III. RESPIRATION IN FISHES

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INTRODUCTION

IN recent years several useful reviews on the respiration of fishes have appeared, some as separate reviews or as sections of reviews on comparative physiology (3, 33, 43, 49, 52, 63), others as dissertations (28), or as monographs (60, 61) or as reference texts (95). The present account consists of an attempt to review recent contributions to the subject matter not covered in the articles by Leiner (52), Krogh (49), and Fry (34). Aspects of respiration emphasized in this paper are restricted to external respiration, and include the means of interchange of respiratory gases between the gills and the external environment.

Respiration of fishes has been approached by descriptive accounts of mechanisms and quantitative changes; by comparing these features with similar ones in other classes of animals; and by relating the respiratory system to the activity of fish, as well as to environmental factors, both external and internal (49, 52, 60, 61, 95). Because such comparisons are made, it is desirable to set out some of the conditions which govern respiration in fishes and mammals (Table 4).

The structure of the gill and its projecting filament has been compared with that of the lung of mammals and its recessed alveolus by Leiner (52), Van Dam (28), and Krogh (49). Krogh has emphasized Van Dam's work in demonstrating that the flow of respiratory water through the gills is opposed to the flow of blood through the gills, thus making for very efficient extraction of oxygen from the external respiratory medium. Associated with this anatomical arrangement is the fact that in teleost fishes at least, the respiratory flow across the gill filaments is in one direction, while the renewal of the respiratory medium in mammals is tidal in nature. The medium of exchange between the external respiratory medium and the gills of fishes is carried out in the same phase (liquid), whereas in mammals there are two phases, a gaseous one entering the respiratory tree down to and within the alveolus, opposing a

TABLE 4

Respiration in Fishes and Mammals

Condition	Fish	Mammal
Type of respiratory organ	Gill (Filament)	Lung (Alveolus)
Circulation	Counter	Direct
Ventilation	Liquid flowing in one direction	Tidal action
Medium of exchange	Tissue (liquid) and liquid	Tissue (liquid) and gas
Body temperature	Variable $-2°$ to $40°C$.	Fixed $37°$ to $40°C$.
p O_2 of inspired medium	1–200 mm. Hg	80–100 mm. Hg
p CO_2 of expired medium	0–10 mm. Hg	40–45 mm. Hg
O_2 Diffusion rate	Low (liquid)	High (gas)
O_2 Capacity of external medium	Low	High
Density of medium	High	Low

liquid phase (tissue of the alveolus, blood, etc.). The exchange between the blood and the tissues is carried out in the same phase (liquid for both fishes and mammals).

Physico-chemical conditions governing respiration in fishes and mammals are also very different (Table 4). The temperature range in inland fresh waters inhabited by fish is approximately $0°–40°C$. and in the sea it is $-1.8°$ to $30°C$. In one downward excursion through the thermocline the temperature may drop from $20°$ to $8°C$. The body temperature of fishes is not greatly different from their immediate environment. These possible ranges for the temperature of fishes are contrasted with the relatively higher and fixed body temperature of mammals ($37°$ to $40°$). Characteristics of the loading and unloading of oxygen to and from hemoglobin will shift with changes in temperature as was shown long ago by Barcroft and his associates (12). These special conditions governing oxygen exchange and hemoglobin at low temperatures were first appreciated in fishes by Krogh and Leitch (50). These workers also were aware of the variable oxygen levels which may confront the fish gill, conditions which may range from near exhaustion of stagnant waters to supersaturation in areas of high photosynthetic activity (Table 4). The pressure head of oxygen within the lungs of mammals at sea level ranges between 80 and 100 mm. Hg (89) although admittedly mammals living at very high altitudes will be

subjected to lower loading pressures. The conditions for unloading carbon dioxide are also different for the two classes, for fishes may respire into a carbon dioxide vacuum (in sea water as pointed out by Dill and others (29)), while for fresh water fish the carbon dioxide gradient will usually be a value of less than 1 mm. Hg in all but acid bogs. Carbon dioxide is ever present in the mammalian lung and the pressure is relatively high (39).

