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Ecological and Environmental Physiology of

Fishes

F. Brian Eddy and Richard D. Handy

Ecological and Environmental Physiology of **Fishes**

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Ecological and Environmental Physiology of **Fishes**

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Preface

Before we started writing and after discussion with the Series Editor, it seemed a reasonably straightforward task to put together a book on *Environmental Physiology of Fishes*. Early on though, it became apparent that this was far from true, and in order to achieve the aims of the book, there would have to be careful selection of content and consideration of how deeply to explore it. The content was already determined to a certain extent, since this series follows a similar format and authors are invited to address general headings such as 'Extreme Environments' and 'New Techniques and Future Developments'. This helped create a focus, but at the same time, the book needed a vision to make the content accessible to a new generation of students. We hope this has been achieved and that this book engages the interest of the reader not only with basic concepts, but also with new and relevant work in environmental physiology, as well as indications as to how the subject may develop in the future.

In recent years, there has been a huge expansion in research into the many facets of animal biology, and disciplines that were once considered separate have now begun to overlap or even merge. Ecophysiology is a prime example. Having developed from areas of common interest in animal ecology and animal physiology, it now receives input from related disciplines including animal behaviour, comparative endocrinology, conservation biology, and importantly, the biomolecular sciences. Over the last few years, most branches of biology, including the ecophysiology of fishes, have been and continue to be reshaped by advances in the biomolecular sciences, particularly in areas such as comparative genomics. Very soon new insights may emerge from the application of DNA sequencing using the new-generation sequencing techniques and related methods. Even a brief survey of the literature reveals that research into the 'ecophysiology of fishes' occurs in all these areas and in many more as well. Material relating to the 'ecophysiology of fishes' appears across a wide range of publications including internet sources, and in writing this book, three things became clear to us. First, that it would be almost impossible to locate and appraise every relevant source for this volume. Second, that discussion with experts in the field together with relevant review material would be important in shaping the book. Third, that it would not be possible to cover all aspects of the subject, and thus some major areas would receive only a brief mention or be omitted altogether. Hopefully the topics selected more or less represent the meat of the subject and by them, the reader will be informed about core aspects, areas of current interest, and possible future developments in these areas.

The book would not have been possible without reference to earlier publication in fish biology and related topics. These are listed in the General References. Each of these works receives special recognition and acknowledgement since they helped shape some of the sections. I hope the points made by the authors are reflected reasonably and receive acknowledgement. Many sections of the book are based on books and papers from the literature. Whenever possible, these are cited in the text and appear in the Bibliography. Material from these sources is gratefully acknowledged. My thanks go to my co-author Richard Handy for substantial contributions that shaped much of Chapters 2 and 5, and for critical evaluation of the other chapters. I would also like to thank Dr Nic Bury of Kings College, London, for helpful and critical comments on Chapters 4 and 5. There have been useful contributions from discussion with other colleagues and experts in this field, and we thank them too. Thanks go also to the Editor of this series, Warren Burggren and to my editor, Helen Eaton, for her help and encouragement. Financial support from the Leverhulme Trust is gratefully acknowledged.

Brian Eddy
September 2011

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Ecological and Environmental Physiology of Fishes

1.1 Introduction and Opening Remarks

Over two-thirds of the earth's surface is covered by water, and the first 150–200 million years of vertebrate evolution was dominated by adaptation to the aquatic habitats. More than half the living vertebrates are aquatic. Fishes have evolved to colonize almost every type of aquatic habitat and today they are a hugely diverse group of over 25 000 species. Evolution of this great diversity has resulted in fascinatingly different designs for special modes of life, as well as solutions to the problems common to them all. Comparisons of fishes in different habitats help to reveal the biological and physiological compromises fishes have to make to satisfy the often conflicting demands on their lives.

