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CERTAIN ASPECTS OF THE RESPIRATORY FUNCTIONS OF THE BLOOD OF THE SPOTTED GAR, LEPISOSTEUS OCULATUS

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CHAPTER I

INTRODUCTION

The bony fishes vary considerably in their ability to extract oxygen from their environment and in their toleration of high concentrations of carbon dioxide. These differences have been brought out in a large number of studies in this century of the respiratory functions of the blood of various fishes. Some of the earlier studies are those of Marsh (1902, 1906) who studied hemoglobin and red blood cell counts of the brook trout, Salvelinus fontinalis, and the rainbow trout, Salmo gairdneri. Krogh and Leitch (1919) found remarkable differences in the oxygen tensions required to saturate the blood of different species of fishes. They noted also that fish blood responded to carbon dioxide much more variably than did mammal blood. Powers (1939) investigated the hydrogen ion content of the blood of the carp, Cyprinus carpio, and of Salmo iridius. Hall, et al. (1926) studied changes in the hemoglobin and red cell count of the menhaden, Brevoortia tyrannus, as affected by asphyxiation.

Further questions regarding the respiratory physiology of fish blood arise when the several species of freshwater fishes that are known

to utilize both aquatic gill-breathing and aerial breathing are considered. Black and Irving (1937) studied oxygen dissociation of the blood of the bowfin, Amia calva, an air-breather. Willmer (1934) investigated three air-breathing fishes of British Guiana, the yarrow, Erythrinus erythrinus, the electric eel, Electrophorus electricus, and the hassa, Hoplosterum littorale. G. R. Fish (1956) included Clarias mossambicus, an air-breather, in his studies of the oxygen dissociation of the blood of several fishes of Uganda. None of these studies showed the blood of air-breathers to be distinctly different from that of certain other fishes that are restricted to aquatic respiration. Dubale (1959) compared the iron content of the blood of five air-breathing fishes, Macrones gulio, Bolephthalmus dussumieri, Osphronemus gourami, Ophiocephalus striatus, and Heteropneustes fossiles with that of five fishes that are restricted to aquatic respiration. He found that all the air-breathers had more blood iron than non-air-breathers. Horn (1965) found that the rate of breathing in the bowfin increased with temperature from 50 to 90 ^{o}F. Air-breathing was more frequent in darkness than in light.

The comparison of the efficiency of bloods of different animals necessitates a more complete description than is found in the literature for air-breathing fishes. A minimal set of parameters that would allow a comparison are hemoglobin content, red cell numbers, hematocrit, pH, oxygen capacity, oxygen dissociation, and total blood volume. In this study, those parameters are investigated for the spotted gar, Lepisosteus oculatus, an air-breather. This species was chosen because it was the most easily available local air-breathing fish.

The Subject of the Study

Although several investigators of the 19th and early 20th centuries had suggested the likelihood that Lepisosteus uses the air bladder as an organ for aerial respiration, Potter (1927) was apparently the first to demonstrate the fact conclusively. His work done on the longnose gar, L. osseus, and the shortnose gar, L. platystomus, showed that these fishes would die within a few hours in water with 1.9 cc/l oxygen content unless allowed to gulp atmospheric air. Analyses of the gases in the air bladder showed a decrease in oxygen and an increase in carbon dioxide during the intervals between successive surfacings. He concluded that the swim bladder functioned as an accessory respiratory organ in these fishes. Saksena (1963) investigated four external factors--temperature, light, activity, and feeding--and found that all influenced the rate of aerial breathing in the longnose gar and the spotted gar. Winston (1967) found that both temperature and light affect aerial breathing rate in the alligator gar, L. spatula.

The spotted gar is one of five species of gars found in the United States. According to Moore (1957, page 55) it ranges from Lakes Erie and Michigan through the Mississippi river basin south to Texas and along the Gulf coast to Florida. Trautman (1957, page 163) gave the maximum size of the spotted gar as 44 inches total-length and 6 pounds in weight. In the southern part of its range where it inhabits edges of bayous (Goodyear, 1967), it frequently encounters high water temperatures.

CHAPTER II

MATERIALS AND METHODS

Experimental Animals

The gar used in these investigations were captured in Lake Texoma in the environs of the University of Oklahoma Biological Station, either by electrical shocking or in hoop nets. They were transported in large tanks to the Norman campus of the University and kept in either metal or concrete tanks supplied with continuously changing tap water. The water temperature varied seasonally from 18.0 to 26.5 ^{o}C. The fish were fed regularly a variety of living and frozen fishes including commercial bait minnows, goldfish, Mississippi silversides, mosquitofish, and white bass.[1]

Method of Drawing Blood

In all of the studies except those of blood volume, blood was obtained by heart puncture. After being weighed and measured for total length, the fish was immobilized by wrapping it tightly in wet cloth and newspaper. Then a scale on the ventral midline of the body in the region of the heart was loosened at the posterior edge with a small, stiff

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[1]All common names of North American fishes used herein conform to the American Fisheries Society Special Publication No. 2, Second Edition, 1960, "A List of Common and Scientific Names of Fishes from the United States and Canada."

scalpel. Penetration of the heart was made through the body wall under the loosened scale with a 22 gauge needle attached to a syringe and blood was drawn into the syringe. Both the syringe and needle were rinsed before use with heparin solution to prevent clotting of the blood. Of several hundred samples taken in this manner, in only a very few was there any clotting. This is contrary to the experience of several investigators. Hendricks (1952) experienced great difficulty in retarding clotting of the blood of the white sucker, Catostomus commersoni, and G. R. Fish (1956) found that the blood of Tilapia esculenta clotted frequently when oxalate anticoagulant was used.

Determinations of blood hemoglobin, hematocrit, and red cell number were made repeatedly on 39 individually marked gars over a period of several months. Sampling of individuals was done at intervals of approximately one month.

Hematocrit

Hematocrit, the relative volume of packed red cells, was measured by the "micro" method of taking whole blood into a glass capillary tube of uniform bore, sealing one end by fusion in a flame and centrifuging it for five minutes in an International micro-capillary centrifuge at 14,000 x G. The hematocrit value was then read with an International Model CR micro-capillary reader. This method of measuring hematocrit has largely replaced the older Wintrobe method and has been used for fish blood by Hesser (1960), Snieszko (1960), Larsen and Snieszko (1961b) and Normandeau (1962).

Hemoglobin

Hemoglobin was determined by the quantitative cyanmethemoglobin

method of Wintrobe (1956). Hemoglobin is here converted to stable cyanmethemoglobin and the light absorption of the solution is measured spectrophotometrically. Standard absorption curves were prepared using the commercial Hycel hemoglobin standards and diluting solution. A Coleman Model 14 Spectrophotometer was used to measure optical density of the solutions at 540 millimicrons. This technique has been employed successfully on fish blood by Gelineo and Gelineo (1955), Larsen and Snieszko (1961a), Haws and Goodnight (1962), and Larsen (1964).

Red Blood Cell Numbers

The standard clinical technique for counting red blood cells was employed (Wintrobe, 1956, p 387-389). Hendricks (1952) reported difficulties in using Haymes solution as a diluent for the blood of Catostomus but I encountered no such trouble with gar blood.

Hydrogen Ion Concentration

A Beckman Model 160 Physiological Gas Analyzer with Micro Blood pH Assembly was utilized for all pH measurements.

Blood Volume

The procedures used to estimate blood volume were slightly modified from those reported by Conte, et al. (1963) in their studies of blood volume of the steelhead trout, Salmo gairdneri gairdneri. A commercial solution of human serum albumin with radioactive iodine (I^{131}) was used for the determination of plasma volume. For estimation of the total red cell volume, red cells were tagged with radioactive chromium (Cr^{51}) in the form of sodium chromate.

Red cells were tagged for injection into a subject fish in the

following manner:

(1) Blood taken by heart puncture from a donor fish was centrifuged[1] for five minutes and most of the plasma was decanted.

(2) Sodium radiochromate solution was added to the cells, allowing approximately three microcuries of activity per milliliter of cells.

(3) Cells and isotope solution were incubated together for one hour at room temperature (23-25 ^{o}C) with occasional agitation.

(4) Cells were washed three times in approximately ten times their volume of isotonic saline, centrifuged for five minutes following the first two washes and ten minutes following the third, the supernatant wash solution being discarded each time.

(5) The tagged cells were resuspended in one-third to one-half their volume of isotonic saline and drawn into a hypodermic syringe, ready for injection.

A 0.020 ml sample of the cell suspension was measured into a counting tube as a standard to determine the total radioactivity of the cells injected into the subject fish. The radioactivity of the treated red cells ranged from 24,000 to 400,000 counts/min/ml of cells.

