INTRODUCTION TO FISH PHYSIOLOGY

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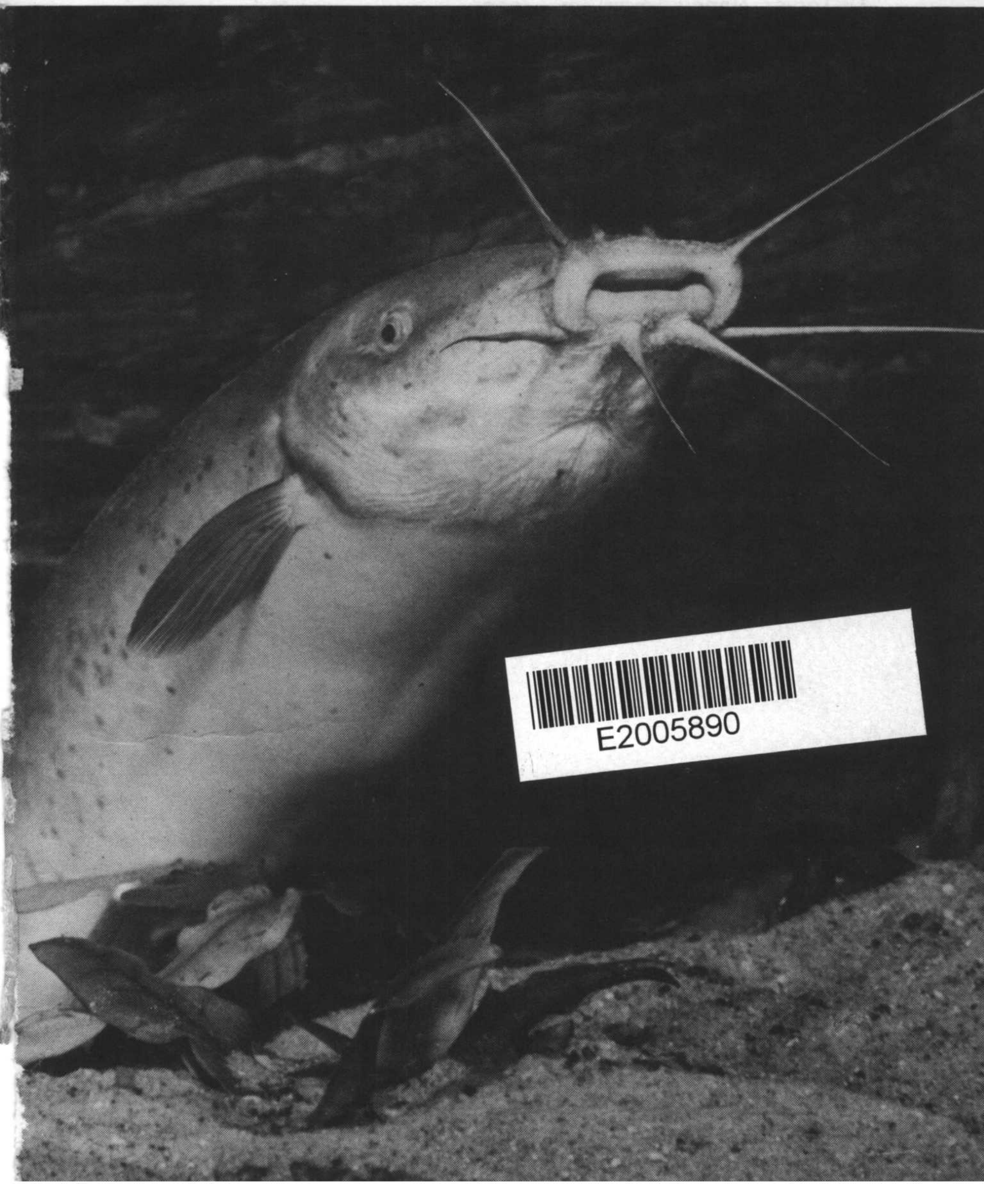