The significance of the differences in diffusion rate of oxygen in gaseous and liquid media to respiration is discussed by Leiner (52). The differences in oxygen capacity together with the equally marked differences in the density of the external respiratory media are discussed by Leiner (52), Van Dam (28), and Krogh (49). The relationship of these various factors to the high oxygen utilization (extraction) rate from the respiratory media is expounded by Van Dam (28).

It is clear that a comparison of respiratory mechanisms between fishes and mammals is not easily made. Moreover, particular adaptations in respiratory mechanisms can be related only to particular sections of the environment (49). Nevertheless attempts have been made to relate respiration to environment as well as to activity (60, 61). In many of the papers entitled respiration, a wider use of the word has been given than employed in this review. In particular, oxygen consumption, or respiratory metabolism has been used often as an index of respiration. While no one will deny that respiration and gaseous metabolism are related, and that the latter must determine the former, it seems wise to separate the two phases in any attempt to study the effects of either environment or activity upon the physiology of respiration. There are further difficulties in connection with using oxygen consumption of fishes as an index for any study, for at the present time, no paper upon oxygen consumption in fishes appears to be comparable with any other paper, for the reason that not all the various conditions now known to influence gaseous metabolism have been controlled. These conditions include temperature (30, 79), activity (22, 31, 71), biological condition (48, 78, 80), history (31, 71), diurnal variation (80), and previous another field which has a very restricted application, for as yet the means of measuring the activity of fishes in absolute terms are limited (34).

The special subject of emergency respiration (Notatmung) has been considered in a recent monograph by Olthof (57).

ANATOMY OF RESPIRATORY SYSTEM

Leiner (52) has reviewed the literature on the anatomy of the respiratory system, and in addition he has given considerable attention to the accessory organs of respiration. Hora (45) has reviewed a series of papers on the physiology of the air-breathing fish, *Monopteris javanensis*. For a comprehensive treatment of respiration and the physiology of the swimbladder, the works of Rauther (62) and von Ledebur (51) should be consulted. Krogh (49) has discussed adequately the anatomy of fishes in relation to respiratory mechanisms, and has given timely emphasis to Van Dam's (28) careful work in describing the relation of the circulatory system of the gills to the course that respired water takes. (The earlier paper by Woskoboinikoff (88) on circulation of blood through the gills has not been seen by this reviewer.) The blood of lowest oxygen content is conducted to the gills as the respired water leaves, and the oxygenated blood leaves at the point where inspired water (with its higher oxygen tension) enters the gills (28). This principle of counter circulation obtains for the exchange of metabolites between maternal and foetal circulations in mammals (12).

Bevelander (14) noted in his detailed study of 36 species that the respiratory epithelium of the teleosts was of the flat, squamous type while in elasmobranchs it was a thicker polyhedral or cubical type. Bevelander also reported that mucous cells appear larger and more numerous on the gill filament proper, and smaller and less numerous in the interlamellar spaces and on the free surfaces of the lamellae. By the use of specific stains, Copeland (26) demonstrated the presence of chloride-secreting cells distinct from the mucous-secreting cells in the respiratory epithelium.

Willem (82, 84, 85, 86) has published a series of anatomical papers on the reduction and modification of the respiratory apparatus in certain members of the teleost Plectognaths.

Gray (35, 36) has determined the number of gills, the number and the length of gill units and the number of respiratory units (secondary lamellae) in 8 species of marine fishes. The number of respiratory units differs distinctly from species to species, and is relatively great for surface active migratory fish and relatively small for sluggish bottom fishes.

Gudger (38) has called attention to the occurrence of oral breathing valves in 150 species of fish.

Balabai has written a series of papers on the detailed musculature of the respiratory apparatus in cyclostomes and jawed fishes (6,

7, 10). Tatarko has described the relationships of the hyoid and maxillary bones to the branchiostegal apparatus in the Acipenseridae (73) and Polyodontidae (74). Much of the Russian work in this field was initiated by Woskoboinikoff who wrote on the anatomy of the hyoid and branchial arches in the lower Gnathostomata in relation to respiration (90, 91, 92).

The paper by Pliszka (58) has not been available to the present reviewer.