Today, fishes are found in almost every imaginable watery habitat. These include the shallows and depths of the oceans, coastal waters and estuaries, rivers, streams, lakes, ponds, and ephemeral water bodies. Many species inhabit freezing waters in polar regions and have low-energy life styles whilst others thrive in ponds fed by thermal springs. Some periodically emerged from the water and have become air breathers. Some fishes species show high performance swimming and extreme feats of endurance, making them interesting models to understand the energetics of vertebrate animals. Tunas in the open oceans have a high, sustainable swimming speed that allows them to swim rapidly and outperform their prey. The anatomy and physiology of tunas give an insight into how they generate the forces required for high speed swimming. Study of these fishes shows they have large masses of warmed red muscle, and the unusually large amounts of oxygen required to sustain fast swimming are delivered by highly efficient respiratory and circulatory systems. Some freshwater carp are able to survive long periods of very low oxygen levels occurring periodically in some ponds and lakes. How is their metabolism switched from aerobic to anaerobic pathways so that they can survive without oxygen for long periods? The challenges of living in a particular environment are in part met by adaptations of body form and physiological function, yet there are wider and equally important questions, such as why these are species successful in their particular environments. Answers to such questions may be found in the study of behaviour, in the dynamics of populations, in the ecology and physiology of the species, and in evolution. The study of environmental physiology aims to understand how the organisms regulate and tolerate or even adapt to the natural and anthropogenic changes in their environment.

Traditionally the focus of fishes biology has been on systematics, anatomy, and geographical distribution of fishes, but recently interest has extended beyond these areas. Fish biologists seek ways to improve fisheries and aquaculture, and to assess the impact of human activities on aquatic environments. They seek to extend understanding in rapidly developing fields such as the interrelationships of physiology and behaviour, as well as to deploy molecular biology techniques to investigate topical issues such as comparison of genomes, phylogenetic relationships, control of gene expression, the use of transgenic fishes to investigate cellular processes, and fishes as molecular models of vertebrate developmental biology. Amateur fishes biologists want to increase their knowledge of the fishes they keep in aquariums or ponds, or of those they attempt to lure with hook and line. This book is aimed at fishes biologists with some basic knowledge who may wish to acquire enough elementary physiology to extend their understanding of how living fishes function in their environments. It is aimed at enthusiastic amateur fishes biologists, undergraduates with an interest in vertebrate biology, and researchers who may have specialized in related areas but now require some physiological input.

1.2 Water as a Habitat

1.2.1 Sea Water and the Marine Environment

Approximately 71% of the earth is covered by sea water (Table 1.1). The deepest parts lie more than 10 000 m below the surface and the average depth is about 3400 m. Near the land masses, the sea is often shallow and the sea bed, called the continental shelf, gradually slopes from the coast to a depth of about 200 m. About 8% of the total sea area lies above the continental shelves and at their edges the slope of the sea bed is steeper, called the continental slope, descending to the ocean basins reaching depths of 3000–6000 m. Here the sea bed may be almost flat over large areas—abyssal plains—though there are extensive areas of submarine mountains whose peaks may approach the surface. Parts of the sea bed are furrowed by deep troughs where the bottom may descent to 7000 m or more. Some submarine ridges and trenches are associated with volcanic activity, and areas of warmed water support unique and varied forms of life.

The deep sea environment is relatively stable, characterized by lack of sunlight, isolated from tides and external rhythms, and the hydrostatic pressure is high. In contrast, shallow oceans and seas are subject to seasonal and physical changes but

Table 1.1 By far the greatest amount of water on earth is contained in the oceans. Most forms of life including humans are dependent on freshwaters even though they are a small proportion of the waters on earth. Approximate renewal times for freshwater in rivers are days or weeks; for lakes, tens of years; and for glaciers and most oceanic waters, thousands of years. Modified from Wetzel (1983).

Compartment	Volume (1000 cu.km)	Per cent
Oceans	1 370 000	97.61
Saline lakes	100	0.008
Total freshwater	37 000	2.8
Glaciers, ice, snow	29 000	2.08
Subsurface	4067	0.295
Freshwater lakes, rivers	126	0.009
Saline lakes	104	0.008
Atmosphere	14	0.001

not to the extent of coastal waters and estuaries which may experience significant variation in flow, temperature, salinity, and radiation.

The chemical composition of the sea has changed little over the period of about 700 million years when evolution occurred. It is believed that a small increase in alkalinity occurred and that oxygen levels gradually increased from 600 million years ago. Changes generated by the increasing biomass are probably of equal importance. Organisms, including the fishes, form part of a dynamic equilibrium both physiologically, as individuals, and ecologically (as populations), with their aquatic environment. The study of environmental physiology aims to understand how the organisms regulate and tolerate or even adapt to the natural and anthropogenic changes in their environment.

