THE ORIGIN OF THE LANDLOCKED HABIT IN SALMON

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The salmon is recognized as the most valuable and highly prized of all fish. In nature its distribution is confined to the northern hemisphere north of 40° N. L. Only one species (Salmo salar) is found in the northern Atlantic. To spawn it ascends rivers both on the European and on the American coasts. Five species belonging to the genus Oncorhynchus are found on the Pacific coast of North America, and at least one additional species occurs on the northern Asiatic coast of the Pacific. All these fish have the similar habit of passing the major part of their life in salt water and ascending fresh water streams to find spawning grounds in the upper reaches. However, in some of the river systems that carry these salmon, certain fresh water lakes are known in diverse regions bordering the northern Atlantic and Pacific oceans, which contain salmon that never run to salt water. These fish, sometimes recognized by systematists as separate species, are generally regarded as descendants of the seagoing types which they resemble very closely. They are much smaller than their sea-run relatives and are sometimes spoken of as dwarf salmon. They are generally designated as landlocked salmon. The lakes in which they are found are widely scattered and unrelated to each other. Such landlocked salmon occur usually in elevated lakes and belong to both the Atlantic and the Pacific genera.

Landlocked Forms of the Genus Salmo.—The forms which belong to the genus Salmo may be considered first. The most extended study of a landlocked salmon yet made has been published by Dahl (1927). The form in question is found in an elevated lake in southern Norway, 84 km. from the ocean. Dahl stated that access to the lake is cut off by a waterfall only 15 km. from the sea. The original study made in 1914 led him to believe that the specimens were the result of fortuitous planting of salmon fry or else a landlocked form of Salmo salar. Ten years later other specimens taken from the same water possessed exactly the same characters as those previously examined and he concluded that they were landlocked. This type is common in the watershed of the Otra, occurring at several places other than that at which it was first captured. It is the object of seasonal fishing which is celebrated in a local rhyme of very ancient origin indicating thus its age. Dahl records in detail the specific characters of this fish, its habits, food and other biological features. A study of the stream showed that barriers now existing in the river prevent access from the sea to the region in which these salmon occur, and Dahl was led to the conclusion that
according to current ideas of the geological chronology of this region, the immigration and landlocking of this form occurred, roughly speaking about 9000 years ago. In personal correspondence Professor Dahl writes that he has found this landlocked or dwarf type in the waters of another river system in that country and believes it occurs in a few other rivers in southern Norway where elevated lakes of a similar character are to be found.

Corresponding dwarfed, non-seagoing or landlocked forms of *Salmo salar* have long been known in North America. Lake Sebago, Maine and some other waters in New England are inhabited by a type known as the Sebago salmon so similar to the Atlantic species that it is difficult to separate the two forms. However, the Sebago type never descends to the sea although the outlet to Sebago Lake is not barred by any impassable obstacles. This salmon is regarded as the same as the ouananiche, famous in literature as well as in sport and found in various waters in Quebec and Labrador. This species has been transplanted in the egg stage into Lake George and other eastern lakes as well as into glacial lakes of the Sawtooth range in Idaho and elsewhere in the mountain regions in the northwestern United States. It has become well established in certain places. In native waters it does not go to sea though in some lakes it spawns in the outlet. When introduced into new waters this landlocked salmon sometimes shows a tendency to desert them and then it does not return. This may indicate that factors which inhibit movement seaward are absent in the new environment.

*Salmo Salar in the Southern Hemisphere.*—In nature all salmon are limited to the northern hemisphere and numerous attempts have been made to transplant both genera to southern waters. According to C. Tate Regan the Atlantic salmon was introduced in 1864 into Tasmania but the experiment was not successful as the ocean waters were probably too warm. The experiments in New Zealand resulted very differently. A fine run was established in Lake Te Anau on the Waiau River near the southern end of the south island. Regan to whom specimens were sent states that they are certainly *Salmo salar*, resembling somewhat the ouananiche, and adds: "There appears as yet to be no evidence that the salmon of the Waiau system ever goes to sea." His view was confirmed by Hutton's study of the scales. The lake is some thirty miles long, very deep and has an abundant supply of small fish for food. This is suggested as the reason why the salmon stop there and do not go down to the ocean. These fish are clearly landlocked salmon even the unintentionally so. Some minor peculiarities of structure and habit described are no doubt related to the food supply and the character of the waters they inhabit; so one may well regard it as a new species in the making.