MECHANISMS OF BREATHING

Van Dam (28) has shown for the rainbow trout, *Salmo shasta*, that water is expressed over the gills during both the inspiratory and expiratory phases of the respiratory cycle. During inspiration when the oral cavity is being widened and the opercula are being abducted, the oral valves are open, the opercular valves are closed, and water is drawn along the gills by the widening of the gill cavities. During expiration when the oral cavity is being decreased in size, the opercula are abducted, the oral valves are closed, the opercular valves are opened, water is driven along the gills by the decrease in volume of the oral cavity. "In other words, during inspiration the gill cavity acts as a suction pump, during expiration the mouth cavity acts as a pressure pump; in both cases water is drawn along the gill." (28). The significance of the continuous flow of water across the gill to the counter flow of blood through the gill filaments is expounded by Van Dam (28). Earlier, Woskoboinikoff (89) published a lengthy treatise on the suction pump system and the relation of the suction pump to the pressure pump in a number of teleosts. In 1939 Balabai showed that the alternate suction and pressure pump action is characteristic of the breathing of elasmobranchs (8) and sturgeon (9).

Of considerable interest are Van Dam's observations on the unilateral ventilation and also periodic ventilation in the eel. The respiratory pauses may extend to five minutes. The pauses are not seen when the animal is using unilateral gill ventilation. Both the respiratory pauses and the unilateral ventilation occur when the animal appears to be in a resting condition (28).

In papers on the mechanism of movement of gill filaments in Teleosti, Bijtel (15, 16) discusses the position of the tips of the gill filaments. During normal respiration the tips from adjacent gill arches touch, and thus the respiratory water is forced through the lamellae. This arrangement was deduced by Van Dam (28) from

the high percentage oxygen utilization rates (80%) and observed in living *Tinca tinca* by Hofdijk-Enklaar (44) and confirmed by Bijtel (15, 16). During the so-called cough reflex the tips of the filaments are retracted to permit the sudden flow of water through the gills (15, 16).

REGULATION OF BREATHING AND RESPIRATORY REFLEXES

Respiratory centre

Babkin and M'Gonigle (4) in their studies on the respiratory mechanism in skates, review the literature pertaining to their subject up to 1930. They recount the views of Baglioni (5) who asserted that the initiation of the respiratory act in fishes is central; of Bethe (13) who contended that the respiratory act is accomplished through peripheral reflexes; and those of Babak (3) who assumed an intermediate position by claiming that respiration is actuated primarily by an autonomous centre and modified secondarily through peripheral reflexes. Babkin and M'Gonigle stated that much of the early controversy was due to the variety of species studied, and further, since the place occupied in the evolutionary scale by elasmobranchs and teleosts is not the same, the respiratory mechanisms may also be different. To these statements should be added that the variety of mechanisms of respiration in different fishes (5, 49) and even in the same fish (27, 28), and the variety of experimental methods used including the use of anaesthetics which may depress respiration, have not aided physiologists in formulating a general scheme of respiration in fishes.

Lutz (53) and Babkin and M'Gonigle (4) have furnished indirect evidence that respiration is maintained by an autonomous centre in certain elasmobranchs. These studies add to the early experimental work of Vulpian (77), Steiner (72) and Hyde (46) who demonstrated that in fishes all respiratory movements failed when the medulla was sectioned. Recording electric potentials from the isolated brain stem of goldfish, Adrian and Buytendijk (1) observed close correspondence between impulses and respiratory activity.

More recently Powers and Clark (59) sectioned various combinations of the IXth and Xth cranial nerves immediately medial to the gills in three species of fish (brook trout, *Salvelinus f. fontinalis*; rainbow trout, *Salmo gairdnerii irideus* and the bluegill, *Lepomis macrochirus*). Their results showed that the integrity of the

afferent pathways from receptors in the gill regions is essential to the maintenance of respiratory action. From these results the authors contend that the reflex system dominates the control of respiration for these species.

Van Dam (28) in his observations on the respiration of the eel *Anguilla vulgaris* in a resting condition found that there were respiratory pauses up to five minutes' duration; at other times the eel ventilated on one side only, although no respiratory pauses intervened when the animal ventilated unilaterally. These peculiarities in the respiration of the eel suggest a stronger dependence of the respiratory centre upon metabolism than appears in other fishes.