The radioiodinated human serum albumin solution was used as supplied by the manufacturer or was diluted further with isotonic saline to reduce the radiation count per unit volume. An amount calculated to yield about 1500 counts per minute per gram of fish was taken into a hypodermic syringe for injection. An equal volume of the isotope

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[1]All centrifugations were made in an International clinical centrifuge at 1790 x G unless specified otherwise.

preparation was diluted to 100 ml in a volumetric flask, and a measured sample was pipetted into a counting tube for a standard.

The subject fish was immobilized by wrapping it in wet newspaper and then tied ventral side up in a V-shaped wooden trough arranged to hold the head at a lower position than the tail. Water containing 166 ppm of tricaine methanesulfonate (Sandoz Pharmaceutical MS-222) was pumped over the gills through the opercular openings. The water drained into a catchpan and from there into a reservoir from which it was recirculated to the gills. Air was continuously bubbled into the anesthetic water in the reservoir. Irrigation of the gills continued throughout the operation.

When the fish was anesthetized, as indicated by a slack lower jaw, an incision was made into the pericardial cavity to expose the heart and most of the ventral aorta. A blood hematocrit sample was removed by puncturing the ventricle. The volume of this initial sample was approximately equal to the volume of the isotope preparations that were subsequently injected.

The previously prepared and measured isotope materials were injected slowly into the ventral aorta with the needle directed anteriorly.

Beginning ten minutes after the injection of the isotope preprrations, blood samples of 0.25 ml were taken from the ventricle at approximately five-minute intervals. A total of five such samples was usually made. There was no chronic cannulation of the circulatory system, so each injection or withdrawal constituted a separate penetration of the system.

The blood samples were centrifuged for ten minutes. Measured

samples of the plasma and of the packed cells were then pipetted into tubes for radiation counts.

Radiation counts of the samples and standards were made with a Tracerlab Single-Channel Gamma Spectrometer, Model SC 67 or with a Packard Alphagamma Two-Channel Spectrometer, Model 500C. Sufficient counts were made to reduce counting error to 2%. Corrections were made for background radiation and for the presence of the two different isotopes, when both were present in the same sample, by using the method of Berman, et al. (1964). This method utilizes the gamma energy peak of I^{131} at 0.600 MEV to estimate the radioactivity of the iodine in the mixed sample. This is subtracted from the combined counts of the two isotopes, I^{131} and Cr^{51} which occur at 0.31 MEV.

When the total radioactivity--either Cr^{51} or I^{131}--injected into the subject and that of a measured volume of the cells or plasma was found, the blood volume was computed according to the formula:

$$\text{Estimated Volume of Cells (or plasma)} = \frac{\text{Total count of injected material (counts/minute)}}{\text{Counts/minute/ml of cells (or plasma) extrapolated to zero-time.}}$$

The zero-time counts were computed from the radiation counts at successive time intervals by use of the formula:

$$b_o = \frac{\Sigma x_i \; \Sigma x_i y_i - \Sigma y_i \Sigma (x^2)}{(\Sigma x)^2 - n\Sigma (x^2)}$$

where b_o is the intersect of the straight line with the Y-axis, and x_i and y_i are respectively, the successive times of withdrawal of blood and the observed radiation counts of those samples. Table 1 lists the activity of the injected isotopes, the activity of each successive post-injection sample and the calculated values of the zero-time radiation count. Table 2 gives calculated values of plasma, red cells, and whole blood

for each fish examined.

Oxygen Dissociation

Solutions of hemoglobin were prepared for studying oxygen dissociation as follows:

(1) Whole blood from two or more fish was centrifuged for ten minutes and the plasma was discarded.

(2) The cells were washed twice with isotonic NaCl solution by agitating the cells with the solution for thirty seconds, centrifuging and discarding the supernatant and then repeating the washing process and centrifuging.

(3) The washed cells were lysed with a few drops of diethyl ether and the hemoglobin was taken up in a quantity of buffer estimated to yield a hemoglobin solution of approximately 4.2 g/100 ml.

(4) The buffered hemoglobin solution was centrifuged for ten minutes to yield a clear solution free from cellular debris.

The buffers consisted of mixtures of 0.1 M citric acid and 0.2 M disodium phosphate mixed to give the desired pH. The pH 7.2 buffer contained the two solutions in a ratio of about 6.7 ml of disodium phosphate to 1 ml of citric acid. The pH 7.6 buffer contained about 14.7 ml of disodium phosphate to 1 ml of citric acid. A Beckman Model 160 Physiological Gas Analyzer equipped with the accessory micro blood pH assembly was used to determine the pH of the buffers and also for all measurements of blood pH.

The hemoglobin solutions were equilibrated with mixtures of oxygen and nitrogen at 20 ^{o}C in swirl-type tonometers of the type described by Laue (1951) and by Finley, et al. (1960). Mine were constructed

from 50 ml round-bottom distillation flasks. The necks of the flasks were cut off to a length of 2 cm. Three additional openings were made in the flasks by installing two gas ports made of 2 cm length of 7 mm glass tubing and a sampling opening made of a 2 cm length of 14 mm glass tubing. These were equally spaced around the shoulder of the flask. During equilibration of the samples, gas was circulated into one and out the other of the smaller tubes. A clamp attached to the original neck of the flask held the tonometer to its rotating mechanism.

The gas mixtures were forced from large storage carboys by water pressure first through a drying tube filled with Ascarite to remove carbon dioxide and then through a bubbler containing distilled water to saturate the gas with water vapor. The gas then passed through the tonometer at a rate sufficient to effect a complete change of the gas content of the tonometer in one minute.

As described by Laue (1951) the swirling motion of the tonometer keeps a thin film of the hemoglobin solution along the walls of the vessel, insuring efficient equilibration. The tonometer was open to room air only long enough to fill a 100 λ pipette inserted through the sampling port. The solutions were equilibrated at least 15 minutes between samplings.

The oxygen content of the hemoglobin solutions was analyzed with the micromanometric Van Slyke blood gas analysis system described by Van Slyke and Plazin (1961). Of the three chemical systems described by them, experimentation indicated that the one which utilized ferricyanide solution acidified with lactic acid was the most operable since there was less coagulation of the hemoglobin solutions with it than with

either neutral or basic ferricyanide solutions. Even with this best system some coagulation usually occurred in the extraction chamber, tending to trap and hold gas bubbles. For this reason, an extraction time of 4 minutes with continuous shaking was used instead of the period of 50 seconds recommended by Van Slyke and Plazin (1961) for human blood. Triplicate determinations of each sample were made whenever the sample was adequate. Oxygen content in volumes percent was computed for each determination by use of the equations and factors given by Van Slyke and Plazin (1961). Dissolved oxygen in the samples was computed and subtracted.

After the oxygen content of the hemoglobin solutions had been measured, the equilibrating gas mixture was analyzed. Samples of the gas were removed from the stream of inflowing gas into a greased hypodermic syringe and analyzed with the apparatus described by Fry (1949). Table 3 lists the oxygen content of the hemoglobin solutions measured at various partial pressures of oxygen and at two pH levels, 7.2 and 7.6. In Figure 1 these values are graphed to show the dissociation behavior at the two pH values.

Because of the great difficulty encountered in using whole blood in the Van Slyke apparatus, I made only three attempts to measure total oxygen capacity of the blood. All three were made using pooled blood from three fish equilibrated with room air for at least 20 minutes. Table 4 gives the results of these experiments. Although I was concerned at the time that some oxygen was probably being trapped by the viscous coagulum formed during analysis, it appears that these values are likely to be valid. The expected source of error, trapping of released gas, would cause lower than actual values to result.

CHAPTER III

RESULTS AND DISCUSSION

Red Cell Numbers

Fishes have been shown to exhibit wide variations in red blood cell numbers, both among and within species. Wintrobe's (1934) data showed that certain fishes have red blood cell numbers that are lower than those of mammals and birds, but higher than those of the other vertebrates. He listed counts for 16 species of bony fishes ranging from 0.71×10^6 in the wrymouth, Cryptacanthodes maculatus, to 4.2×10^6 cells/mm^3 in the Atlantic mackerel, Scomber scombrus; the mean count for all 16 species was 1.95×10^6 cells/mm^3. Individuals, too, are known to have wide ranges at different times. Hall (1928) found an increase in the red blood cell numbers of the Atlantic menhaden and the northern puffer, Sphaeroides maculatus, during asphyxiation. Schaefer (1925) studied a starving laboratory population of pumpkinseed, Lepomis gibbosus, and noted an 85% decrease in erythrocyte numbers after 97 days of starvation. After 71 days of additional starvation the numbers were nearly up to their initial values. He believed such a reduction and recovery might occur in hibernating fishes in nature. Higgenbotham and Meyer (1948) associated low red cell numbers with poor physical condition in the southern channel catfish. Phillips (1947) found that the red cell numbers in the brook trout increased rapidly when the fish was subjected

to low oxygen concentrations. Red cell counts for a variety of fishes are given by Field, et al. (1943); Katz and Donaldson (1950); Katz (1951); Haws and Goodnight (1962); and Cairns and Scheier (1964).