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Preface:

This book describes in general how fish function, particularly at the level of organs and organ systems. In many ways, fish are typical vertebrates differing only slightly from humans. In other ways, their aquatic environment imposes strict requirements or offers unique opportunities which have resulted in some most unusual functions having no counterpart in man. I have tried to present both such kinds of physiological functions in simple, direct language accompanied by examples of typical experimental data. Most of these examples come from experiments on salmon and trout because salmonids are by far the most studied fish. Readers desiring further information on any of these examples should use the author(s) and year given at the end of the Figure or Table caption to find the full bibliographic listing at the end of the book and then go to the original source at a library. Since fish physiology is a rapidly-growing subject, readers can pursue a wealth of materials which are beyond the scope of this book.

Readers should have a minimum of difficulty with technical vocabulary in this book, although technical words could not be avoided completely. A collegiate or other large dictionary should suffice to define the occasional unfamiliar word. If basic concepts need further clarification, readers should consult a textbook on vertebrate or even biomedical physiology—fish mostly function similarly to other vertebrates. Sadly, such books will also probably impress you how much is known about mammals and how comparatively little is known about fish.

I hope that readers find this to be a satisfying and useful book. The intended audience includes college students, professional fisheries people of all kinds, and interested laymen, particularly pet fish hobbyists and growers. If this book provides some insight into the functional opportunities and limitations of the many lifestyles of fishes, then it will have been successful.

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Chapter I: INTRODUCTION

A. COMPARISON BETWEEN AQUATIC AND TERRESTRIAL LIFE

Fish are typical vertebrates in many respects, and most people already know something about the physiological functioning of familiar vertebrates—dogs, cats, farm animals, themselves. While fish have many functions which are comparable to those of land vertebrates, others of their functions relate to their living in water. You may have some reasonable insight into what it would be like to live a dog's life, but it is quite another thing to imagine what it could be like to live like a fish. Their aquatic realm is too different from our terrestrial one for there to be relationships between them.

The physical and chemical properties of water dominate the lives of aquatic organisms in ways largely unknown to most land mammals. The density of water slows movement and demands streamlining for those species which choose to move rapidly, but at the same time it makes possible neutral buoyancy and almost effortless control of posture. Most land vertebrates function on the surface of their environment, while fish can operate in three dimensions with different problems of orientation and location. Air-breathing animals (including some fish) have an abundant supply of oxygen available, while water-breathers have only about 5 percent or less as much oxygen available in water, even when it is saturated. (Table I-1). Fish thus have a double problem of pumping a heavy respiratory medium over their gills and then having to pump relatively large amounts of it because of the low oxygen content. The site necessary for making adequate exchange of respiratory gases is also necessarily an excellent site of the transfer of water, ions, and heat. This leaves the fish in a compromising situation in which optimum respiration is not possible because of the associated problems in osmoregulation.

At standard temperature and pressure (STP = 0° C and 760 mm HG)
1 liter O_2 weighs 1,428 mg.

Air is approximately 20% O_2 = 285 mg O_2/liter air.

AT STP, 1 liter of air-saturated water contains 14.6 mg O_2 or 5.1% as much as air.

Solubility of O_2 in water decreases at higher temperatures. Water saturated with air contains:

At 10° C	11.3 mg O_2/liter
At 20° C	9.1 mg O_2/liter
At 30° C	7.5 mg O_2/liter

For O_2 dissolved in water, 10 mg O_2 = 7 ml O_2 at any temperature.

Table I-1. Some comparisons between the oxygen content of water and air. (See also Table IV-1.)

