Environmental Physiology of Fishes

Edited by

M. A. Ali

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Environmental Physiology of Fishes

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PREFACE

A very good piece of work, I assure you, and a merry.
-Now, good Peter Quince, call forth your actors by the scroll.
-Masters, spread yourselves.

A Midsummer Night's Dream. Act 1, Sc. 2

This volume is the outcome of a NATO Advanced Study Institute held in August 1979 at Bishop's University, Lennoxville, Québec, Canada. About 130 participants from all the countries of the alliance as well as India and Japan attended this event which lasted two weeks. Seventeen of these participants had been invited to present reviews of chosen topics, usually in their specialty. This book is constituted mainly of these presentations, which were prepared as chapters. In addition, six of the participants, whose seminars were found to complement the main chapters, were coopted by the invited lectures/authors to provide additional chapters. Although a lecture was given on electric fields, a chapter on this matter is unfortunately absent due to the lack of preparation time.

One may say that Environmental Physiology of Fishes as a discipline originated in Canada. Having been involved as a teacher and worker in this field since 1954, it was but natural that I was tempted to organise an ASI and get a volume out on the matter. I was encouraged by discussions with colleagues and the acceptance on the part of a large number of eminent colleagues to attend the ASI, deliver lectures and write chapters. It was felt that participants made up of a heterogenous group varying from pre-doctorate students to workers nearing retirement, on the one hand and, workers interested in the entire animal, e.g. organs, tissues, even cells, chemicals factors, physical factors, behaviour, rhythms etc., on the other would have nothing but to gain much from the company of one another, were they to spend two weeks working, eating and playing together. I am glad to say that this proved to be correct judging by the constant discussions which took place at all times, the friendships which were made and the post-ASI contacts which were established. I feel that more than the impact the volume may have on the field, the interaction between younger and older workers and among workers from so many different fields will prove to be more advantageous for the advancement of this field of endeavour in the next ten or even twenty years.

Fishes form the largest class of vertebrates and occupy a very wide variety of habitats, some even non-aquatic. In every aspect of their physiology they demonstrate a larger repertoire of adaptive features, more than any other class of animal with the possible exception of the crustaceans. My hope is to have this volume reflect these numerous physiological adaptations in them, with the different environmental factors and variations. I asked the authors to prepare critical, or general reviews, and encouraged them to be as provocative and speculative as they wanted. This book was planned to be reasonable in length and yet cover as much of the field as possible. Obviously not all fields could be covered due to the paucity of space, time or lecturers/authors. In a volume of this sort a certain amount of overlap or repetition is unavoidable. I have tried to keep it to a minimum but may not have entirely succeeded since I am certainly not expert in all aspects of the physiology of fishes. As the director of the ASI, I attended every lecture and seminar and, as the editor I have read every chapter in this volume carefully. This has considerably broadened my knowledge and I am grateful for having had this opportunity and hope that the reader will find the effort worthwhile.

It appears also desirable to explain briefly the process by which the lecturers/authors are selected for the ASI and the ensuing volume. Being a NATO-ASI, lecturers have to be drawn from as many member countries of the alliance as possible. In most cases, travel costs have also to be taken into consideration. Other factors which are not insignificant are lecturing and writing ability of the person, his (or her) ability to deal with a heterogenous group scientifically and socially over a two-week period. Taking all these points into consideration a list is drawn up with the help of the advisory committee and correspondence begins - often as early as two years before the ASI is to take place and chapters are to be submitted. In spite of such early arrangements some persons found it unavoidable to withdraw their presence a few months before the event. In this case they have usually been replaced but if the withdrawel was just a few weeks before the ASI it was virtually impossible to ask someone else to take their place. The presentations at the ASI are followed by discussions and towards the end a meeting of the authors and the editor takes place. At this meeting matters are discussed openly and suggestions are made to fill the lacunes in the volume by inviting one or two or more of the other participants, generally those whose seminars were found to fill such a need, to contribute chapters on subjects and lines established by the consensus. After this, of course, matters are between the editor and the individual author.

I am grateful to Dr. Mario di Lullo of the NATO-Scientific Affairs Division and his predecessor Dr. Tilo Kester for the advice and encouragement they gave during the planning and organising of this ASI. I thank Dr. René J.A. Lévesque, vice-rector for research of my University and Prof. Jean-Guy Pilon, chairman of my department, for the material and moral

support they provided, in the organisation of the ASI and the preparation of this volume.