Little is known of the conditions existing in the lake and of the habits of
the salmon in this new environment; hence judgment must be suspended on the validity of the explanation suggested for the origin of the landlocked condition. While the abundance of small native fish in the lake certainly serves to maintain the plant of salmon, it is not safe to conclude that these fish fail to continue their migration to the sea because of the abundant food supply in the lake.

The steelhead, often spoken of as a trout, belongs to the genus Salmo. While a migratory species that often inhabits seasonally both fresh and salt water, it accommodates itself readily to a permanent fresh water home and the landlocked type is found in many places in the Pacific coast region. A subspecies, the Kamloops trout,4 "has been landlocked for so many generations that it has no inclination to return to the sea." (Keil 1929.) I have found no records of exact observations on the habitat of this species or of experiments with eggs or fry of the Kamloops trout.

The Pacific Salmon and Its Habitat.—The outstanding difference in habit between the Atlantic salmon, or the genus Salmo, and the Pacific genus Oncorhynchus lies in the fact that, whereas the former after spawning returns to the sea to feed there, and at a later date repeat the migration, the Pacific salmon spawns but once. All the fish both male and female make but a single trip to the spawning grounds and all die at the end of the reproductive period. The race is replenished from the progeny that spring from the eggs deposited at this single reproductive period. No adults ever go down-stream to the ocean.

The Pacific salmon seek spawning grounds in the upper reaches of rivers which come from glacier fed or spring fed lakes and streams in the high mountains. In their natural state these rivers are turbulent, rapidly flowing streams. Even though in places stretches of quiet water occur the current is still clearly in evidence. Under the conditions indicated the water is richly supplied with oxygen and is kept at a constant temperature. The temperature of the stream rises gradually as the water moves down to the sea, although under certain conditions occasional diurnal fluctuations may be rather marked. Thus in a canyon where the afternoon sun is reflected from a rocky face full into the stream the water temperature on an extremely hot day may be strikingly high in the midafternoon but as the sun sinks toward the horizon usual temperatures are rapidly restored. Because of their rapid descent from higher levels these rivers offer marked advantages for the development of water power projects and some sites on important salmon streams have already been provided with dams while many more dams are projected.

In studying groups of animals under natural conditions it is difficult to employ the experimental method because of the magnitude of the factors involved. In nature conditions are modified but usually too slowly to permit of ready observation of the effects of change. Thus it is impossible
ordinarily to modify stream conditions experimentally. However, in some cases industrial developments bring about radical changes on a large scale as has in fact been effected on certain salmon streams. These changes follow the erection of power dams. The relation of these changes to the salmon is most intimate.

The extremely radical character of the changes brought about by the erection of a power dam needs to be reviewed in some detail. Viewed in the large the stream bed may be considered as a plane descending from the lake where the sockeyes were spawned to the sea. The average depth, velocity, oxygenation and temperature of the water moving down this plane are subject to minor variations, but do not vary greatly. In other words, the environment which influences the young sockeye is relatively stable.

Into the plane of water moving rapidly and under stable conditions the power dam by forming a reservoir introduces a huge wedge of nearly static, i.e., not flowing, water presenting very different and previously entirely unknown environmental conditions. The inflowing water is small in quantity compared to the volume of the reservoir and the outflow is also minimal. In consequence the stream current has been eliminated except for short distances near the inlet and outlet. In fact, the outlet current in a power plant reservoir often cannot be detected by any current meter except the latter be located very close to the intake of the power plant. Furthermore, this intake is situated at a considerable depth so that at the surface of the reservoir there is nowhere any current leaving the lake unless the water is being wasted at some gate or spillway. In contrast with the original stream in which the salmon lived, the reservoir is a large mass of deep, quiet water.

Temperature conditions are also greatly modified. The summer heat warms up the surface water in the reservoir to a level probably never reached previously even under extreme and brief conditions in the stream, and this high level is maintained at the surface for a long period. Furthermore, the winter temperatures which had disappeared in surface water at the season when the young salmon deserted the original lake home are maintained in the depths of the reservoir since in midsummer the deep water is at or near 4°C. The stream water entering the reservoir at its head does not flow along the bottom but sinks only as far as its own temperature level and the water below that remains unchanged until the stream temperature drops in the fall. The water of the reservoir is warmer at the surface and colder in the depths during the migratory season than young salmon had found in the river before the construction of the dam.