Further, it is impossible for the average fish to maintain a body temperature different from that of the environment. Tunas, for example, can do this only by the possession of a heat exchanger system in their muscle comparable to that in the gills; most of the heat in the blood leaving the muscle is transferred to the arterial blood entering the muscle by an elaborate counter current heat exchanger. All other fish have a body temperature which strictly follows that of the environment, for better or for worse. The temperature stability of water protects fish from rapid (e.g.—diurnal) temperature changes and is generally advantageous in this regard in temperate climates. If the water eventually becomes too warm for survival, however, the fish has no way to avoid it unless able to leave for cooler places—deeper water, for example. Fish are similarly exposed intimately to everything which is dissolved in water, good or bad.

Most sensory organs of fish are not greatly different from those of land verterbrates, but the resulting sensations which they perceive underwater are probably quite different in several respects from what we sense. Most fish can probably see as acutely and over about the same color range that we do. However, visibility in water is a few hundred meters at best and a small fraction of a centimeter at worst. In humans experiencing little or no vision, maintaining a balance is often a problem—our equilibrium is predominantly visual. In fish there appear to be no such problems, and they orient effectively even in poor visibility. In humans, taste and smell, pressure and hearing are distinct senses. In fish, each of these pairs probably constitutes a single, continuous spectrum. Some fish even have one sense that that humans do not—detection of low level electrical fields.

Thus, while we can have some generally useful insight into what a fish's life may be like, it is very difficult to apply one's intuition to the details. At the same time, it is important that a fish physiologist try to do so. It is an important part of many physiological experiments that data be obtained from "happy" fish rather than distressed ones. Recognizing the difference between these two extremes of behavior becomes an intangible factor in research in fish physiology. One must try to think like a fish.

B. SWIMMING MECHANICS

There are two related problems which a fish must solve to swim efficiently. One is to produce a minimum of energy-robbing turbulence while moving through the water. The other is to convert muscular contraction into some kind of effective propulsive motion. Although the two problems are somewhat interrelated, let's look at turbulence problems first.

The general idea of streamlining is recognized by most people. A streamlined object is smoothly-rounded and spindle-shaped with no sudden changes in outline. In fish, for which swimming is important, however, the minor details also become important. For a fish of any given weight, a long, slim fish goes through the water with less effort than a short, fat fish. For this reason, fast-swimming fish have very compact viscera and many have no swim bladder, both acting to minimize the fish's cross sectional area and the accompanying form (pressure) drag which is proportional to the cross sectional area. If the maximum diameter of the fish exceeds about 15 percent of the body length, hydrodynamic data suggest that the flow over the body is probably turbulent downstream from the thickest part of the body. Most fast-swimming fish have the widest part of their body as far posterior as possible so as to delay the initiation of turbulence as long as possible. Thus fish like sculpins, ling cod or catfish will never be famous for their swimming prowess—their head is the widest part of their body and produces lots of turbulence.

The amount of surface area of a fish also influences the amount of drag to be overcome during swimming. A body which is flattened has much more surface area than the one which is round in cross section. Large fins also add dramatically to surface area. Spines which project at right angles into the flow of water create huge amounts of drag. When form drag and friction (surface area) drag are combined, drag increases by perhaps as much as the cube of the velocity. In practical terms, this means that for a fish to double its swimming velocity it must increase its energy output by about five or six times. Such numbers must be taken with a certain amount of caution because they are extrapolated from data on plaster models of fish tested in wind tunnels. Tests on living, swimming fish have been made only a few times and have given variable results. However, it appears probable that a living, swimming fish has less drag than a dead, limp one being towed through the water or a model fish in a wind tunnel. A more complete discussion of the factors appears in Webb, 1975.