Respiratory reflexes

1. *Mechanical.* Baglioni (5) described changes in respiratory rhythm for teleosts and elasmobranchs when air was introduced into the respiratory passages. Lutz (53) studied the effect of suddenly starting and stopping the respiratory flow of water conducted to the spiracles of the dogfish, *Scyllium canicula,* and found that inhibition of respiration occurred, followed by reflex ejection of water from the mouth and gills. When the respiratory flow was increased gradually, respiratory movements increased; on gradually reducing the flow, the rate of respiratory movement decreased to the starting level. Ogden (56) observed in the dogfish, *Mustelus californicus,* a simple quantitative relationship between the respiratory water pumped over the gills and the hydrostatic pressure between the mouth and the gill slits from −7 to 3 cm. water, yet the breathing frequency remained constant.

2. *Chemical.* The response of some fishes to changes in the oxygen and also the carbon dioxide content of the inspiratory water is shown in Table 5. Where possible, cases have been listed where the authors included a simultaneous accounting of the frequency of breathing and the quantity of water moved during each respiratory cycle. Observations by Baglioni (5) and Westerlund (81) were made on frequency only.

The response in the dogfish, *Mustelus californicus,* to lowered oxygen and also to increased carbon dioxide is one of struggling according to Ogden (56). No change was noted in either breathing frequency or quantity of water shifted. Clear indication of a similar response in elasmobranchs is to be found in the earlier studies of Schoenlein and Willem (69) for the ray, *Torpedo ocellata,* and dogfish, *Scyllium canicula,* and by Bethe (13) for the dogfishes, *Scyl-*

TABLE 5

EFFECTS OF DECREASED OXYGEN AND INCREASED CARBON DIOXIDE
UPON RESPIRATION IN FISHES

Species	Author	Effects of lowered O_2	Effects of increased CO_2
ELASMOBRANCHS			
Torpedo ocellata	Schoenlein and Willem (69)	None on rate	....
Scyllium canicula	Schoenlein and Willem (69)	None on rate	....
Scyllium catulus	Baglioni (5)	Increased rate and swimming	....
Scyllium canicula	Bethe (13)	None on rate	None on rate
Scyllium catulus	Bethe (13)	None on rate	None on rate
Mustelus californicus	Ogden (56)	None on rate None on volume Struggling response	None on rate None on volume Struggling response
TELEOSTS			
"Karausch" *Carassius vulgaris?*	Westerlund (81)	Increased rate	Increased rate
Serranus scriba	Baglioni (5)	Increased rate and activity	Increased rate and activity
Scorpaena ustulata	Baglioni (5)	Increased rate and activity	Increased rate and activity
Spheroides maculatus	Hall (40)	....	Increased rate None on volume
Uranoscopus scaber	Meyer (55)	Increased rate None on volume	Increased rate None on volume
Salmo shasta	Van Dam (28)	None on rate Increased volume	None on rate Increased volume
Anguilla vulgaris	Van Dam (28)	Increased rate Increased volume	Increased rate Increased volume; or apnea

lium canicula, and *S. catulus.* In all these studies the experimental animal was held in a fixed position. Baglioni (5) studied the behaviour of the dogfish, *Scyllium catulus,* when allowed to swim freely in oxygen-free sea water. He found that within three minutes the fish became restless, swam aimlessly and that the respiratory frequency increased from 54 to 66 per minute. During the experimental period of 1 hour and 56 minutes, the respiratory frequency rose at one point to 90 per minute; the activity and the frequency

of breathing seemed to correspond. The control animal remained in the same position throughout the experiment, and except for one observation of an increased rate to 60 respirations per minute, the rate remained at 54 per minute.

From studies made on teleosts (Table 5) it appears that a decrease in oxygen tension or an increase in carbon dioxide in water flowing over the gills brings about changes in respiration. The response is not always the same in detail. In *Uranoscopus scaber,* Meyer (55) found that the frequency alone changes; in the rainbow trout, *Salmo shasta,* Van Dam (28) found that both factors changed. Struggling, dyspnea and apnea also occurred in the eel in response to carbon dioxide depending on the concentration used (28). Woskoboinikoff and Balabai (94) showed that the carp responded to oxygen lack by an increase in breathing activity.