It would have been impossible to conduct the ASI without the kind support and cooperation of Monsieur J.L. Grégoire, vice-principal and his assistant Mrs. Lillian Garrard and Mr. Ivan Saunders, directors of buildings and grounds of Bishop's University. I am grateful to them for everything they did to make my task less arduous and our stay enjoyable. I thank also the members of my advisory committee for their help in the choice of lecturers and participants. I am grateful to my colleague Dr. Mary Ann Klyne for all the assistance she so willingly gave in the organising and running of the ASI as well as the editing of the volume. My librarian, Miss Margaret Pertwee returned from her second retirement to help in the preparation of the volume, particularly the bibliographies and indices and I wish to record my thanks to her for that.

I thank Mesdemoiselles Marielle Chevrefils and Jocelyne Trudeau for preparing the camera ready manuscript with a Xerox word processing system.

Montréal
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GENERAL INTRODUCTION

GENERAL INTRODUCTION

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Bait the hook well; this fish will bite.
Much Ado about Nothing, Act II, Sc. III.

Almost half of the vertebrate species are fishes. These are estimated to be about 18,800 living species as compared to 21,100 living tetrapods. However, estimates vary greatly, ranging from 17,000 to 30,000. The eventual number of piscine species may well be 50% greater than presently known, going perhaps as high as 28,000.[1] This vast group is also very heterogenous with tremendous diversity in morphology, habitats and physiology. Despite this diversity, members of the super class Pisces can be defined as aquatic poikilothermic vertebrates that have gills throughout life and, if present, fins as appendages. Thus, forms varying from lamprey, rays, eels, flatfishes and lungfishes are distantly related.

Fishes range in size from a 12 mm goby from the Philippines (Pandaka pygmaea) to the 15 m whale shark (Rhincodon typus). Some have stringlike bodies while some others are ball shaped. Some, such as the reef living forms are highly coloured while benthic forms are usually drab. Some, as the salmon and tuna are sleek, graceful and fast while some others, as the chimaeras and stonefishes are grotesque and slow. Fins, when present, may be modified as holdfast organs or as a lure for attracting prey. Some Cyprinids, Silurids, Amblyopsids, Ophidiids and Gobiids lack eyes, mainly as an adaptation to cave dwelling while in a number of forms inhabiting the great ocean depths, which are also devoid of light, eyes may either get to be very large or, greatly reduced. In fishes inhabiting turbid waters also, the eyes may either be reduced or, be of normal size but with reflecting layers to facilitate the capture of light quanta. In many species, bodies are inflatable or encased in inflexible armour. Scales may be present and indeed be very conspicuous as in the carp or, may be totally absent as in eels and catfishes. Internal anatomy too is very diversified.

Fishes inhabit every conceivable aquatic habitat. They are found in lake Titicaca, the world's highest (3,812 m), and in lake Baikal, the world's lowest (7,000 m below sea level) and deepest (1,000 m). Some are found in almost distilled water containing only 0.01 parts per thousand (ppt) dissolved solids, while some live in very salty lakes with 100 ppt dissolved solids. Most lakes have between 0.05 to 1.0 ppt dissolved solids while the value for average seawater is about 35 ppt. One finds fishes such as the African Tilapia in hot soda lakes (44°C) while some, such as Trematomus occur under the Antarctic ice sheet at temperatures of - 2.0°C. Many have acquired the ability to breath air in order to sustain life in stagnant tropical swamps. Some of these, such as the Dipnoi (lungfishes) have become almost amphibious being capable of living outside water for long periods. On the other hand, fishes such as the Salmonids need fast flowing, well oxygenated waters to survive. Similarly, considerable variation is also manifested as far as the ability to withstand differences in salinity and temperature is concerned. Those able to cope with wide variations are termed euryhaline or eurythermal while those restricted to a narrow range are called stenohaline or stenothermal. Dissolved matter has direct and indirect effects upon fishes. Dissolved oxygen is affected by temperature and pressure and is often a determining factor in the occupation of a habitat. Let us recall that water is about 800 times denser than air. Air contains about 21% oxygen by volume but freshwater can dissolve very little, with about 10.23 ml/l at 0°C. This becomes even lesser as the temperature increases. Seawater of 35 ppt salinity has about 8.8 ml/l oxygen at 0°C. Some fishes need saturated conditions (about 6.5 ml/l at 20°C) but most can exist at about 50% of this value. Dissolved carbon dioxide (in the free state) can affect the ability of the blood of fishes to take up oxygen.