Among the spotted gar that I sampled, there were large differences both among and within individuals. In a group of 39 fish that were sampled at approximately 30-day intervals from 7 to 11 months, the lowest individual mean red cell count was 2.44×10^6 cells/mm^3. Within individuals, one had a high count of 4.58×10^6 cells/mm^3 and a low of 2.31×10^6 cells/mm^3 within a 7-month period. This variation, 2.27×10^6, is significantly greater than the difference between the low and high individual means, which was 1.16×10^6. Table 5 lists red cell numbers and other parameters for individual gar over the period of study. Table 6 is a summary of these results. I was not able to discover any cause of these variations. The mean quantity that I found for the spotted gar, 3.08×10^6 cells/mm^3 is greater than that of most bony fishes that have been studied.

Hemoglobin Concentration

Wintrobe (1934) listed hemoglobin amounts for 16 species of bony fishes with a range from 2.1 g/100 ml in the yellowtail flounder, Limanda ferruginea, to 15.2 g/100 ml in the Atlantic mackerel. Gelineo and Gelineo (1955) gave 10.4 g/100 ml as the average hemoglobin value in several freshwater species that they studied. As did Wintrobe (1934), they pointed out that the hemoglobin amounts of bony fishes are typically higher than those of other poikilotherms but lower than those of the homeotherms. Field, et al. (1934) compared hemoglobin concentrations in carp and brook trout; the carp averaged 10.5 g/100 ml and trout 8.5 g/100

ml hemoglobin. Kisch (1949) found that the hemoglobin of ten species of marine teleosts averaged 8.7 g/100 ml.

Korzhuev (1963) suggested that high values of hemoglobin which he found in three species of sturgeon might be ecological adaptations for maintaining high blood oxygen tensions during their breeding season. His specimens averaged 12 g/100 ml hemoglobin and individuals reached 15 g/100 ml. Haws and Goodnight (1962) found little difference in the hemoglobin content of the blood of the channel catfish and the brown bullhead, which have quite different ecological requirements. Black (1955) found that hemoglobin in the blood of the largemouth bass, Micropterus salmoides, increased from 8.1 ± 0.43 g/100 ml to 9.9 ± 0.42 g/100 ml after 15 minutes exercise.

These cited results point up the great variability found in studies of the hemoglobin content of the blood of a number of different fishes. The group of 39 spotted gar that I studied had an average hemoglobin concentration of 9.9 g/100 ml which would appear to be very near the average for the freshwater fishes that have been investigated. As with red blood cell counts, there were greater differences within individual fish over a period of several months than between the means of individuals. The lowest hemoglobin value recorded during the period of monthly samplings was 5.6 g/100 ml (Table 5, fish #52); this fish also had the lowest individual average over a 10-month period--7.9 g/100 ml. The highest value recorded, 18.9 g/100 ml was recorded for the individual that showed the greatest variation--from 9.9 g/100 ml to 18.9 g/100 ml--within two months (Table 5, fish #15). The highest individual average was 13.2 g/100 ml (Table 5, fish #43).

One individual, not included in the group mentioned above because of an apparent diseased condition, had hemoglobin amounts ranging from 5.3 g/100 ml to 18.9 g/100 ml during an 8-month period. The blood plasma was colored orange or red, apparently due to hemolysis. The microhematocrit capillary tube showed several volumes percent of debris, which I assumed to be cell fragments, resting over the packed red cells. At the time of the highest hemoglobin values, hematocrit and red cell counts were also abnormally high. The blood was so viscous that it would not readily flow into the microhematocrit capillary.

Hematocrit

The data of MacCay (1930), Wintrobe (1934), Field, et al. (1943), and Haws and Goodnight (1962) indicate that when two or more species of fishes are compared, values of the hematocrit are correlated positively with those of the red cell count, as might be expected. Wintrobe's (1934) low value of 8.4% and high value of 59.0% were given for the yellowtail flounder and the Atlantic mackerel, respectively. These are the extremes, so far as the literature is concerned, for recorded hematocrits among fishes. Normandeau (1962) reported mean values up to 47.8% for the brook trout and up to 44.9% for the rainbow trout. Schiffman and Fromm (1959) reported an average of 31.8% for the rainbow trout.

Young (1949) found that in the opaleye, Girella nigricans, variation in the hematocrit of individuals at different times was as great as differences between individuals. This was true in only 7 of the 39 fish in my study. The lowest individual average hematocrit was 26.1% (Table 5, fish #37) and the highest average was 41.1% (Table 5, fish #43).

The mean of all individual means was 32.0 ± 0.41% (Table 6). This value is considerably lower than the values found by Normandeau (1962) for several salmonids, approximately equal to the values found by Field, et al. (1943) and by MacCay (1930) for the carp, and slightly higher than most of the values given by Wintrobe (1934) for 16 species of bony fishes.

Blood Volume

Of the several vertebrate classes, the bony fishes appear to have the lowest blood volumes (Prosser and Brown, 1961, p 389). This parameter is conventionally expressed in milliliters of blood per 100 grams of body weight, or volume-percent and herein will be expressed as percent (%). The few studies that have been made on bony fishes indicate values ranging from 1.5% to 3.0%. Derrickson and Amberson (1934) obtained a value of 1.5% for the tautog, Tautoga onitis, by washing out the blood with oxygenated Ringers solution. Lennon (1954) bled anesthetized white suckers by caudal severance and estimated the blood volume to be 1.4% This method, according to Prosser and Brown (1961, p 388) characteristically yields low values when compared to other methods of estimating blood volumes. The results of Prosser and Weinstein (1950), Martin (1950), Schiffman and Fromm (1959), and Thorson (1961) are summarized by Conte, et al. (1963). These investigators found volumes ranging from 1.8% to 3.8% in a variety of freshwater and saltwater bony fishes. The average value was 2.9%. All but Conte, et al. (1963) used dilution of some dye, usually Evans blue, also designated as T-1824, as a measure of the plasma volume and then calculated total blood volume from the hematocrit value. Conte, et al. (1963) employed Evans blue, radioiodinated human serum albumin (I^{131}) and sodium radiochromate (Cr^{51}). These substances were used

separately and in combination. Using Evans blue, they estimated the blood volume of steelhead trout to be 3.3 ± 0.7%. Using radioiodinated serum albumin to estimate plasma value, they obtained the value 2.5 ± 0.7%. Simultaneous use of serum albumin and radiochromate-tagged red blood cells gave the value 2.8 ± 1.0%.

In my study, the plasma volumes of 17 gar were estimated by the use of radioiodinated human serum albumin. The blood volumes were calculated from these estimates and the hematocrit values. In 9 of the 17 fish, radiochromate-tagged red cells were also injected for estimation of total red cell volumes. In one fish, red cell volume only was estimated by use of Cr^{51}. Table 2 lists the results of these experiments. Mean plasma volume for the 17 gar, based upon the estimate with I^{131} was 1.36 ± 0.46 ml/100g body weight. Mean whole blood volume for this group, based on total plasma volume and hematocrit was 2.22 ± 0.36 ml/100g body weight. Mean red cell volume for the group of 10 gar was 0.71 ± 0.39 ml/100g body weight when red cell volume was estimated by use of Cr^{51}. When both estimated plasma and estimated red cells were considered, mean whole blood volume for the 9 gar was 1.83 ± 0.55 ml/100g of body weight. These results indicate that blood volume of the spotted gar lies within the range of previous measurements of blood volumes in bony fishes, perhaps somewhat less than the average of all species that have been investigated.

Blood pH

When blood was taken from the gar for the oxygen dissociation studies, to be discussed later, the pH was measured with the equipment mentioned previously. A total of 40 such determinations was made.

Measured values of blood pH ranged from 7.08 to 7.73 (Table 7).

