1958) defined adaptation as the sum total of changes which occurred within the animal as a result of a change or changes in the external environment (e.g., environmental temperature changes). These alterations or responses on the part of the organism favour survival in the changed environment. Heart rate and blood pressure were cited as examples of specific characteristics or adaptates thus modified. Acclimation was considered to be composed of those adaptates possessing time-course characteristics measurable in terms of days or weeks.

Precht (1958) classified acclimation or short-term adaptation into two types: (a) capacity adaptation; (b) resistance adaptation. The first, capacity adaptation, was considered to be an adaptation occurring within the normal temperature range of the animal. Precht (1958) regarded adjustments within this category to be primarily concerned with the maintenance of a relatively constant metabolic rate. Resistance adaptation was classified as that associated with enhancing the animal's ability to tolerate extremes in temperature according to the direction of acclimation. For example, a cold acclimated animal would be able to

withstand lower environmental temperatures than would a warm acclimated animal.

a. Capacity Adeptation. The phenomena of capacity adaptation has been extensively treated by Precht (1958) and Prosser (1958). Precht (1958) used oxygen consumption as a measure of the metabolic rate of animals shifted from an acclimation temperature (T_1) to a higher or lower test temperature (T_2). It was noted that in experiencing such changes the animal may overcompensate or undercompensate immediately following transfer. Complete acclimation was said to have occurred if the rate of oxygen consumption at the test temperature (T_2) returned to that observed at the acclimation temperature (T_1). In all Precht (1958) noted five possibilities with respect to the steady state finally achieved at the test temperature:

- i The rate function increased when the animal was transferred to T_2 and remained at this point with no apparent acclimation occurring
- ii The rate function showed an initial increase when the animal was transferred to T_2 , but returned to that equivalent to the rate at T_1 with complete acclimation occurring.
- iii Partial acclimation occurred with the rate function reaching a steady state somewhat higher than that recorded at T_1
- iv Hypocompensation occurred with the rate function at T_2 becoming slightly lower than that at T_1
- v Hypercompensation occurred with the rate function reaching, and remaining at, a position considerably higher than that recorded for T_1 .

Prosser (1958), in his review of the general field of physiological

adaptation, was of the opinion that information regarding the nature of compensatory adaptation might best be obtained by observing reaction rates (e.g., oxygen consumption) of warm and cold acclimated animals transferred to various temperatures above and below the acclimation temperature. In extending the theory presented by Precht (1958), Prosser reviewed the literature and came to the conclusion that nine possible types of rate-temperature relationships could be distinguished in animals transferred from an acclimation temperature to different test temperatures. These represented various combinational changes in the parameters of the classical Krogh and Belehradek temperature metabolism equations.

Of particular interest to the present study was the work of Kanungo and Prosser (1959) in which the standard and active oxygen consumptions of cold and warm acclimated goldfish were reported for various test temperatures. In this publication it was noted that the results obtained corresponded to a type IVA rate-temperature relationship (see Prosser, 1958).

b. Resistance Adaptation. Resistance adaptation was illustrated by the work of Fry, Brett and Clawson (1942) on Carassius auratus. Upper and lower lethal temperatures (LD₅₀) were observed and represented graphically by a tolerance polygon. It was noted that upper and lower incipient lethals increased to maximum values with increase in acclimation temperature. The area bounded by the polygon was designated as the zone of thermal tolerance. This increase in upper and lower lethal temperatures represented resistance adaptation or adaptation as previously defined.

GENERAL HAEMATOLOGICAL PICTURE OF FISH

The general haematological situation of fishes will be discussed under the following headings:

1. Cell types
 - a. erythrocytes
 - b. leukocytes
2. Haematocrit
 - a. general considerations
3. Haemoglobin
 - a. haemoglobin content
 - b. haemoglobin polymorphism
4. Blood oxygen combining capacity.