Of the five North American species of the Pacific salmon only one is well known to occur as a landlocked type. This is the little red fish or silver trout (*Oncorhynchus kennerlyi*). It is found naturally in numerous
lakes in the mountains from Alaska south to Oregon and is reported also from Hokkaido, Japan. The parent species spawns regularly in a lake and that habit as will be shown would contribute to its frequent occurrence as a landlocked type. Fish culturists have planted the latter widely as silver trout. The origin of this species is generally recognized by ichthyologists and fish culturists, many of whom refer to it specifically as the fresh water descendant of the big red fish, also called the blue-back salmon or sockeye (O. nerka). It lives and propagates well in many fresh water lakes and is thoroughly acclimatized to a fresh water existence. In details of structure except as to size, and in habits, the landlocked form agrees with the sea-going sockeye.

When the migrating young sockeye is studied under unmodified natural conditions one observes a definite sequence of reactions. After living in the lake in which they are hatched or planted for about a year, they move toward the outlet and pass into the outflowing stream. Once embarked on the down-stream journey they continue moving with the current leisurely until they reach salt water. Here they disappear into deep water which constitutes the habitat of the sockeye during the active growing period of the life cycle. From these feeding grounds they migrate two years later upward into surface waters and shoreward into fresh water, where the reproductive function is discharged. The new conditions created by the erection of a dam modify conspicuously these habits. I have had an opportunity to study such a case and wish next to record the recent results of that study. Two previous papers6,10 (Ward, 1927, 1929) have given data secured earlier and only special or more recent observations bearing on the problem under discussion are included here.

Studies on Baker River Sockeyes.—The sockeye salmon spawns in very few places in the state of Washington. The most valuable run there ascends the Skagit and Baker rivers to spawn in Baker Lake. I studied these fish first in 1912 when natural stream conditions were mostly unmodified and have followed their relations to the changes in the Baker River associated with the modifications in their surroundings; these are particularly those due to the erection of a high power dam at Concrete, Washington. As the result of these studies, I ventured to predict in 1927 that the life cycle of the fish would be radically effected by this sudden change in stream conditions and that probably one of the results would be the production of a landlocked variety of the sockeye. A year later a good many such fish were caught on the sockeye spawning grounds at Baker Lake. The number increased in the following year and fell off considerably in 1930. In that fall only 10 such fish were taken at Baker Lake and all were males. In 1927 some aind in 1928 and 1929 considerable numbers of such fish were seen spawning along the lake shore where the sea-run sockeyes were wont to spawn before the hatchery was established. In 1931 only 18 were taken,
all males; none were observed spawning. This evidence though too scanty to be conclusive suggests that the landlocked type consists preponderantly of males. It indicates also that a regular run of these fish cannot be depended on. Perhaps conditions at the dam in 1928 were favorable for the escape of all the migrators and none became landlocked. However, the number of landlocked sockeyes in Lake Shannon is larger than indicated by the figures just given. Local fishermen recognize this type among fish caught in the lake at certain seasons. Some such fish have been taken with eggs in early stages of growth and at points which might indicate that they were on the way to spawning grounds in Baker Lake. The evidence is too incomplete to justify any conclusions as to the frequency of the landlocked sockeye in Lake Shannon or to determine whether all go to the ancestral spawning areas in Baker Lake.

The fish were clearly a dwarf variety of the sockeye and corresponded closely to the landlocked variety of that species as found in other waters. Eggs from these dwarf sockeyes have been secured, fertilized and hatched in different years. They have produced typical sockeye fry. In 1929 a total of 8615 fingerlings were raised from such eggs.

An analysis of the physical features of the region shows some basis for this fluctuation in numbers. The usual variations in climatic conditions have manifest themselves even in the few years that have elapsed since the dam was built. The total annual precipitation, and also its distribution by seasons especially, determine the water level in the reservoir. If this is high and water is wasted at the time when the migrators reach the dam, these young fish pass on down-stream with little delay. If, on the contrary, the reservoir is low and water is infrequently or not at all discharged, then the migrators are held at the surface of the lake. Under such circumstances some young fish descend into deep water in the lake. They remain there during the growth period of the life cycle until they attain the adult condition and go up to the spawning grounds. At this time they are evidently sockeye salmon, dwarfed and landlocked by virtue of the conditions that exist in the lake.