There are few reports in the literature of pH measurements made on fish blood. Powers, et al. (1939) recorded values for the carp ranging from 6.90 to 7.56; for the rock bass, Ambloplites rupestris, 6.70 to 7.47; and for the smallmouth bass, Micropterus dolomieui, 6.44 to 7.55. Willmer (1934) reported pH values from 6.2 to 6.8 for oxygenated blood of several freshwater fishes of British Guiana, which included three air-breathers, the hassa, the yarrow, and the electric eel. His method of estimating pH, using a dialysate of the blood, seems rather crude. Field, et al. (1934) reported values of 7.65 to 7.69 in the carp, and 7.28 to 7.37 in the brook trout. Haws and Goodnight (1962) found that the pH of the blood of the brown bullhead ranged from 7.54 to 7.91 and that of the channel catfish from 7.49 to 7.65. Since these last two mentioned groups of workers kept their fishes under conditions similar to mine, and since their determinations were made on freshly drawn venous blood, as mine were, their values should be more nearly comparable with mine.

Oxygen Dissociation

The oxygen dissociation curve of the gar hemoglobin solutions made at pH 7.6 indicates a moderately high affinity for oxygen (Fig. 1). The oxygen pressure for half-saturation, P_{50}, which is often taken to characterize the entire oxygen dissociation curve (Black, 1940) is 9 mm Hg. This value, 9 mm Hg, is essentially the same as Willmer recorded for the haimara, the hassa, and the electric eel, all air-breathers. These values are lower than 10 of the 15 P_{50} values listed by Prosser and Brown (1961, p 210) for various marine and freshwater teleosts, denoting

a higher oxygen affinity in these air-breathers. G. R. Fish (1956) gave data on oxygen dissociation for three other freshwater fishes having lower P_{50} values than I found for the spotted gar. These were Tilapia esculenta, Mormyrus kannume, and Bagrus docmac. The latter is an air-breather. Black (1940) found the P_{50} value of bowfin blood to be 5 mm Hg.

Krogh and Leitch (1919), Black (1940), Willmer (1934), and G. R. Fish (1956) showed that among fishes there is great variety as to the effect of acidification on the affinity of the blood for oxygen. This "Bohr effect" has been seen to some degree in nearly every species of fish investigated, but the variations are far greater than those found in the different species of mammals. Krogh and Leitch (1919) considered the large Bohr effect in freshwater fishes to be an adaptation to low environmental temperatures, allowing higher unloading tensions of oxygen in the tissues. Root (1931) found that the blood of the Atlantic mackerel, the sea robin, Prionotus carolinus, and the toadfish, Opsanus tau, all displayed large Bohr effects. Black (1940) demonstrated the same thing for the white sucker. He found that the bowfin and the brown bullhead have blood that is much less affected by increased acidity than is that of the sucker. Burke (1965) found a larger Bohr effect in the smallmouth bass, than in the largemouth bass.

Examination of the findings of the investigators just mentioned indicates that high affinity for oxygen is almost uniformly associated with a small Bohr effect in the blood of fishes. Black (1940) suggested that the principal advantage of the high oxygen affinity may lie in the ability of the fish to extract oxygen from water at high environmental temperatures. This is borne out by the findings of Irving, et al. (1940)

that increasing temperature brought about a corresponding increase in the P_{50} of the bloods of three species of trout, Salmo gairdneri, S. trutta, and Salvelinus fontinalis.

I found that the effect of lowering the pH from 7.6 to 7.2 had a moderate effect upon the oxygen affinity of the hemoglobin of the spotted gar, compared to the results of other such studies (Figure 1). Little of the work reported in the literature was done at constant pH; rather, dissociation curves at constant CO_2 tensions are usually given. However, the data of Root (1931) suggest that my results at pH 7.6 may legitimately be compared with those of other workers at 0-2 mm of CO_2 and that pH 7.2 would correspond to more than 10 mm CO_2. Such a comparison indicates that the blood of the spotted gar behaves similarly to that of the hassa and of the electric eel studied by Willmer (1934) and also to that of Clarias mossambicus and of Protopterus aethiopicus studied by G. R. Fish (1956). It appears to be only slightly less sensitive to acid than that of the bowfin, investigated by Black (1940). Two other freshwater fishes, the brown bullhead and the carp, which seem to have habitat preferences very near those of the spotted gar were shown by Black (1940) to have oxygen affinities as high as or higher than that of the spotted gar and to display a Bohr effect of about the same magnitude as that of the spotted gar.

A comparison of the two dissociation curves reveals an additional effect that has been noted before in fish bloods; namely, the reduction in total oxygen capacity of the hemoglobin at lowered pH values. Root (1931) noted loss of oxygen capacity in mackerel blood with increasing hydrogen ion concentration; Irving, et al. (1940) found that trout hemoglobin is unsaturated at oxygen pressures of 150 mm Hg in the presence

of CO_2; Scholander (1957) showed that for the blood of the silver hake, Merluccius bilinearis, at pH 7.0, saturation was achieved only with oxygen pressures over 40 atmospheres.

Oxygen Capacity of Whole Blood

Examination of the literature revealed that higher oxygen capacities than those reported here for the spotted gar (Table 4) are known for only three species of fishes. Root (1931) reported the Atlantic mackerel to have a blood oxygen capacity of 15.77 vol. % and Willmer (1934) reported 18.14 vol. % and 19.75 vol. % respectively for the hassa and the electric eel, both of which are air-breathers. Most other reported capacities are much lower, especially those of marine fishes. Five marine species reported by Root (1931), the goosefish, Lophius americanus, the toadfish, the northern puffer, the northern sea robin, and the scup, Stenotomus chrysops, all had oxygen capacities of less than 8 vol. %. Root's conclusion that active fishes have greater oxygen capacity than more sluggish fishes has not been borne out by subsequent investigators. My own observations suggest that the spotted gar is quite sluggish under most circumstances and that it has a high blood oxygen capacity.

CHAPTER IV

SUMMARY

The foregoing investigations of various respiratory functions of the blood of the spotted gar have revealed that this fish is not unique in any of the parameters that have been studied. It appears to be somewhat outstanding in having a definitely higher red blood cell count and higher blood oxygen capacity than most other bony fishes that have been studied. Like most other freshwater species of fishes that may be found in warm, shallow waters in at least part of their range, the spotted gar has hemoglobin with a high affinity for oxygen which is not markedly lowered by acidification. Since both oxygen affinity and oxygen capacity may be expected to diminish as environmental temperature increases, these characteristics may be adaptations that allow the fish to withstand the increased temperatures without an injurious loss in blood oxygen capacity.

It appears from this study and other studies that the various respiratory functions of the blood of fishes are much more closely related to the habitats of the fishes than to the source of their oxygen. Since most air-breathing fishes inhabit warm, shallow waters where oxygen tensions are low and carbon dioxide tensions are often high, their blood is similar to that of fishes restricted to aquatic respiration in the same types of habitats.