Ogden (56) states that the response in the dogfish to increased carbon dioxide or decreased oxygen in respired water is one of swimming. Tracy (75) found that carbon dioxide initiated the "random" body movements in the larval form of the teleost toadfish, *Opsanus tau.* However the earlier work of Baglioni (5) for the dogfish *Scyllium catulus,* still must be recognized; in this study the dogfish responded to oxygen-free sea water by swimming and by an increase in respiratory frequency. In Ogden's (56) experiments, the fish was held in a fixed position, and the response was one of struggling only. It is possible to argue that in the natural environment the increase in frequency of respiration in the dogfish, *Mustelus californicus,* may be due to the increased metabolism which followed the swimming movements caused by the unfavourable environment. It is possible too that the mechanism in the species studied by Baglioni is different from that in the species studied by Ogden. The response to changes in respiratory gases in elasmobranchs should be tested further. As far as the teleosts are concerned the respiratory response is positive, though variable.

RESPIRATION AND CIRCULATION

Schoenlein and Willem (69) long ago reported for the dogfish, *Scyllium canicula,* and the ray, *Torpedo ocellata,* that the heart was reflexly inhibited when the spiracles closed, the sensory limb of the reflex originating in the pharyngeal cavity. Bethe (13) and Baglioni (5) stated that cardiac and respiratory inhibition occurred together in elasmobranchs. Lyon (54) reported for the shark, *Carcharias,* that the cardiac rate was intimately related to the

respiratory rate, and that there were indications that the heart normally takes its rate from respiration. Nevertheless the myogenic nature of the heart-beat is shown by the fact that the heart usually beats long after respiration has ceased (54). Lutz (53) studied respiratory and cardiac reflexes in the dogfish, *Scyllium canicula*, and reported that electrical and mechanical stimuli applied to various parts of the body and certain viscera caused reflex inhibition of both respiration and cardiac activity. Stopping or starting the flow of respiratory water over the gills caused respiratory inhibition and sometimes cardiac inhibition; stimulation of the ventricle caused cardiac inhibition and sometimes respiratory inhibition (53). Willem (83) has recounted the published work on synchronism of respiratory movements and heart-beats in fish.

Hart (42) investigated the stroke volume of the heart in four species of freshwater fish and noted that the values correlated inversely with the Bohr effect of the bloods of the same species investigated by Black (17) as discussed below. Hart suggested that the differences in circulation may compensate for differences in oxygen transport imposed by the differences in the bloods for transporting oxygen.

RESPIRATORY BLOOD-GASES AND TISSUE TENSIONS

Methods

Since the comprehensive review by Redfield (49) appeared on the respiratory functions of blood, more evidence has been obtained on the fragility of fish blood. Black and Irving (21) reported that hemolysis abolished the Bohr effect for the bloods of at least two teleosts, and that hemolysis of the blood of the carp, *Cyprinis carpio*, may be brought about by the use of the anticoagulant potassium oxalate. Hamdi and Ferguson (41) found that fluorides used to prevent glycolysis of mammalian blood, caused hemolysis of fish blood. Krogh and Leitch (50) used leech head extract in their studies of fish blood; they also used defibrinated fish blood. Irving, Black and Safford (47) and Black and Black (20) found that blood which had been drawn from fish for longer than 12 to 18 hours could not be used for blood-gas studies, although no reasons were presented for the anomalous changes in both CO_2 combining power and oxygen capacity. Ferguson and Black (31) noted that the CO_2 combining power in bloods from the carp, *Cyprinus carpio*, and rainbow trout, *Salmo gairdnerii*, increased when the

blood was stored fully oxygenated, and decreased when stored in nitrogen. The importance of lactic acid in altering the properties of fish blood has been emphasized by Von Buddenbrock (24), Root (64), Redfield (63), Black and Irving (21), Secondat and Diaz (70) and Auvergnat and Secondat (2).

Transport of carbon dioxide

Redfield (63) has reviewed the literature relating to the equilibria of carbon dioxide with the blood of fishes. In a number of groups of animals which carry hemoglobin as the respiratory pigment the form of the curve is much the same, although the quantity of bicarbonate increases as the hemoglobin content increases. This is borne out by the work of Root (64) on marine fishes.