The waters of the oceans are in constant movement through the action of oceanic currents. The direction of surface currents is mainly determined by the earth's rotation and wind action. Deeper oceanic currents are generated mainly by regional changes in density and salinity of sea water. Warm surface waters of low density from low latitudes are carried by surface currents to higher latitudes, where cooling causes an increase in density and sinking to deep levels. The course of deep water currents is determined by complex factors including the earth's rotation, position of the land masses, and temperature.

Over the ages the processes of weathering and sedimentation have produced remarkably uniform composition of the oceans with reference to the major dissolved constituents (Table 1.2). There may be local differences through addition of fresh water from rivers and rainfall or removal by spray or evaporation. It is widely held that life began in sea water and many of the simplest animals living today are small and surrounded by sea water. Indeed, sea water provides the most constant environment for animal life. The chemical composition and

Table 1.2 Concentration of the principal inorganic ions in 'normal' sea water, salinity 35–36 parts per thousand (ppt or ‰). Sea water may become more concentrated, e.g. by evaporation or diluted by fresh water from rivers or rainfall, but the relative concentrations of ions remains the same. Together with trace elements, the osmotic concentration is about 1000–1200 mOsm and the freezing point depression about 1.8–1.9 °C. Below about 1000 m depth salinity is relatively constant at about 34.5–35 ppt while at the surface there is variability according to evaporation or dilution by precipitation. (Modified from Willmer *et al.*, (2004.)

	1 litre sea water	
Ion	g per litre of sea water	mmol per litre of sea water
Chloride	19.4	548.3
Sulphate	2.7	28.25
Bicarbonate	0.14	2.34
Calcium	0.41	10.23
Magnesium	1.3	53.57
Potassium	0.39	9.96
Sodium	10.8	470.2

osmotic pressure of the extracellular fluids of most marine invertebrates is similar to sea water.

The principal inorganic ions of sea water are shown in Table 1.2. In addition, it contains almost every element, often at low or trace concentrations. Two elements, in particular, are of importance in the marine environment since their availability may be limiting; that is, once taken up organisms they are unavailable for further biological production. Nitrogen is present in sea water as dissolved gaseous nitrogen, as inorganic forms such as ammonia, nitrite, and nitrates and also as organic forms, e.g. amino acids. Some micro-organisms such as blue-green algae (*Cyanobacteria*) are able to fix dissolved nitrogen and so, in certain locations, add to the availability of this element. Phosphates normally are present in sea water at sub-micromolar concentrations and yet are essential for growth and proliferation of micro-organisms and some algae are able to release phosphatases to the environment to help release phosphate from dissolved organic phosphates.

1.2.2 Freshwater and Freshwater Environments

On a geological timescale, lakes and rivers are short-lived and offer an environment quite different to the seas and oceans. In all but the larger water bodies there may be significant daily and seasonal changes in temperature, and some smaller water bodies may exist only intermittently, according to climatic conditions. Freshwaters impose osmotic conditions on animals quite different to those in the marine environment.

Freshwaters make up less than 1% of the world's waters yet running and standing freshwater systems play a vital role in life on planet earth. On evolutionary and ecological timescales, running water (lotic systems) are more permanent than most standing water habitats. Running waters may have been a primary pathway for the evolutionary movement of animals from the sea to land and are likely to have been the ancestral habitat for many organisms. Flowing water habitats are a small proportion of the earth's freshwaters yet they are rich and diverse habitats offering important resources to mankind. They range from trickling streams flowing along a narrow channel to massive rivers such as the Amazon, over 3400 km in length and over 3 km wide in places.

Lakes and ponds show tremendous variation in size and permanence and these too support varied ranges of organisms. Water bodies range in size from puddles to the Great Lakes of North America, the Rift Valley Lakes of Africa, and Lake Baikal in Russia. Some lakes have existed for millions of years whilst others are seasonal and may contain water for only part of the year. Standing water bodies are present in all climatic conditions, from ice covered lakes in the polar regions to tropical lakes which may experience high temperatures all year. Organisms from different freshwater systems may vary greatly in their adaptations to particular habitats, yet they have a surprising number of ecological features in common.