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APPENDIX

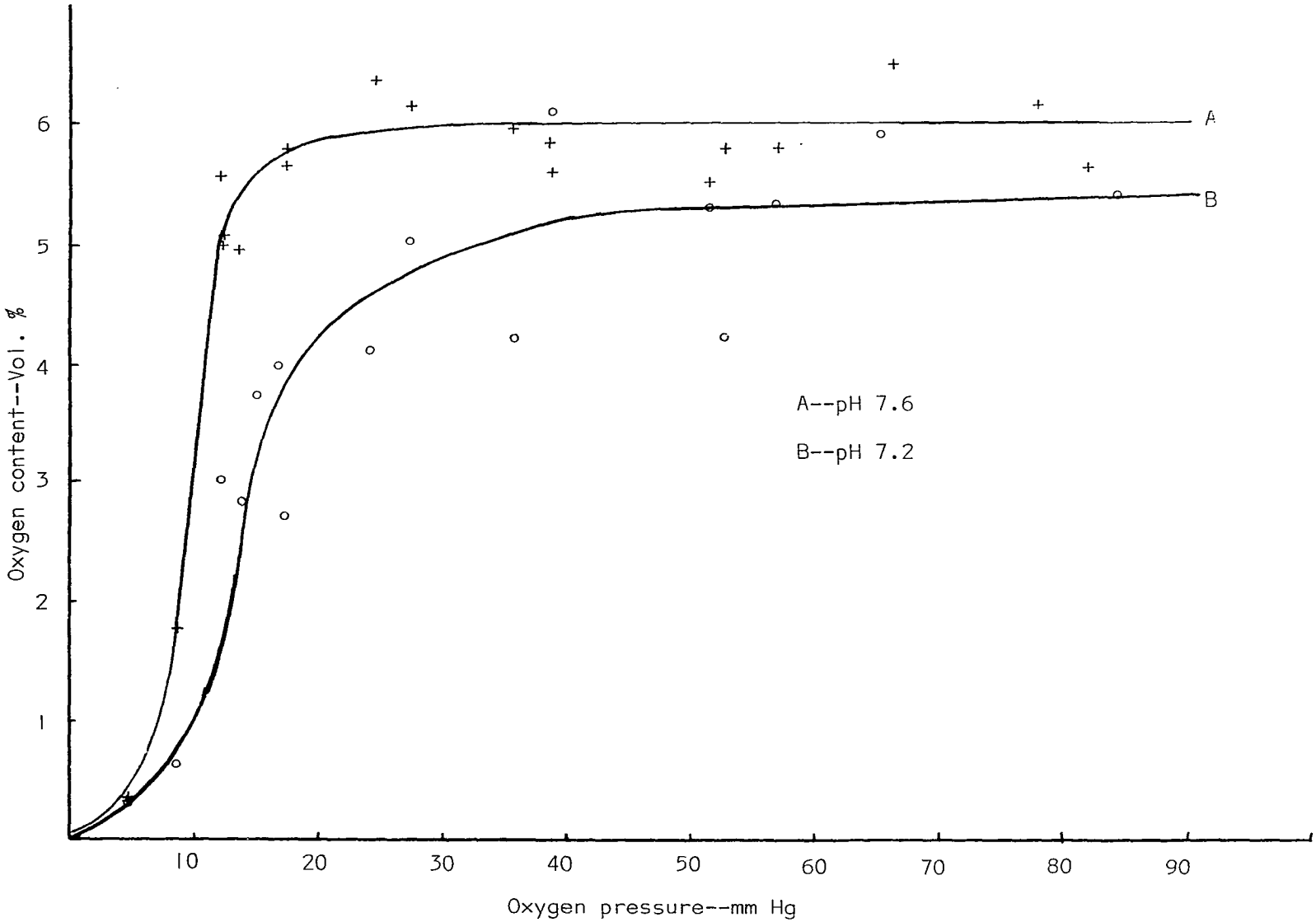

Figure 1. Oxygen dissociation curves of solutions of hemoglobin of the spotted gar.

TABLE 1

Radiation Counts of Injected Materials, Plasma, and Cell Samples

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
1	202,400		10	9,500			
			20	9,210			
			30	8,180			
			40	7,980	10,175		
2	683,000		10	127,000			
			15	140,000			
			21	114,000			
			27	129,000			
			32	132,000	151,000		
3	670,000	53,700	10	87,800		42,170	
			16	75,000		42,200	
			22	69,000		34,900	
			28	55,630		32,400	49,510
			34	54,140	100,238	-	

TABLE 1--(Continued)

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
4	741,600	14,800	10	78,120		7,600	
			15	77,760		6,240	
			21	66,240		6,700	
			26	70,000		5,920	
			31	59,380	87,900	5,800	7,956
5	659,600		10	99,740			
			22	82,400			
			27	76,520			
			32	72,460	111,608		
6	984,700		10	86,900			
			15	87,700			
			20	92,540			
			25	83,660			
			30	84,500	90,566		

TABLE 1--(Continued)

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
7	1,346,000	95,660	10	328,300			
			16	314,400		48,760	
			22	315,400		42,900	
			28	290,500	347,740	39,900	72,851
8		163,600	10			32,700	
			15			30,970	
			21			30,400	
			26			31,540	
			32			33,000	31,247
9	1,363,000	162,700	10	105,980		17,100	
			15	105,360		16,280	
			20	102,700		15,400	
			25	102,050		16,560	17,210
			30	90,620	114,968	-	

TABLE 1--(Continued)

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
10	720,800		10	84,170			
			16	74,140			
			22	73,200			
			27	60,400			
			32	57,450	95,899		
11	450,500	145,800	10	63,520		39,860	
			15	63,620		33,080	
			20	57,720		27,460	
			26	49,500		25,300	
			31	50,100	72,778	22,120	46,105
12	901,000	211,680	11	80,160		16,990	
			16	79,870		17,270	
			21	73,860		16,440	
			26	70,150		14,820	
			32	70,740	86,465	15,720	18,242

TABLE 1--(Continued)

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
13	1,359,500	393,480	10	120,400	-	-	
			15	110,090		47,900	
			20.5	-		41,170	
			25.5	107,550		31,820	
			30	101,114	126,077	26,730	70,065
14	1,579,900		10	57,480			
			15	45,470			
			22	41,340			
			27	33,180			
			32	29,920	66,869		
15	560,700		10	61,310			
			15	59,920			
			20.5	62,500			
			25.5	60,320	60,975		

TABLE 1--(Continued)

Run no.	Radiation counts of injected isotopes counts/minute I^{131}	Cr^{51}	Sampling time, minutes after injection	Radiation counts of plasma and cell samples: I^{131} counts in plasma counts/min/ml	Calculated zero-time radiation counts/min/ml	Cr^{51} counts in cells counts/min/ml	Calculated zero-time radiation counts/min/ml
16	1,839,100	197,100	10	105,700		-	
			15	93,700		17,860	
			20	100,900		15,040	
			25	105,500		14,730	
			30	90,800	106,502	17,060	17,378
17	3,678,200		10	164,800			
			15	155,200			
			20.5	149,500			
			25	134,200			
			30	149,100	177,629		
18	1,399,100	192,096	10	93,650		15,920	
			15	104,420		18,530	
			20	107,120		15,450	
			27	102,240		15,640	
			32	94,810	100,910	14,000	18,369

TABLE 2

Red Blood Cell, Plasma and Blood Volumes of the Spotted Gar

Run no.	Sex	Length cm	Weight g	Hematocrit %	Plasma volume ml	Plasma ml/100 g body wt	Red cell volume ml	Red cells ml/100 g body wt	Based on hematocrit and plasma volume: Total blood ml	Based on hematocrit and plasma volume: Whole blood ml/100 g body wt	Based on plasma and cell volume: Total blood ml	Based on plasma and cell volume: Whole blood ml/100 g body wt
1	M	64.4	1022	49.0	19.9	1.95	-	-	39.0	3.82	-	-
2	M	-	468	38.5	4.52	0.97	-	-	7.35	1.57	-	-
5	M	52.0	480	32.0	5.68	1.18	-	-	8.35	1.74	-	-
6	M	57.5	713	50.0	10.3	1.44	-	-	20.6	2.89	-	-
10	M	59.1	770	46.0	7.51	0.98	-	-	13.9	1.80	-	-
14	F	63.3	1028	24.0	23.6	2.30	-	-	32.0	3.02	-	-
15	M	56.3	380	31.5	9.20	2.42	-	-	13.4	3.53	-	-
17	F	76.3	1572	29.3	20.7	1.32	-	-	29.3	1.86	-	-
3	F	55.7	608	29.2	6.68	1.10	1.08	0.18	9.44	1.55	7.76	1.28
4	-	60.0	802	51.6	8.43	1.05	1.86	0.23	17.4	2.17	10.3	1.28
7	M	49.5	370	28.8	3.84	1.04	1.31	0.35	5.39	1.46	5.15	1.39
9	F	64.6	1162	44.0	11.8	1.02	9.45	0.81	21.4	1.84	21.2	1.83
11	F	56.9	664	44.5	6.19	0.93	3.16	0.48	11.2	1.69	9.32	1.41
12	M	60.9	922	48.0	10.4	1.13	11.6	1.26	20.0	2.17	22.0	2.39
13	M	65.1	828	45.8	10.7	1.29	5.61	0.68	19.7	2.38	16.3	1.97
16	M	64.5	1010	39.4	17.3	1.71	11.3	1.12	28.5	2.82	28.6	2.83
18	F	62.9	1118	38.8	13.9	1.24	10.4	0.93	22.7	2.03	24.3	2.17
8	M	54.4	478	40.0	-	-	5.23	1.09	-	-	13.1	2.74 *
					Means	1.36 ± 0.46		0.71 ± 0.39		2.22 ± 0.36		1.83 ± 0.55

* This value not included in computing mean.