1. Cell Types

a. Erythrocytes. The erythrocytes of fishes have, in their mature form, been described by Jordan (1938) as elliptical discoid bodies with central nuclei. In the teleosts studied, the erythrocytes ranged in length from 6 to 13 microns. Varying numbers of immature erythrocytes, or large and small lymphoid haemocyto blasts, have been described in the blood vascular system of fishes (e.g., Dawson, 1933; Jordan, 1938; Duthie, 1939; Catton, 1951; Bondar, 1957). Jordan (1938) noted that the large lymphoid haemocyto blasts showed intravascular differentiation into erythrocytes, while the smaller lymphoid haemocyto-

blasts differentiated intravascularly into thrombocytes.

Several investigations on erythrocyte numbers and mean corpuscular volumes have been carried out in teleost species. The salient findings, with variations related to thermal conditions, have been recorded in Text Table I. It will be noted from this table that erythrocyte counts and mean corpuscular volume have been observed to vary with environmental temperature. Contrary to the findings of Spoor (1951) and Bondar (1957), Anthony (1961), in experiments on the goldfish, obtained results which indicated a decrease in the number of erythrocytes with increased acclimation temperature. This decrease in erythrocytes coincided with an increase in mean corpuscular volume. It is also of interest to note that Straub (1957, cited by Precht, 1958), who conducted experiments on the amphibian, Rana esculenta, found increases in erythrocyte counts and decreases in mean corpuscular volume with an increase in acclimation temperature.

b. Leucocytes. Considerable difficulty has been experienced in identifying certain leukocytes found in fishes. Jordan (1938) noted that lymphoid hemoblasts (stem cells), or large, small, and intermediate lymphocytes gave rise to granulocytes, monocytes, thrombocytes, and also erythrocytes. Intravascularly, the large and small lymphocytes differentiated into erythrocytes and thrombocytes respectively. Extravascularly, identical cells produced finely granular oxyphilic heterophils and coarsely granular eosinophils. Yuki (1957) cites the observation of Chuin (1920) who observed the presence of numerous lymphoid hemocytoblasts

TEXT TABLE I

ERYTHROCYTE NUMBERS AND MEAN CORPUSCULAR VOLUMES
IN VARIOUS SPECIES OF TELEOST FISHES,
INDICATING VARIATIONS RELATED TO
THERMAL CONDITIONS

SPECIES	TEMPERATURE °C	RBC (10^6)	MCV (μ^3)	REFERENCE
<u>Carassius auratus</u>	5.0	2.0	172	Anthony (1961)
	6.0	2.1	181	
	26.0	1.7	219	
	30.0	1.8	176	
Pike (no species given)	----	1.7	175	
Roach (no species given)	----	1.9	238	
<u>Notropis blennius</u>	9.5	1.3		Bondar (1957)
	16.5 (after 21 days)	2.7		
<u>Carassius auratus</u>	13.9	1.6		Spoor (1951)
	30.0	2.2		
<u>Carassius auratus</u>	----	0.5		Baker & Kline (1932)
Scomber (no species given)	----	3.9		Kisch (1952)
Tautog (no species given)	----	2.1		Kisch (1952)
<u>Cyprinus carpio</u>	----	0.8	311	Field, Elvehjem, and Juday, (1943)
<u>Salvelinus fontinalis</u>	----	1.0	314	

in the circulatory system of fishes, and stated that such a situation resembled that of hemopoiesis at the beginning of the third stage of the foetus in higher vertebrates. The position of the lymphoid hemoblast in hemopoiesis was diagrammatically represented by Catton (1951) and has been reproduced in Figure 1.

Due to the similarity of erythrocytic stem cells to lymphocytes, it has been virtually impossible to obtain accurate and consistent counts of the leukocytes of fish blood. Thus, recorded leucocyte counts made in fishes show significant differences. Lagler, Bardach, and Miller (1962), for example, noted that white cell counts as determined by various investigators showed a range of 20,000 to 150,000 per cubic millimeter in different groups of fishes. Yuki (1957) noted that the work of Onoda (1934) and Irie (1932) showed large discrepancies among the ratios of granulocytes, monocytes, and lymphocytes in the blood of the crucian carp examined in winter.