Most fish swim by moving the caudal fin back and forth by alternate contractions of the muscles on each side of the body. A few fish use other fins for propulsion, often the dorsal or the pectorals. When fin motions are analyzed in slow-motion movie films, the motions are seen to be quite complex and to vary widely according to the body shape and muscle arrangements of the fish. The wave-like nature of the swimming motions is best seen in long, slim fish such as eels, but also occurs in short fish. This wave of muscular contraction begins just behind the head, alternately in each side of the body, and progresses posteriorly as an S-shaped wave whose amplitude increases as it travels posteriorly. The wave has a component of its motion which pushes backward against the water, thus propelling the fish forward. The propulsion wave travels down the fish about 15 percent faster than the fish travels forward—i.e., there is about 15 percent slippage. The side-to-side component of the propulsion wave carries the caudal fin from side to side, also providing for-

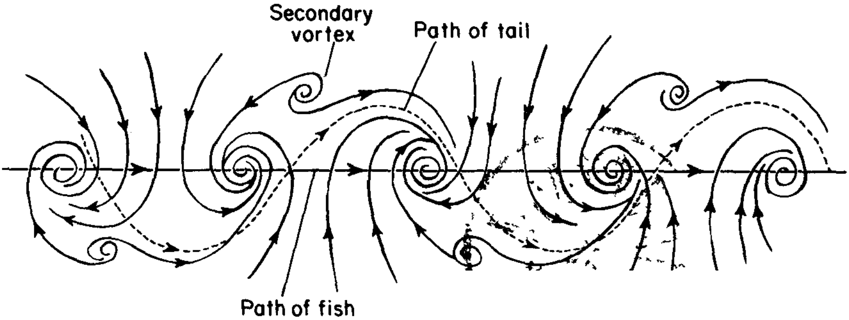

Fig. I-1. Schematic representation of the wake vortices produced by a fast-swimming fish. Swirls (vortices) develop alternately along each side of the body and then move into a relatively straight line behind the fish. Energy savings may occur as the fish's tail passes in front of each swirl, traveling in the same direction as the water in the swirl. (Redrawn from Rosen (1959), from Wedemeyer, et al., 1976, by permission of TFH Publications.)

ward propulsion in somewhat the same fashion as the use of a sculling oar. The relative importance of body undulation versus caudal fin oscillation for propulsion varies from perhaps 80 percent body and 20 percent caudal for eel-like fish to 20 percent body and 80 percent caudal for swimmers like tunas or swordfish. Most fish are intermediate between these extremes.

It should not be overlooked that fins do a great many things for fish besides propel them. They are used for equilibrium (upright balance), braking, turning, walking and climbing. Some are modified for making sounds, providing a spiny defense or acting as feelers. Even the adipose fin of salmonids and catfish probably serves some significant but presently unknown function at some time in the life cycle and is not simply a vestigial remnant of a fin that was once useful.

The water flow near a fish also turns out to be quite a bit more complex than might be supposed. There are small whirlpools (vortices) formed on either side of a fish behind the head as the propulsive waves originate. The vortices grow and are left behind the fish as a swirling wake, not unlike the whirlpools left by each stroke of an oar (Fig. I-1). There is also crossflow above and below the caudal peduncle which complicates any analysis of the propulsive pressure on the tail. In general, fish seem to be masters at taking advantage of any favorable water flow that they can produce, that is produced by other fish in a school or that they can find in a stream. This ability to take advantage of water moving in favorable directions may be one of the reasons why free-swimming fish appear to have substantially less drag than inanimate models of fish in wind tunnels. Fish have been swimming for a very long time and have learned how to do it very well.

As a final comment on swimming mechanics, it should be pointed out that one way to solve all the problems and to deal with the energy needed for swimming is to not swim. A number of fish have adopted lifestyles which require little swimming. They can be sedentary and filter food out of their respiratory water or develop means of attracting food to come to them rather than chasing it. They can escape predators by camouflage rather than speed or can develop bony plates or spines for defense. Strong-swimming, often predatory fish have sophisticated streamlining and gimmicks which are stimulating to an engineer and satisfying to analyze, but streamlining isn't the only way to be a fish.