These adult landlocked fish varied from 6 to 12 inches, averaging about 10 inches in length. When first caught their blue backs, marked with small black spots and the silvery bellies gave the fish a likeness to the sockeye that was instantly noticed. At spawning time the males were very thin; most of them were red on back and sides with the black spots still showing. The females had only a little coloring and that of a darker shade. The females were found to be ripe and spawned in October and November. The eggs hatched between March 8 and May 24. The study of the scales showed that the ripe males were 3 years old and the spawning females were 4-year fish. They constitute unquestionably a new race of sockeyes passing their entire life in fresh water and properly designated as landlocked. The
modified conditions which produced this race, experimentally as it were, serve to explain the origin of the landlocked races found in nature.

*Origin of Races Naturally Landlocked.*—Factors that interfered with the seaward movement of the young sockeye might be either (1) such as prevented the fish from leaving the lake, or (2) such as enticed it to remain. Evidently these influences might be equally well physical or physiological. Only two factors have been previously suggested; of these stream barricades, especially falls, come under the first category noted above and a rich food supply under the second. My study of the cases known leads to the conclusion that neither of these is adequate. I purpose to show that the ruling factor is temperature. Each of the factors may be discussed in detail to bring out values in each.

When one comes to consider the factor which has conditioned the change from the dual existence to a permanent fresh water habitat one finds difficulty in accepting the mechanical explanation suggested in the expression landlocked. As a matter of fact there is in many cases no impassable barrier between the fresh water lake in which these fish live and the salt water. At Sebago Lake the entrance to the river is free and open, the distance to the ocean relatively short and despite a small dam found in the stream today, the journey would be easy for any salmon that essayed to make the trip. In the lakes of the Pacific coast the distance though greater is not more than covered by other salmon in other streams of the same region. In some streams no obstacles of a serious nature oppose either the descent of the migrants or the ascent of the adult fish so that any mechanical interpretation of the situation seems untenable.

Even in those cases in which the stream is barred by impassable falls or rapids so that no salmon coming from the sea could possibly gain access to the waters in which a landlocked variety is found today, the origin of a landlocked variety can hardly be traced to the obstacles in question. If these barriers were formed gradually as is likely in most cases, the upstream journey would be barred long before it was even dangerous to go down-stream. More than that if the young salmon had not lost its urge to go down to the sea or been held back by a stronger impulse, it would have followed with the current even had that carried it over one of the impassable falls which we are told block the way at present. When one sees young salmon, moving seaward by thousands, go over the spillway of a high dam without hesitating, it is evident that no sense of impending danger retards their movements. One must conclude that the salmon which tarry in those elevated lakes that are the home of the landlocked types remain there in response to present-day influences that hold them back. If they are descended from forms which once went down-stream to the ocean, some later generations were impelled at some time to give up the urge to go with the current and desert the lake by some more powerful influence, some at-
traction that held them back or turned them aside and thus kept them from carrying out their primal impulse. If there had not been some such influence all the salmon would have gone on out of the lake and down to the sea just as have the generations of young salmon in other streams in the same region. The landlocked type resembles sea-run species so closely that at first sight men recognized their relationship; the name given to these fish represented the simplest explanation of their origin, but as suggested it seems to be inadequate to account for present conditions. If ancestral habits had ruled, the lake would be barren today of these fish.

These thoughts led me to search for a more adequate cause. Another and better interpretation of the situation did not offer itself at once. I recall distinctly that while on Lake Sebago, Maine, many years ago, I talked of this matter with Dr. W. C. Kendall who was also there studying the Sebago salmon. This type was so like the Atlantic salmon (Salmo salar) that it was difficult to find criteria to separate them, yet the Sebago salmon never went to sea even though the way was wide open. We could not see why and had to satisfy ourselves with the comment that probably the type was physiologically landlocked. Only recently has evidence come to me which seems to provide an adequate explanation of the phenomenon. That evidence was secured while studying the behavior of young sockeye salmon under changed conditions in the Baker River following the erection of a power dam at Concrete.