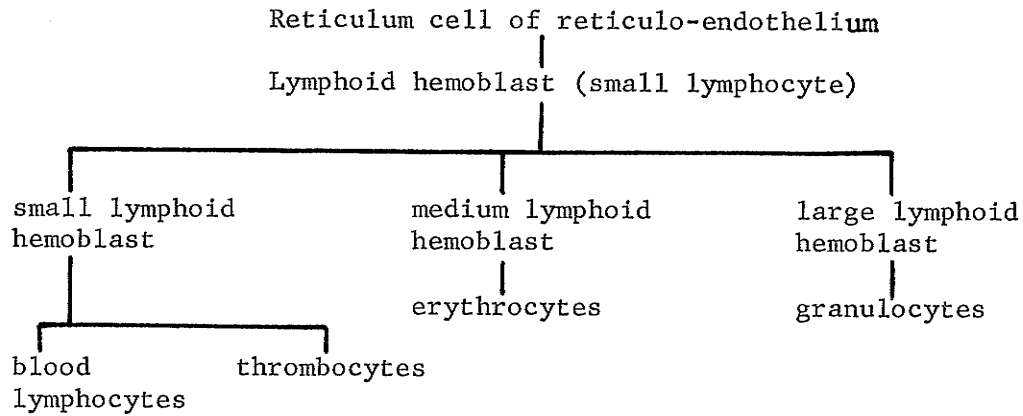
The effect of thermal environment upon the leucocytes of fishes has been largely neglected, however, Slicher and Pickford (1962) have studied the effect of cold shock on the white cell counts of fishes and observed a triphasic response elicited by immersion in ice water. This triphasic response was composed of an initial leucocytosis which occurred 15 minutes after immersion, a leucopenia reaching a maximum at one hour, and a leucocytosis at two hours.

Perhaps the most apparent difference between fish blood and human blood has been found to exist in the erythrocytes. As compared to the erythrocytes of fishes those of human blood have been described