TABLE 3

Oxygen Content of Hemoglobin Solutions Equilibrated at Various Partial Pressures of Oxygen

Run no. at pH 7.2	PO_2 mm Hg	O_2 content vol. %	Hemoglobin g/100 ml	Calculated O_2 content w/ 4.2 g/100 ml Hemoglobin
108	24.7	3.91	4.0	4.10
110	35.7	4.24	4.2	4.24
113	52.9	4.45	5.0	4.16
116	12.4	2.88	4.0	3.02
120	12.9	3.69	4.2	3.69
122	57.1	4.97	3.9	5.35
124	17.4	2.57	3.9	2.77
126	27.3	5.42	4.5	5.06
128	66.0	6.32	4.5	5.90
130	8.7	0.67	4.2	0.67
134	13.7	2.77	4.15	2.80
138	4.9	0.37	5.2	0.30
140	17.3	4.38	4.6	4.00
143	82.0	5.90	4.6	5.39
145	38.9	6.42	4.4	6.13
147	51.3	5.54	4.4	5.29

TABLE 3--(Continued)

Run no. at pH 7.6	PO_2 mm Hg	O_2 content vol. %	Hemoglobin g/100 ml	Calculated O_2 content w/ 4.2 g/100 ml Hemoglobin
107	24.7	4.83	3.2	6.33
109	35.8	4.50	3.2	5.91
111	38.5	5.82	4.2	5.82
112	52.9	5.79	4.2	5.79
115	12.4	5.58	4.2	5.58
118	12.4	6.06	5.0	5.09
119	12.4	4.79	4.0	5.03
121	12.9	5.88	4.6	5.37
123	57.1	5.78	4.2	5.78
125	17.4	4.76	4.2	4.76
127	27.3	6.53	4.4	6.23
129	66.0	6.83	4.4	6.52
131	8.7	1.63	3.9	1.76
133	13.7	4.75	4.0	4.99
137	4.88	0.46	4.9	0.39
139	17.3	5.63	4.2	5.63
141	77.8	8.79	6.0	6.15
144	82.0	5.92	4.4	5.65
146	38.9	6.10	4.6	5.57
148	51.3	5.50	4.2	5.50

TABLE 4

Oxygen Capacity of Whole Blood of the Spotted Gar

Run no.	Oxygen partial pressure mm Hg	Oxygen Capacity vol. %
76	150+ (atmospheric)	16.72
77	150+ (atmospheric)	14.99
78	150+	15.26
	Mean	15.66

TABLE 5

Red Cell Counts, Hematocrit, Hemoglobin, and pH Data for Individual Fish

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
1	12/18/62	3.38	37.9	-	-
	4/18/63	2.28	27.6	7.9	-
	5/18/63	3.75	35.5	10.7	-
	7/4/63	3.12	35.4	11.0	-
	8/3/63	2.36	32.0	10.3	-
	9/6/63	2.94	36.2	11.7	-
	10/4/63	2.11	24.6	8.5	-
	11/1/63	3.41	35.8	10.3	-
	11/25/63	3.06	30.1	9.6	-
	8/11/65	-	-	10.1	-
	8/23/65	-	-	9.8	7.40
	11/2/65	-	-	9.8	7.58
2	12/10/62	2.92	34.7	-	-
	4/18/63	1.64	25.4	7.3	-
	6/17/63	2.77	35.0	11.8	-
	7/17/63	3.33	37.1	11.5	-
	8/19/63	3.64	39.6	12.5	-
	9/20/63	1.64	21.2	7.1	-
	10/18/63	3.66	33.5	10.3	-
	11/15/63	3.48	34.4	9.9	-
	12/13/63	3.18	28.3	8.3	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
4	12/11/62	3.00	38.6	-	-
	4/3/63	2.34	28.7	8.3	-
	5/7/63	3.02	36.7	11.2	-
	6/7/63	3.15	34.3	10.9	-
	7/8/63	2.98	37.2	11.3	-
	8/8/63	3.09	34.1	9.5	-
	9/6/63	3.60	32.8	11.3	-
	11/1/63	3.22	38.2	10.9	-
	12/6/63	2.89	33.0	9.7	-
5	12/17/62	2.83	36.6	-	-
	4/18/63	2.44	36.4	11.2	-
	5/17/63	3.09	36.1	11.6	-
	6/17/63	2.90	38.5	11.4	-
	7/17/63	2.60	33.2	10.6	-
	8/3/63	3.23	35.8	12.4	-
	8/19/63	2.24	25.6	8.4	-
	9/20/63	3.53	37.6	12.0	-
	10/18/63	3.24	36.2	11.8	-
	11/15/63	3.14	35.4	11.2	-
	12/13/63	2.63	31.8	8.6	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
7	12/18/62	2.28	-	-	-
	5/7/63	2.10	30.3	11.0	-
	6/7/63	2.38	28.4	8.7	-
	7/8/63	2.68	28.6	9.5	-
	8/8/63	2.74	30.2	10.0	-
	9/6/63	2.98	36.2	11.5	-
	10/4/63	2.32	29.0	9.5	-
	11/1/63	2.68	27.4	8.8	-
	11/25/63	2.40	25.8	8.2	-
9	12/4/62	2.25	27.8	-	-
	1/9/63	2.21	24.4	-	-
	4/23/63	2.26	25.5	7.9	-
	5/23/63	2.50	26.6	8.8	-
	6/22/63	2.31	23.7	7.7	-
	7/23/63	2.72	27.6	8.7	-
	8/23/63	2.49	32.0	10.1	-
	9/22/63	2.44	25.6	8.3	-
	10/18/63	2.80	26.8	8.4	-
	8/17/65	-	-	8.3	7.47
	9/18/65	-	-	5.8	7.48

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
13	4/18/63	2.68	32.7	10.7	-
	5/16/63	2.83	28.4	8.4	-
	6/17/63	2.52	32.6	10.0	-
	7/17/63	2.92	32.4	10.2	-
	9/20/63	3.51	32.4	10.7	-
	10/18/63	2.78	30.3	9.5	-
	11/15/63	3.13	32.6	10.0	-
	12/13/63	3.02	32.0	8.9	-
15	3/27/63	2.58	35.2	10.8	-
	4/26/63	3.66	41.0	18.9	-
	5/30/63	3.81	37.4	12.0	-
	6/30/63	2.88	33.1	9.9	-
	7/31/63	4.22	40.4	11.7	-
	8/28/63	3.46	36.6	10.8	-
	11/25/63	3.63	35.8	11.0	-
	8/21/65	-	-	9.0	7.56
17	3/26/63	3.56	29.2	9.0	-
	4/25/63	1.91	20.7	5.8	-
	6/29/63	3.21	25.2	8.0	-
	7/31/63	3.74	29.0	9.2	-
	8/28/63	3.15	29.6	8.9	-
	9/27/63	3.30	26.8	8.1	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(17)	10/25/63	3.34	27.0	7.8	-
	11/22/63	3.12	25.8	7.3	-
18	2/6/63	3.39	35.8	-	-
	4/22/63	3.85	57.2	15.6	-
	5/22/63	4.12	42.6	12.9	-
	6/21/63	2.58	34.0	10.2	-
	7/22/63	3.98	35.5	12.0	-
	8/22/63	3.42	38.4	13.2	-
	9/20/63	3.62	41.8	13.7	-
	10/18/63	3.40	39.1	12.0	-
	11/18/63	3.50	38.8	12.0	-
	12/13/63	3.40	36.8	10.3	-
19	3/13/63	-	35.0	-	-
	3/28/63	2.31	28.8	9.4	-
	6/7/63	2.76	28.0	9.4	-
	7/8/63	3.40	29.0	9.9	-
	8/8/63	3.18	35.0	11.3	-
	9/6/63	3.60	36.2	10.9	-
	10/4/63	3.30	35.8	10.6	-
	11/25/63	4.58	35.5	10.4	-
	8/10/65	-	-	10.9	7.5