These conditions have already been described in good part. When the migrators, dropping down-stream from Baker Lake reach the reservoir, Lake Shannon, they move along the shore seeking an outlet. Under natural conditions they should find one and make their way out but when the water is low and no discharge from the surface exists, the migrants linger there until with advancing summer conditions, the surface water becomes warmer than the species likes. It has already been pointed out that in the reservoir the surface water heated by the summer sun reaches a temperature considerably warmer than the flowing stream ever attained. There is only one way for the fish to escape the warm waters and they take it. They move downward to cooler levels and disappear from the surface zone. How far they go could not be ascertained but probably they move below the thermocline which forms soon after the time at which they disappear from the surface. With that they have lost all chance of leaving the lake and continuing the journey to the sea. Nothing further is known of them until sexually mature they appear at the spawning grounds of the species. They have lived and grown to maturity in the reservoir and like their sea-run ancestors have responded to approaching maturity by moving up-stream against the current to the place where fulfilment of the reproductive function terminates their existence. In this manner there has been produced experimentally a race of landlocked sockeyes.
Origin of a Natural Race of Landlocked Salmon.—The question now arises how do conditions in nature resemble those which were artificially created by the erection of the dam, and do somewhat similar influences ever interfere to prevent the young salmon from completing the journey to the sea? Earlier in this paper attention was called to the fact that landlocked salmon planted in certain lakes tend to desert those waters. One will naturally assume that in such cases some influence is lacking which in other localities inhibits the fish from deserting the lake. I am of the opinion that temperature is the ruling factor and that changes known to have occurred in the recent geological history of the northern hemisphere are calculated to afford an adequate explanation of the formation of landlocked races of salmon in widely scattered lakes.

During the period of glaciation the salmon, attracted no doubt by the fresh water inflow from ice-fed streams, must of necessity have spawned nearer the sea. In the changes that were wrought as the glaciers retreated some lakes near the shore were cut off from connection with streams and being spring fed kept their outflow, ascending which came the migrating sockeye to spawn in the lake. In other cases the salmon followed the re-treating glaciers into newer and higher reaches of the streams and the sockeye found there often lakes for spawning but did not reach all lakes, for many with suitable spawning areas have never sheltered a run of red salmon even though the species occurs abundantly in other parts of the same river system. Conditions in these streams should be studied to ascertain whether unfavorable temperature conditions do not in general bar access to such lakes as they apparently do in isolated instances which I have found. But that is another problem and need not be discussed here. It is necessary to follow further the life cycle of the sockeye as climatic changes occurred which affected this lake spawning species.

The adult sockeyes spawned in these cold lakes and the young salmon when hatched found in the lakes sufficient juvenile food to hold them over the first year. In the streams where other species of Oncorhynchus spawned the food supply was of course very scanty and so the young seeking food drifted down-stream earlier and went out to sea in their first year. The lake feeding young sockeyes stayed in that environment until the following year when in the spring the urge for more food—or different food—led them to leave the lake and journey down-stream toward the ocean. So long as the water remained cold in the lake when they were spawned or in lakes lower down on the stream through which they had to pass, the journey to the sea was uninterrupted. But with the gradual melting of the ice the climate warmed up and changes occurred in the water. While the streams became warm, the temperature was uniform in the entire mass and they were still glacier fed so that the water remained relatively cool.

One can speak of temperature changes in exact figures only at the present.
When the surface water of the lake passes 10°C. the migrators which have been continuously at or near the surface appear to desert that level and withdraw into deeper layers. Much before the surface temperature has reached 15°C. the fish are no longer seen; apparently they have taken up their abode permanently in deeper, cooler waters. The conditions seen today in these lakes are the result of gradual changes in climate following the glacial period. As the summer became longer and warmer, the temperature of the surface water rose and the critical temperature for migrating salmon was reached earlier in the season. When conditions were reached where the salmon were influenced to seek deeper, cooler waters before they had reached the outlet of the lake, or when they found the outflowing stream unattractive because its temperature was to them too high, then they abandoned the movement down-stream and seeking deeper, cooler waters were at the end of their migration.

In the lakes conditions were different. With the gradual climatic change the lake water also became warmer in summer than it had been previously. But in the absence of a current adequate to mix the mass thoroughly the surface water reached a higher temperature than was found in the stream. The effect of this on the movements of the sockeye depended on the relation between the time of the salmon migration and the amount of change in temperature of the water.