Fishes show a remarkable ability to overcome barriers and one often observes some kind of a continuity in their distribution. Exceptions are some marine genera which occur in the temperate and polar regions of both hemispheres but not in the tropics (anti-tropicality). But the vast majority of genera are tropical and most of the others are found either in the Northern or the Southern hemisphere.

The majority of species live entirely either in freshwaters or in the oceans. A few are diadromous, living part of their lives in freshwater and part in the sea. Among these, most are anadromous which spawn in freshwater but spend most of their lives in the oceans. Catadromous forms do the opposite. However, in the case of some species it is not possible to classify as marine, freshwater, catadromous or anadromous since variations may be found between populations and in some cases even individuals may differ. Of course, one often finds many marine and freshwater species in brackish water whose salinity undergoes remarkable variations even during a 24 h period. It is also interesting to note that freshwater, which covers only about 1% of the earth's surface and accounts for a little less than 0.01% of its water has about 6,850 species of fishes while saltwater which covers about 70% of the globe with 97% of its water has only about 11,650 species! Most of the freshwater species are found in Southeast Asia and in the Amazon basin. As far as the marine forms are concerned, the Indo-Pacific is the richest region, followed by the Caribbean area. Fish fauna is sparse in areas recently exposed from the last ice age such as Western Europe, the West African marine region, Arctic and Antarctic.

The habits of fishes vary as much as their morphology, physiology and ecology do. Some are territorial, others form schools. Some take care of their young, some others just lay millions of eggs and leave their survival to chance. Some feed on plants, some on corals and some on plancton. Many are voracious predators, even capable of swallowing an entire large prey. A few are parasitic, some even on their own females! Quite a few are capable of producing sound, light, electricity or, venom. Some are hermaphrodites, others show sex reversal. Some migrate far, some not so far and some not at all. Some migrate vertically during a 24 h period. In many species the habitat of the juveniles is different from that of the adults. For example, tide pools and marshy areas may serve as nursery grounds for the young of many species.

Economically, the interest in, and the importance of fishes is considerable. The quantity of fish caught in 1978 exceeded 45,000 metric tons. Recreational fisheries yielded millions of dollars to a number of countries. The aquarium trade is worth about a billion dollars per year in North America alone and over 25 million persons all over the world indulge in this hobby. Fishes are used for industrial products and food; for such things as fish meal (for agriculture), food of trout, catfish, poultry, pigs, etc. Fish (cod) liver oil is a supplement to diet in many areas and oil from a number of other speciesis another important product of reduction plants and is used in many manufacturing processes and in foodstuffs. Fishes are used for making glue, are a source of leather, and a source of guanine for some paints. Nearly 30% of the fishes caught are used for industrial purposes. Fish culture is getting to be more and more important every year, not only in the warmer but also in the temperate countries. Much greater use could be made of fishes as biological control agents (algal, insect and fish control). Knowledge of poisonous and dangerous fishes (those that attack humans, vectors of parasites and diseases) would also enable us to better control them.

Our purpose is to examine the physiology of fishes in relation to variations in environmental factors so that we could understand the manner in which they adapt themselves to various habitats. This has two points of interest. First, we would be able to comprehend how different species adapt to different habitats; how the same family, genus or species adapts to different environments and, how different species, genera, or families adapt to the same environmental conditions. Second, environmental pollution is being studied more methodically and frequently and in view of their importance, as outlined above, the effect of pollution on fishes is receiving greater attention. Since pollution is essentially an artificial modification of the environment, its effect on the physiology of a fish may be considered to be the study of an aspect or of aspects of its environmental physiology. Also, in order to understand what a pollutant does to a fish, one must first know what the physiological responses of a fish to its "normal" environmental factors are.

Environmental physiology of fishes has not existed as a discipline or sub-discipline for long although papers may be found sporadically in the literature even in the latter part of the 19th century. It is probably correct to say that a concerted effort to study the environmental physiology of fishes commenced in Canada, particularly in Professor F.E.J. Fry's laboratory. Persons who were trained there and some of us who were trained elsewhere in the country have spread out literally almost all over the globe, establishing groups studying various aspects of the environmental physiology of fishes. It is thus a signal honour that Professor Fry was a member of the advisory committee of the Advanced Study Institute which led to this volume. This volume was planned so that it would be as complete as possible yet not put too much emphasis on matters that have been dealt with thoroughly in the recent past, such as Vision in Fishes (Vol. A1 in this series, 1975), Electroreception (Handbook of Sensory Physiology, Vol. III/3, 1974, Springer-Verlag, N.Y.). The chapters dealing with light for example have been written with the theme of this volume in mind and try to bring a fresher perspective. On the other hand, considerable space has been given to gases, gas exchange organs, ions, pressure, sound, temperature, photoperiods, rhythms and reproduction. It is hoped that it will give an overall view of the effect of various environmental factors and a combination of them on fishes, both at the organ's and individual's level. It will be evident from the chapters that the gaps in our knowledge of the environmental physiology of fishes are still much too large to permit generalisations and it is hoped that this volume would succeed at least to a small extent in encouraging further concerted work in this field.