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
20	4/23/63	1.71	21.9	6.9	-
	5/22/63	3.93	39.6	12.4	-
	6/21/63	3.26	38.8	11.7	-
	7/22/63	3.56	38.8	13.1	-
	8/22/63	2.64	32.2	9.9	-
	9/22/63	3.84	41.6	13.3	-
	10/18/63	3.77	39.0	12.0	-
	11/15/63	3.87	39.2	12.2	-
	12/13/63	3.06	33.8	9.7	-
24	4/18/63	3.55	37.5	12.0	-
	5/17/63	3.10	36.1	10.8	-
	6/18/63	3.54	38.3	12.3	-
	7/22/63	3.72	43.6	14.5	-
	8/19/63	3.36	41.0	13.6	-
	9/20/63	4.08	42.6	13.9	-
	10/18/63	3.54	40.7	13.5	-
	11/15/63	3.67	43.1	12.8	-
	12/13/63	3.66	38.0	11.2	-
	8/16/65	-	-	11.3	7.43
25	4/23/63	2.45	33.0	9.6	-
	5/30/63	3.15	30.6	10.6	-
	6/30/63	2.60	32.6	10.5	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(25)	7/31/63	2.96	31.6	10.6	-
	8/28/63	1.78	20.8	6.9	-
	9/28/63	2.47	26.9	8.3	-
	12/6/63	3.28	32.5	9.1	-
26	4/24/63	2.44	26.4	7.7	-
	5/24/63	-	25.3	8.2	-
	6/25/63	1.71	18.6	7.7	-
	7/25/63	3.43	28.4	9.2	-
	8/26/63	3.46	30.9	10.3	-
	9/27/63	2.96	26.5	8.3	-
	10/25/63	2.78	25.8	7.6	-
	11/22/63	3.56	29.7	8.3	-
27	4/22/63	2.84	38.8	11.2	-
	5/23/63	3.39	39.0	12.1	-
	6/23/63	2.85	32.2	10.6	-
	7/25/63	2.58	24.2	7.5	-
	8/26/63	2.76	33.0	10.8	-
	9/28/63	3.48	35.2	11.3	-
	10/26/63	3.12	34.8	10.5	-
	12/6/63	3.46	33.6	9.8	-
28	4/4/63	2.82	32.2	9.5	-
	5/2/63	3.18	32.8	10.8	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(28)	6/4/63	2.64	28.2	8.6	-
	7/4/63	2.60	28.9	8.9	-
	8/3/63	2.40	24.6	8.3	-
	9/6/63	2.51	30.4	9.8	-
	10/4/63	3.32	29.1	9.6	-
	11/1/63	3.78	26.2	8.2	-
	11/25/63	3.24	30.2	9.1	-
30	3/28/63	2.52	32.8	10.7	-
	5/1/63	2.86	30.7	9.9	-
	5/31/63	2.92	31.5	10.2	-
	7/2/63	2.44	31.4	9.1	-
	8/1/63	3.22	34.2	11.1	-
	9/29/63	2.72	29.6	10.0	-
	10/26/63	3.42	34.4	10.2	-
	12/6/63	3.48	35.3	10.3	-
31	4/22/63	2.74	35.7	10.4	-
	5/22/63	3.36	33.2	10.5	-
	7/23/63	2.89	32.7	10.3	-
	8/23/63	3.63	40.0	12.2	-
	9/22/63	3.50	40.0	11.1	-
	10/18/63	3.54	36.0	11.2	-
	11/15/63	3.39	37.0	10.9	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(31)	12/13/63	3.77	34.8	9.9	-
32	4/22/63	2.48	34.2	10.1	-
	5/23/63	3.80	38.6	11.6	-
	7/23/63	3.42	38.0	12.6	-
	8/23/63	3.15	41.2	13.1	-
	9/22/63	4.09	38.2	12.9	-
	10/18/63	3.54	40.4	12.4	-
	11/15/63	3.66	39.0	12.1	-
	12/13/63	4.05	38.8	10.8	-
33	4/22/63	1.71	22.3	6.6	-
	5/23/63	3.20	30.2	9.6	-
	6/22/63	2.26	25.6	8.9	-
	7/23/63	1.83	22.4	7.6	-
	8/23/63	2.30	26.0	9.0	-
	9/20/63	2.32	30.6	9.9	-
	11/15/63	4.88	51.5	13.5	-
	12/13/63	2.91	28.5	8.0	-
35	4/23/63	3.08	32.6	9.5	-
	5/23/63	3.96	32.3	9.9	-
	6/24/63	2.82	32.5	9.3	-
	7/25/63	4.24	32.8	9.9	-
	8/26/63	3.01	30.3	9.9	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(35)	9/28/63	2.82	27.6	9.1	-
	10/26/63	3.63	30.2	8.8	-
	12/6/63	3.36	30.6	8.5	-
37	4/4/63	3.77	27.6	7.8	-
	5/2/63	2.74	27.2	8.1	-
	5/31/63	3.00	29.9	8.4	-
	7/2/63	2.76	26.1	8.2	-
	8/1/63	2.69	22.8	8.0	-
	8/29/63	3.32	26.3	8.0	-
	10/4/63	2.94	22.4	7.3	-
	11/1/63	3.37	26.6	8.0	-
	8/3/65	-	-	8.1	7.48
	9/28/65	-	-	6.6	7.65
	10/12/65	-	-	5.4	7.58
38	3/15/63	-	28.0	9.4	-
	3/28/63	-	28.6	-	-
	5/1/63	2.56	33.1	8.3	-
	5/31/63	3.24	32.2	9.6	-
	7/2/63	3.25	33.4	10.3	-
	8/1/63	3.94	36.5	11.6	-
	8/29/63	3.16	28.6	10.6	-
	9/27/63	3.14	32.1	-	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(38)	10/28/63	3.11	32.4	9.0	-
	11/22/63	3.54	32.0	8.9	-
	12/23/63	3.86	31.2	9.2	-
39	4/24/63	2.40	37.1	10.3	-
	5/24/63	2.96	38.7	11.5	-
	6/25/63	2.68	35.0	10.7	-
	7/25/63	2.63	38.0	11.8	-
	8/26/63	3.08	38.2	12.2	-
	9/27/63	2.86	33.4	9.7	-
	10/26/63	2.66	31.2	10.6	-
	12/6/63	3.03	33.5	9.8	-
40	4/4/63	2.69	37.4	11.2	-
	4/23/63	2.68	27.0	8.1	-
	5/30/63	2.78	34.7	10.8	-
	6/30/63	2.50	28.8	9.1	-
	8/29/63	3.19	36.4	11.4	-
	9/28/63	3.52	35.4	11.8	-
	10/26/63	3.18	38.3	11.3	-
	11/25/63	3.57	39.0	11.4	-
41	5/23/63	2.60	33.1	9.9	-
	6/24/63	2.82	29.6	9.4	-
	7/25/63	3.05	35.2	10.6	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(41)	8/26/63	3.40	34.0	11.1	-
	9/28/63	3.39	41.0	13.2	-
	10/26/63	3.15	32.2	9.8	-
	12/6/63	3.03	30.3	9.2	-
43	3/13/63	-	41.1	-	-
	4/8/63	3.30	41.2	13.7	-
	5/7/63	2.70	38.7	12.2	-
	6/7/63	2.89	38.8	12.9	-
	7/8/63	3.65	41.3	13.8	-
	8/8/63	4.63	47.1	15.3	-
	10/4/63	3.79	42.8	13.6	-
	11/1/63	4.26	41.0	12.8	-
	11/25/63	3.62	38.1	11.7	-
44	3/27/63	2.66	31.6	9.8	-
	4/26/63	2.96	31.9	13.5	-
	5/30/63	3.68	30.4	9.0	-
	6/30/63	2.58	24.9	8.4	-
	7/31/63	3.42	32.8	10.9	-
	8/28/63	2.20	28.9	9.0	-
	9/28/63	2.88	32.6	10.3	-
	10/26/63	3.52	33.1	9.7	-
	1/25/64	3.21	36.2	10.3	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
45	3/26/63	2.92	33.9	9.2	-
	4/25/63	2.35	-	8.7	-
	5/29/63	3.31	-32.8	9.7	-
	6/29/63	2.49	30.4	10.0	-
	7/30/63	2.90	31.2	10.9	-
	8/27/63	3.50	30.8	9.8	-
	9/27/63	3.04	24.8	8.8	-
	10/25/63	3.50	29.8	7.7	-
	11/23/65	3.42	29.6	8.5	-
47	3/27/63	3.05	35.0	11.0	-
	4/27/63	2.46	30.0	8.7	-
	5/30/63	2.87	29.6	9.2	-
	6/30/63	2.78	30.3	8.4	-
	7/31/63	3.49	31.2	9.8	-
	9/6/63	2.14	20.2	6.1	-
	10/4/63	2.44	19.5	6.0	-
	11/1/63	2.84	23.0	6.6	-
	12/6/63	2.52	24.5	6.8	-
48	4/17/63	3.40	32.2	9.0	-
	5/16/63	3.19	28.2	11.3	-
	6/18/63	2.52	27.0	8.0	-
	7/22/63	4.34	36.8	11.6	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(48)	8/19/63	2.84	28.4	8.4	-
	9/20/63	2.82	25.9	8.3	-
	10/18/63	3.38	33.1	9.4	-
	11/22/63	2.96	-	8.4	-
	12/23/63	3.34	31.7	9.3	-
49	4/3/63	2.45	31.0	7.8	-
	5/2/63	3.08	30.8	9.5	-
	5/31/63	2.92	32.0	9.7	-
	7/4/63	3.06	33.2	10.2	-
	8/1/63	4.07	33.0	10.6	-
	8/29/63	3.13	28.4	9.1	-
	10/4/63	3.26	27.2	9.1	-
	11/1/63	3.26	30.5	9.2	-
	12/6/63	3.66	30.1	8.8	-
51	4/17/63	1.98	21.0	6.4	-
	5/16/63	2.79	30.5	9.0	-
	6/18/63	2.24	26.0	8.1	-
	7/18/63	2.86	33.6	10.3	-
	8/22/63	3.17	37.3	12.1	-
	9/20/63	3.04	-	10.3	-
	10/25/63	3.66	33.0	9.6	-
	11/22/63	3.24	32.6	9.1	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
52	3/26/63	2.02	20.4	7.1	-
	4/25/63	1.72	19.7	5.6	-
	5/29/63	3.22	30.5	8.4	-
	6/29/63	2.83	26.3	8.4	-
	7/30/63	3.02	26.9	8.6	-
	8/27/63	3.22	29.4	9.3	-
	9/27/63	3.16	26.2	8.0	-
	10/25/63	3.71	28.0	8.0	-
	11/22/63	3.50	26.2	7.7	-
	12/23/63	2.84	24.8	7.6	-
53	3/27/63	2.84	27.6	9.9	-
	4/27/63	2.30	26.0	7.1	-
	5/29/63	3.22	32.8	10.3	-
	6/29/63	3.09	28.6	9.4	-
	7/30/63	3.96	32.8	10.6	-
	8/27/63	3.50	29.2	9.3	-
	9/27/63	3.43	26.5	9.1	-
	10/25/63	3.18	27.3	7.9	-
	12/23/63	2.68	25.0	7.3	-
56	3/25/63	2.20	25.0	7.5	-
	4/25/63	1.89	20.5	6.9	-
	5/29/63	2.83	27.8	8.2	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(56)	6/29/63	2.74	25.4	8.2	-
	7/30/63	2.82	26.5	8.8	-
	8/27/63	2.98	28.0	8.5	-
	9/27/63	3.22	27.6	8.5	-
	10/25/63	2.74	28.0	7.7	-
	11/22/63	3.79	28.0	8.0	-
	12/23/63	3.47	32.7	8.7	-
	8/25/65	-	-	7.6	7.43
58	4/4/63	3.49	39.1	10.4	-
	5/2/63	3.16	35.0	11.0	-
	5/31/63	2.76	32.3	9.5	-
	7/2/63	2.97	32.6	10.0	-
	8/1/63	3.94	39.6	12.8	-
	8/29/63	3.84	37.0	12.3	-
	10/4/63	3.32	31.9	11.3	-
	11/4/63	3.34	36.8	10.5	-
	12/6/63	3.20	34.1	9.7	-
59	3/25/63	3.08	32.5	8.6	-
	4/25/63	2.28	23.4	7.1	-
	5/30/63	2.81	27.0	8.0	-
	6/29/63	3.08	28.0	8.7	-
	7/31/63	4.23	32.8	10.0	-