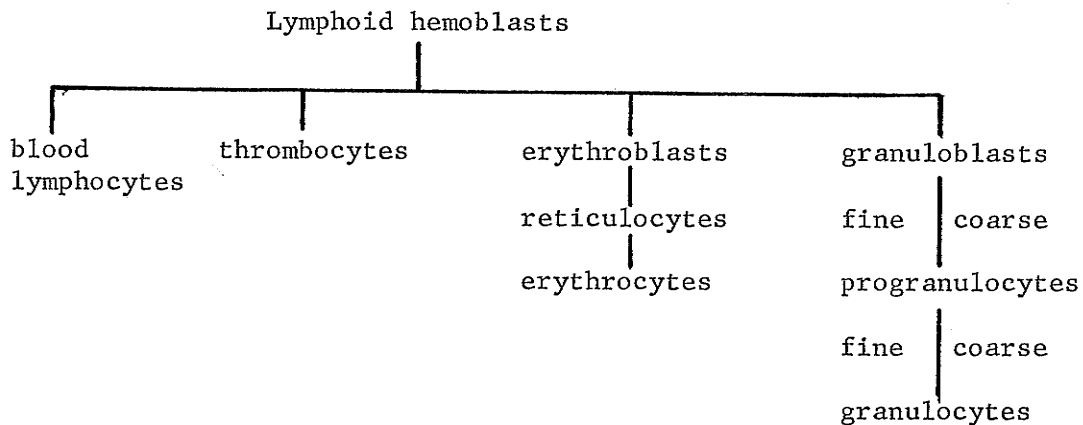
FIGURE 1

PROPOSED SCHEMES OF BLOOD CELL FORMATION IN FISHES

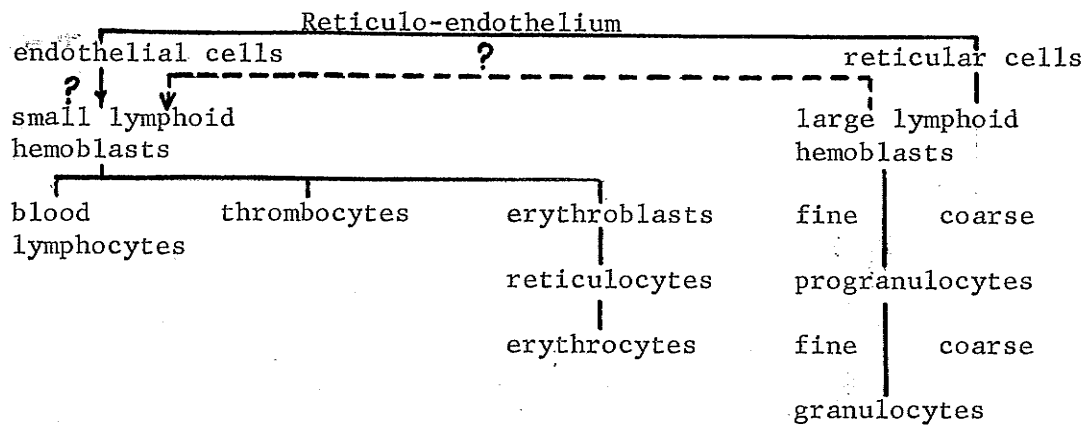
1. Jordan and Speidel (1923)



2. Duthie (1939)



3. Catton (1951)



by Dawson (1948) as flattened, biconcave discs without nuclei. Significant differences in the number of erythrocytes per cubic millimeter have been found in comparisons of fish and human blood. The human female usually has erythrocytes numbering 4.5 million per cubic millimeter, while the male has approximately 5.0 million per cubic millimeter.

Leucocytes of humans may show considerable variation in number according to the physiological condition of the body, but under normal conditions Dawson (1948) has reported them to number approximately 8,000 per cubic millimeter.

Comparisons in the size of the blood cells of humans and fishes have been tabulated in Text Table II. The data used in this case have been taken from Jordan (1938), Lowenthal (1931), and Dawson (1948). As will be noted from the table, variations in the comparative sizes are known to exist, but in general, considerable similarity is shown.

2. Haematocrit

a. General Considerations. Numerous investigators have carried out studies on the haematocrit values of fishes: Snieszko (1961) on rainbow trout, brown trout, and brook trout; Field, Elvehjem and Juday (1943) on carp and trout; Becker, Bird, Kelly, Shilling, Solomons, and Young (1958) on various species of marine teleosts. Anthony (1961) studied the relationship of haematocrit to environmental temperature in Carassius auratus. Characteristic values indicating variations as related to thermal conditions have been recorded in Table III.

TEXT TABLE II
COMPARATIVE SIZES OF THE BLOOD CELLS
IN FISHES AND HUMANS

CELL TYPE	SIZE IN MICRONS	
	Fish	Human
Erythrocyte	6.0-13.0	7.0- 8.8
Lymphocyte	6.0-11.0	6.0-12.0
Monocyte	9.0-16.0	12.0-15.0
Neutrophile	7.5-13.5	10.0-12.0
Basophile	5.0-12.0	8.0-10.0
Eosinophile	5.0-12.0	10.0-12.0

TEXT TABLE III

CHARACTERISTIC HAEMATOCRIT VALUES OF
 VARIOUS SPECIES OF TELEOST FISHES,
 INDICATING VARIATIONS RELATED TO
 THERMAL CONDITIONS

SPECIES	TEMPERATURE °C.	HAEMOCRIT (% RBC)	REFERENCE
<u>Carassius auratus</u>	5	34.2	Anthony (1961)
	6	36.0	
	26	37.5	
	30	30.0	
Rainbow trout (no species given)	Means of samples taken in winter and summer	47.8	Snieszko (1961)
Brook trout (no species given)		50.7	
Brown trout (no species given)		39.5	
<u>Promicrops itaiara</u>	-----	41.0	Becker et. al. (1958)
<u>Thunnus thynnus</u>	-----	41.0	
<u>Mycteroperca venenosa</u>	-----	24.0	
<u>Scromberomorus maculatus</u>	-----	38.0	
<u>Mycteroperca bonaci</u>	-----	28.0	
<u>Cyprinus carpio</u>	-----	31.3	Field, Elvehjem, and Juday (1943)
<u>Salvelinus fontinalis</u>	-----	27.2	