The exact time at which the temperature changes took place varied then as now with the lake and the year. If the young sockeyes passed out of the lake, or through it as the case might be, before the temperature had risen unduly the migratory movement was not interfered with. But if the location of the lake, its exposure to the sun, its scanty outflow or any other factor, warmed up the surface layer before the sockeyes deserted the lake, something else happened.

It may be that in New Zealand the salmon were held in Lake Te Anau by a superabundant food supply as suggested, but similar conditions do not exist in lakes in North America which contain landlocked salmon. In fact reports from certain of these lakes indicate a scanty food supply and especially an entire lack of small fish which were conspicuously abundant in the New Zealand lake. Furthermore, the migrators, or year-old sockeyes, leave Baker Lake when the food supply is still there and the young fish recently hatched are appearing in large numbers, thus making a new and richer food supply. The exact amount of plankton food has not be measured in any of these lakes so far as I can ascertain, nor is its seasonal variation known. Yet what is known justifies us in rejecting the view that any abundance in the food supply is responsible for the landlocked habit.

Conclusions.—In the light of all the evidence one may conclude: The landlocked salmon in a lake were not influenced or held in restraint by the formation of any mechanical barrier that cut off access from the ocean
but by some factors within the lake itself which changed primitive conditions. Some change brought about the disappearance of the current stimulus that would have led them on down-stream to the ocean. These new conditions caused them to hesitate and finally to abandon their journey to the sea. In the Baker River it was the erection of the dam which created a great body of quiet water and thus eliminated the current stimulus. Following that it was the warming up of surface waters which led the young fish to seek deep, cool waters. One should recall also that when in the old unmodified river the migrators had reached the sea, the next move of the young fish was to turn there into deeper, cool waters. The succession of responses is the same in both cases. The changes brought about by the erection of the dam were rapid and the results immediate.

Somewhat similar modifications have resulted from climatic changes in geological eras recognized and recorded in the history of the regions in which landlocked salmon are now found in nature. Reduction in stream flow in many places has left a geological record that is plain. As the volume of water in the stream has decreased gradually, the outlet has been silted up or been blocked by landslides. Seasonal variations in precipitation have also intervened to diminish the stream flow and reduce the current which guided the migrating salmon. As the region warmed up after the recession of the glaciers, the surface water in some lakes finally reached a temperature level unattractive to the cold water loving salmon. Then the fish sought cooler levels in the lake and were thereby prevented from continuing their journey down-stream.

Thus environmental changes in the course of time exercised ultimately similar influences on the salmon to those involved in the erection of the power dam. A large body of quiet water was intercalated in the course of a turbulent stream and the current stimulus disappeared; then the warm surface waters turned the salmon downward and once having left the surface they were held to carry out one part of the life history in the cooler depths of the fresh water lake instead of in the ocean. The migrating salmon had become physiologically landlocked.

1 Contribution from the Zoological Laboratory of the University of Illinois, No. 430.
THE IMPORTANCE OF THE TIME ELEMENT IN THE DETERMINATION OF THE RESPIRATORY METABOLISM OF FISHES

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In experiments involving the determination of the gas exchange of fishes it is necessary not only to handle them but to place them in an environment that is far from normal. As a result of this procedure, the respiratory metabolism is relatively high at first, but it gradually decreases with time. This initial high rate terminates usually, in from four to six hours. Most investigators (Gardner and Leetham, 1914; Ege and Krogh, 1916; Gaarder, 1918; Powers and Shipe, 1928; Hall, 1929, 1930; and others) have not taken into account this initial effect. Keys (1930) was the first to report it and he explained it as being due, in part at least, to the payment of an oxygen debt contracted by the fishes in their struggles incident to being placed in the respiratory apparatus, and possibly in part to sub-minimal stimuli (Winterstein and Hirschburger, 1927). He stated that "in order to be sure that the determinations represent standard or anything like basal metabolism, it is necessary to wait five or six hours after the fish has been placed in the apparatus before beginning the final determinations." He also assumed that if, after six hours in the respiratory chamber, two or more determinations over a minimum period of two hours checked reasonably well, they represented standard metabolism.

The purpose of the present paper is to attempt to show that, with Fundulus parvipinnis, even though there is a temporary equilibrium established five to six hours after the fishes have been installed in the respiratory chamber, this does not represent standard metabolism, but that after 24 hours or more a lower level is attained which is practically constant and represents "normal" metabolism.