The effect of hemolysis of fish blood in reducing the content of CO_2 is very great as shown by Black and Irving (21) for certain freshwater fishes and by Root, Irving and Black (67) for certain marine fishes. The integrity of the red cell is of importance to the transport of CO_2 as well as for oxygen transport (11). Ferguson, Horvath and Pappenheimer (32) and Ferguson and Black (31) have demonstrated that chloride and bicarbonate ions interchange during oxygenation and de-oxygenation of whole blood of fishes, which brings this aspect of the transport of CO_2 carriage in harmony with that of mammalian blood as demonstrated by Van Slyke (76). Ferguson, Horvath and Pappenheimer (32) have also furnished evidence that the transport of CO_2 in the carbamino form is possibly absent in the blood of the dogfish, *Mustelis canis*, but may be present in the bloods of the carp, *Cyprinus carpio*, and rainbow trout, *Salmo gairdnerii* (31).

The buffer power of fish blood is not so great as that of human blood between the partial pressures of 10 to 60 mm. Hg (63), yet the buffer power of fish blood over what is probably the physiological range for fishes (0-15 mm. Hg) is considerable (20, 31, 63, 64).

The Haldane effect (25) or the effect of oxygenation on CO_2 combining power is present in the bloods of certain teleosts according to Root (64), Ferguson and Black (31), Black (17) and Black and Black (20). Dill, Edwards and Florkin (29) found that a Haldane effect is present over the physiological range for the skate, *Raia ocellata*, while Ferguson, Horvath and Pappenheimer found no Haldane effect in the dogfish, *Mustelus canis* (32).

Transport of oxygen

Krogh and Leitch (50) described the properties of fish blood for transporting oxygen and observed a degree of difference in the ability of bloods of different species to combine with oxygen. They also noted a sensitivity of the union of blood with oxygen to the presence of low tensions of carbon dioxide. They contended that the sensitivity of fish blood to carbon dioxide was an adaptation, for these authors appreciated the work that Barcroft and his collaborators (11) had published to the effect that a decrease in temperature increased the affinity of hemoglobin for oxygen, and that this effect was countered by the Bohr effect (23), namely that carbon dioxide reduces the affinity of hemoglobin for oxygen, and hence physiological conditions would operate to augment the tension at which oxygen would be unloaded to the tissues at low temperatures. Krogh and Leitch also appreciated the significance of the Bohr effect on the loading tension of oxygen in bloods of fishes in poor oxygen supply. These various relationships are clearly set out by Krogh (49) and Leiner (28). These reviewers list the fishes showing a very large Bohr effect as first observed by Root (64) in certain marine fishes. Green and Root (37) postulated that the marked reduction of oxygen combining power by carbon dioxide might be due to the inactivation of one or more prosthetic groups of the hemoglobin molecule. At the suggestion of Dr. D. B. Dill, Black and Irving (21) hemolyzed bloods of two freshwater fishes and found that the sensitivity to carbon dioxide was obliterated. These studies were extended by Root, Irving and Black (67), Root and Irving (66) and Black (17), who found that in some instances the Bohr effect was not abolished totally by hemolysis. These findings and later data obtained by Irving, Black and Safford (47) and Black (18, 19) substantiated the early view proposed by Krogh and Leitch (50) that the specificity of fish blood as regards affinity for oxygen must rest partly on the hemoglobin and partly on the special chemical milieu maintained by the intact membrane of the erythrocyte.

In a limited series of four species of freshwater fishes, Black (17) found specific differences in the affinity of fish blood for oxygen and also in the Bohr effect. The indications are that fish blood with a low Bohr effect and a high affinity for oxygen characterize fish which inhabit warmer waters of a temperate lake in summer; and that a large Bohr effect and a low affinity for oxygen characterize fish which inhabit the colder waters in summer. How-

ever as Krogh (49) warned, it is possible to find an ecological adaptation between the physiological machinery and limited environments, but usually the relationship does not hold for larger systematic groups and wider environmental lattices.

Black (18), and Black and Black (20) investigated the blood of the Atlantic salmon, *Salmo salar salar*, and Black (19) the brook trout, *Salvelinus fontinalis*, acclimated to summer and winter conditions, but found no difference in the Bohr effect for the two seasons.