TABLE 5--(Continued)

Fish no.	Date	Red Cells millions/mm^3	Hemato-crit %	Hemoglobin g/100 ml blood	pH
(59)	8/29/63	3.44	29.5	9.4	-
	9/28/63	3.10	26.4	8.5	-
	10/25/63	3.74	31.4	8.8	-
	11/22/63	3.68	28.0	8.0	-
	12/23/63	4.16	32.8	9.2	-

TABLE 6

Summary of Red Cell Counts, Hematocrits, and Hemoglobin of Individual Spotted Gar

Fish no.	Red blood cell count 10^6 cells/mm^3 Mean	Range	No. of Samples	Hematocrit % Mean	Range	No. of Samples	Hemoglobin g/100 ml Mean	Range	No. of Samples
1	2.93	2.11-3.75	9	32.8	24.6-37.9	9	10.0	7.9-11.7	11
2	2.92	1.64-3.66	9	32.1	21.2-39.6	9	9.8	7.1-12.5	8
4	3.03	2.34-3.60	9	30.6	28.7-38.6	9	10.4	8.3-11.3	8
5	2.90	2.24-3.53	11	34.8	31.8-38.5	11	10.9	8.4-12.4	10
7	2.51	2.10-2.98	9	29.5	25.8-36.2	8	9.6	8.2-11.5	8
9	2.44	2.21-2.80	9	26.7	23.7-32.0	9	8.2	5.8-10.1	9
13	2.92	2.52-3.51	8	31.7	28.4-32.7	8	9.8	8.4-10.7	8
15	3.46	2.58-4.22	7	37.1	33.1-41.0	7	11.8	9.0-18.9	8
17	3.17	1.91-3.74	8	26.7	20.7-29.6	8	8.0	5.8- 9.2	8
18	3.53	3.39-4.12	10	40.0	35.5-57.2	10	12.4	10.2-15.6	9
19	3.30	2.31-4.58	7	29.4	28.0-35.8	8	10.4	9.4-11.3	8
20	3.29	1.71-3.93	9	36.1	21.9-41.6	9	11.2	6.9-13.3	9
24	3.58	3.10-4.08	9	40.1	36.1-43.6	9	12.6	10.8-14.5	10
25	2.81	1.78-3.28	7	29.7	20.8-33.0	7	9.4	6.9-10.6	7
26	2.90	1.71-3.56	7	26.4	18.6-30.9	8	8.4	7.6-10.3	8
27	3.06	2.58-3.48	8	33.8	24.2-39.0	8	10.5	7.5-12.1	8
28	2.94	2.40-3.78	9	29.2	24.6-32.8	9	9.2	8.2-10.8	9
30	2.95	2.44-3.48	8	32.5	29.6-35.3	8	10.2	9.1-11.1	8
31	3.35	2.74-3.77	8	36.2	32.7-40.0	8	10.8	9.9-12.2	8
32	3.51	3.15-4.09	8	38.5	34.2-38.2	8	12.0	10.1-13.1	8

TABLE 6--(Continued)

Fish no.	Red blood cell count 10^6 cells/mm^3 Mean	Range	No. of Samples	Hematocrit % Mean	Range	No. of Samples	Hemoglobin g/100 ml Mean	Range	No. of Samples
33	2.67	1.71-4.88	8	29.6	22.3-51.5	8	9.1	6.6-13.5	8
35	3.36	2.82-4.24	8	31.1	27.6-32.8	8	9.4	8.5- 9.9	8
37	3.07	2.69-3.77	8	26.1	22.8-29.9	8	7.6	5.4- 8.4	11
38	3.31	3.11-3.94	9	32.6	28.0-36.5	11	9.8	8.3-11.6	9
39	2.79	2.40-3.08	8	35.6	31.2-38.7	8	10.8	9.7-12.2	8
40	3.01	2.50-3.57	8	34.6	27.0-39.0	8	10.6	8.1-11.8	8
41	3.06	3.60-3.40	7	33.6	29.6-41.0	7	10.4	9.2-11.1	7
43	3.60	2.70-4.63	8	41.1	38.1-47.1	9	13.2	11.7-15.3	8
44	3.01	2.20-3.68	9	31.4	24.9-36.2	9	10.1	8.4-13.5	9
45	3.05	2.35-3.50	9	30.4	24.8-33.9	8	9.2	7.7-10.9	9
47	2.73	2.14-3.49	9	27.0	19.5-35.0	9	8.0	6.0-11.0	9
48	3.20	2.52-4.34	9	30.4	25.9-36.8	8	9.3	8.0-11.6	9
49	3.21	2.45-4.07	9	30.7	27.2-33.2	9	9.3	7.8-10.6	9
51	2.87	1.98-3.66	8	32.0	21.0-37.3	7	9.4	6.4-12.1	8
52	2.92	2.02-3.71	10	25.8	19.7-30.5	10	7.9	5.6- 9.3	10
53	3.13	2.30-3.96	9	28.2	25.0-32.8	9	9.0	7.1-10.3	9
56	2.87	1.89-3.79	10	27.0	20.5-32.7	10	8.9	6.9-8.8	11
58	3.34	2.76-3.94	9	35.4	31.9-39.6	9	10.8	9.5-12.8	9
59	3.36	2.28-4.23	10	29.2	23.4-32.8	10	8.6	7.1-10.0	10
Means	3.08 ± 0.03			32.0 ± 0.41			9.9 ± 0.28		

TABLE 7

Blood pH of the Spotted Gar

pH Range	No. of observations
Less than 7.11 (7.08)	1
7.11-7.20	0
7.21-7.30	3
7.31-7.40	10
7.41-7.50	18
7.51-7.60	4
7.61-7.70	3
Greater than 7.70 (7.73)	1