C. COMPOSITION OF A FISH

1. Gross Anatomy

Salmonids are relatively primitive among the approximately 25,000 species of teleost fishes without being aberrant or archaic. They can be used as being illustrative of a number of general anatomical features which are typical of fish. The general body shape is characteristic of swimming, rather than sedentary fish. The caudal fin is relatively large and there is more muscle in the posterior part of the body to operate the caudal fin than in slowly swimming, hovering or sedentary fish such as in the cod-like fish or the flatfish. In salmonids the pectoral fins are placed below the gill covers and the pelvic fins are below the dorsal fin. In contrast, the more advanced perciform fishes have their pectorals near the midline and the pelvic fins ventral and sometimes even anterior to the pectorals. Muscle is the largest single tissue in the body, with dark muscle being found laterally on either side of large amounts of white muscle. Dark muscle is associated with sustained swimming, white muscle with burst (non-sustainable, emergency) swimming. Muscle is arranged on the axial skeleton in slanting layers shaped in somewhat of a W-shape whose significance is unknown. Contraction of the muscles shortens each side of the body alternately during swimming and produces a compression load on the vertebral column.

The visceral organs of salmonids are compactly arranged and typical of most vertebrates, but with certain notable exceptions. The digestive tract is relatively short, but its surface area is greatly expanded just below the pylorus by the presence of pyloric caecae. The number of pyloric caecae is of taxonomic significance in distinguishing the five species of Pacific salmon. The kidney of salmonids is formed by the fusion of a pair of embryonic kidneys, producing a median structure which runs most of the length of the visceral cavity. The anterior portion is hormonal in function and not excretory, while the posterior portion is called an opisthonephros rather than a metanephros as in the higher vertebrates. The whole kidney also functions in the formation of blood cells (there is no bone marrow as in mammals). The reproductive organs originate anteriorly and dorsally in the visceral cavity in typical vertebrate fashion, but the urogenital ducts are quite confusing in their derivation and in their termination at the urogenital papilla just posterior to the anal opening. There is no definitive study as of the time of this writing on how to properly designate the reproductive and excretory ducts according to their embryological derivation. My policy is to use noncommittal names such as urinary duct and vent and not to worry about whether calling the wide place in a urinary duct a true bladder or not. The functional capacities of these structures are obvious and undisputed. There are certain typical vertebrate organs which appear to be absent because they are diffusely scattered. The pancreas is scattered along the mesenteries of the intestine, and the thyroid gland consists of clusters of follicles scattered in the muscles of the isthmus around the ventral aorta.

A number of salmonid structures are typical of vertebrates as a whole. The swim bladder and its pneumatic duct are

Organ	Wet Weight (as % Body Weight)
Liver	1.22
Spleen	0.13
Intestine	4.69[a]
Heart	1.22
Swim Bladder	0.22
Kidney	0.86
Muscle	55.8
Skin	8.68
Axial Skeleton	13.5[b]
Gills, Gill Bars	2.76
Head	11.83
Total	99.91[c]

[a]Includes visceral fat.

[b]Includes vertebral column and fins with associated bones; excludes head skeleton.

[c]These fish were killed and stored on ice for up to two days before weighing. Weight losses during this storage were adjusted for. Weights of individual organs usually totaled between 90-95% of the total body weight as a result of evaporation during dissection as well as removal of blood from organs such as spleen and heart. Evaporation was particularly noticeable on skin and fins. However, all organ weights were increased proportionately so that the total percentage approximated 100%.

Table I-2. Organ and tissue weights of smolting coho salmon, *Oncorhynchus kisutch*, 130-140 mm fork length, 24-30 g total weight. (Unpublished data, L.S. Smith, 1975.)

homologous to the trachea and lungs of the tetrapod vertebrates. The nervous system and its supporting skeleton are quite typical, with 10 cranial nerves and all of the standard lobes in their normal position and enclosed in a typical cranium. Even in the flatfish where there has been a 90° change in body orientation and the eyes and nostrils have migrated to one side of the head, only the nerve endings and sensory organs have migrated—the brain is still in its original position, along with the semicircular canals and otoliths, i.e., on its side in the adult fish.

Thus there are few surprises in fish anatomy to anyone familiar with other vertebrates, but there are many interesting adaptations of the basic vertebrate body plan.