Oxygen capacity of the blood of fishes is variable both within the species and from species to species (63). In some instances the oxygen capacity is so low that at low temperatures a significant measure of the transport of oxygen must be attributed to the oxygen physically dissolved (29, 32, 64).

Tissue tensions

Conditions for discharging and loading carbon dioxide and oxygen to and from the blood must be known if the transport capacity of the blood for the respiratory gases is to be rationalized. Significant among the conditions are the temperature and the physiological tensions of oxygen and carbon dioxide at the two phases of respiratory cycle, namely, the tissues and the gills. According to the work of Von Buddenbrock (24) on fish and of Scholander (68) on diving mammals, the level of lactic acid in the plasma must also be considered.

The determination of tissue tensions in fishes is difficult indeed, as is recounted by Root (64). Dill, Edwards and Florkin (29) estimated the tension of carbon dioxide in "arterialized" blood taken from the efferent side of the gills of the skate, *Raia ocellata*, to be 1.4 mm. Hg. Root (64) estimated the tension of carbon dioxide of the blood taken from the gills of the sea robin, *Prionotus carolinus*, to be 2 mm. Hg, and the "venous" blood taken from the heart of the toadfish, *Opsanus tau*, to be 10 mm. Hg. Ferguson and Black (31) obtained values of 5 to 10 mm. Hg carbon dioxide for blood taken from the heart of the rainbow trout, *Salmo gairdnerii*, the carp, *Cyprinus carpio*, and the bullhead, *Ameiurus nebulosus*. Black (18), and Black and Black (20) noted that the venous tension of carbon dioxide for the Atlantic salmon, *Salmo salar salar*, acclimated to summer was 6 to 8 mm. Hg and 3 to 6 mm. Hg for winter conditions.

Lactic acid levels have been recorded for fish by Von Budden-

brock (24), Secondat and Diaz (70), and Auvergnat and Secondat (2). These works indicate that lactic acid accumulates in the plasma during activity. Von Buddenbrock (24) discusses the importance of lactic acid to the carriage of oxygen, particularly for fish blood sensitive to CO_2.

Root (64) estimated the venous tensions of oxygen in a series of four marine teleosts ranged from 0 to 20 mm. Hg; in three fresh-water teleosts Ferguson and Black (31) estimated the venous tensions of oxygen to range from 3 to 10 mm. Hg.

SUMMARY

Recent papers on respiration in fishes were reviewed. By respiration is meant the exchange of oxygen and carbon dioxide between the external environment and the gills. Papers on the respiratory function of the blood were included, but the literature on oxygen consumption in fishes was excluded.

Important in the advance of knowledge of respiratory mechanisms has been the description of the principle of counter circulation between the respiratory flow of water and blood through the gills, and the efficient extraction of oxygen from teleost gills made possible by the continuous circulation of respired water in one direction, and by the position of the tips of adjacent gill filaments, which are so held that during normal respiration water is forced through the lamellae. During "coughing" the filament tips separate reflexly.

The importance of the respiratory centre of the medulla to the autonomous activity of respiration has been established by early experiments on sectioning, and by action potential studies which show a correspondence between impulses arising from the brain and respiratory frequency. However, the centre seems to be dominated by reflexes in certain teleosts.

Respiration may be modified by a variety of physical stimuli through reflex patterns. The respiratory response to chemical stimuli such as lowered oxygen tension or increased carbon dioxide tension is definite although variable in teleosts but uncertain in elasmobranchs.

Transport of carbon dioxide by the blood of teleosts follows a somewhat conventional pattern established for mammalian blood with unexplained peculiarities, while the blood of elasmobranchs shows little or no Haldane effect. The buffering capacity is con-

siderable over the physiological range of carbon dioxide tension for fishes.

The blood of teleosts varies in oxygen capacity, in the affinity of the blood for oxygen, and in the Bohr effect. In some instances the oxygen affinity and Bohr effect constitute an adaptation to a restricted environment.

The physiological tensions of carbon dioxide are very much lower than those found in mammals. The tensions of oxygen at unloading in fishes are variable. The importance of lactic acid levels in the plasma to the unloading and loading of both gases is considerable.

ACKNOWLEDGMENTS

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