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I thank Michel Anctil, Naercio Menezes and Mary Ann Klyne for comments on an earlier draft of this essay. However, I alone am responsible for its shortcomings. In preparing this essay I drew heavily from many books dealing with the biology, ecology, physiology and taxonomy of fishes and it does not appear feasible to list them in a bibliography.

OXYGEN AS AN ENVIRONMENTAL FACTOR OF FISHES

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I - ABUNDANCE OF OXYGEN IN NATURAL WATERS

A) Sources of Oxygen

Ultimately the source of oxygen in the aquatic environment is photosynthesis. Bodies of water may be net exporters or importers of oxygen. In circumstances where plant life is abundant and light is available water bodies release a considerable amount of oxygen to the atmosphere.

B) Solubility of Oxygen

The solubility of oxygen in water is low. A liter of air-saturated fresh water at 10 C will contain 11.3 mg of oxygen which corresponds to a concentration of 0.35 millimoles per liter. In contrast a liter of air at the same temperature and at atmospheric pressure will contain about 296 mg or 9.25 millimoles of oxygen.

A number of factors affect oxygen solubility. As water temperature rises oxygen solubility decreases such that the oxygen content of air-saturated fresh water at O C is approximately twice what it is at 30 C. The solubility of oxygen in water declines with increasing salinity. At normal temperatures air-saturated sea water will hold 20-23% less oxygen than fresh water. A number of useful tables on oxygen solubility have been reproduced in a recent review by Davis (1975).

It is important to remember that CO_2 is 25 to 30 times more soluble in water than is oxygen. This means that water is a much better medium in which to carry off metabolic CO_2 than it is as a source of oxygen.

C) Variability of Oxygen in Aquatic Environments

Perhaps the most striking feature about oxygen as an environmental factor of fishes relates to its variability in abundance. In contrast with the atmosphere, in which the pressure and concentration of oxygen (P_{O_2} & $[O_2]$) are relatively constant, the P_{O_2} and $[O_2]$ of water can vary dramatically. Not only can the P_{O_2} of water drop below air-saturation levels or even disappear, it can also rise well above atmospheric levels.

The variations of oxygen in natural waters arise from a number of sources, and the variations may be spatial or temporal. Some of the most spectacular fluctuations are due to the diurnal changes in the balance between photosynthetic oxygen production and overall community oxygen demand from respiration and chemical processes. Such fluctuations are particularly common in shallow freshwater systems (Davis, 1975; Garey and Rahn, 1970; Jones, 1961; Kramer et al. 1978), where P_{O_2} may drop to 20 to 30 torr during the night and rise to 200 to 400 torr during the middle of the day.

For the majority of cases it is only photosynthetic activity which can produce elevations in $[O_2]$ above air-saturation levels. However sudden warming of water such as occurs in industrial and thermal power station effluents can increase P_{O_2} in the absence of an increase in $[O_2]$.

Even large bodies of water may have oxygen levels higher than air-saturation. Fairbridge (1966) reports that oxygen levels in many oceans may be as high as 130% of air saturation in the photic layers. Certainly this extends to the antarctic oceans where productivity is high and summer photoperiod is prolonged (Holeton, 1970).

Variations in oxygen concentration also occur on a seasonal basis and are pronounced in situations where there is density dependent stratification of water bodies. Such effects are particularly pronounced in the temperate fresh water lakes where in summer the formation of a warm surface layer effectively seals off a colder hypolimnion from the atmosphere. Often the hypolimnetic oxygen demand exceeds the supply and $[O_2]$ drops or even disappears as the warm season progresses. In the temperate or high latitudes the formation of winter ice cover effectively seals off water bodies from access to the atmosphere. Under these circumstances the oxygen levels are very dependent upon the balance between photosynthetic activity and community oxygen demand. Often the balance swings in favor of oxygen demand due to the influence of short daylengths and light attenuation due to snow cover. In shallow biologically productive waters this can result in