Most water bodies supporting living organisms have pH values in the range of approximately pH 6–8 although there are many unusual, yet life-supporting systems, where pH values may vary outside this range. The chemical composition of sea water ensures strong buffering, and in most marine environments the pH value is about 8 and varies slightly with changes in temperature and salinity. Some freshwater systems have relatively stable pH values if they are buffered by bicarbonate but ion-poor waters tend to be poorly buffered and are usually sensitive to acidic inputs. Freshwater systems in parts of Scandinavia and North America are ion poor and tend to be poorly buffered. During episodes of acidic precipitation the pH value is sometimes as low as pH 5, causing leaching of aluminium and other metal ions from the substratum. These levels of acidity favour formation of aluminium compounds, particularly certain hydroxides, which are highly toxic to fishes resulting in instances of significant mortalities (Table 1.3, Chapter 3.5).

1.2.3 Estuaries, Brackish Water, Hyposaline and Hypersaline Environments

The meeting of freshwater and sea water, where a river meets the sea, and the resulting interactions of these two major aquatic systems produce a variety of aquatic habitats of which estuaries are but one example. Estuaries have distinct

Table 1.3 Ionic concentration of an ion-poor fresh water (soft water) characteristic of an environment dominated by insoluble rock, and an ion-rich water (hard water) characteristic of water running off soluble rock such as limestone. These examples are towards the extremes of the range and the composition of most fresh waters is somewhere in between. The salt content of fresh waters ranges from almost none to about 0.5 ppt and is typically less than 1% that of sea water. Values for extremely ion-poor fresh water such as the Rio Negro in Brazil are shown in Table 2.1. Some fresh waters contain significant amounts of dissolved organic material, referred to as humic substances, imparting a yellow or brown colouration and often have biological activity (Steinberg *et al.*, 2007).

	Concentration in mmol L^{-1} fresh water		
	Ion-poor water	Between ion-poor and ion-rich	Ion-rich water
Sodium	0.24		2.22
Potassium	0.005		1.46
Calcium	0.07		3.98
Magnesium	0.04		1.67
Chloride	0.23		2.54
Sulphate	0.05		3.95
Bicarbonate	Trace		2.02
pH value	Variable, normally slightly acidic, pH 5.5–6.5	Increasing concentrations of calcium and bicarbonate tend to stabilize pH values	Relatively stable depending on bicarbonate buffering, typically pH7.5–8.5

and variable ecological systems of their own. The upper limit of an estuary is often considered to be the limit of daily tidal influence while the middle reaches are subject to increasingly greater tidal influences as the mouth of the river is approached. Defining the outer limits of estuaries depends on the size and flow of the river. Compared to smaller rivers, some large rivers produce a plume of low salinity far out into the open sea and definition of outer boundaries is probably better based on coastal morphology, hydrology, and management considerations.

The most obvious variable in the estuarine environment is salinity. According to the tide it will vary with both depth and distance from the shore, and an organism at a particular location could be exposed to a wide range of salinities during a tidal cycle. Such extremes of exposure are most likely to occur in mid-estuary areas rather than in the more stable salinity regimes towards the two ends of the estuary. The layering of lighter freshwater over more dense sea water means that the salinity of water filling the spaces between sediment particles (interstitial water) is less subject to dilution, and that many intertidal areas are less likely to be exposed to dilute sea water on the receding tide.

Settlement of organic matter and silt in estuaries often forms extensive mud flats. The high levels of organic matter in the sediment and surrounding water are broken down by aerobic bacteria resulting in removal of dissolved oxygen from the water. Hence some mid-estuary regions show a marked reduction in dissolved oxygen compared to the waters in the head or mouth of the estuary. The metabolic processes of anaerobic bacteria often result in release of a variety of substances including hydrogen sulphide and sulphides which cause the mud to turn black and are responsible for the characteristic 'rotten eggs' smell. However, organisms which can tolerate the severe mechanical and chemical conditions of mud flats can benefit from the rich source of nutrients found in the sediments and often show exceptionally high levels of secondary aquatic production which in turn support large populations of predators such as fishes and birds.

The variation in temperature in an estuary over a tidal cycle is generally small. Seasonal changes in temperature in estuaries at higher latitudes can initiate reproductive and migratory behaviour in larger and more mobile species such as fishes. Degradation processes by microbes are increased at higher temperatures, e.g. in tropical climates and during summer at higher latitudes. Increased biological oxygen demand may often lead to depletion of dissolved oxygen in the water. In urban and industrial areas, estuarine organisms may be exposed to further hypoxic stress through human activities such as discharge of organic materials or heated water. Estuaries are amongst the most fragile ecosystems and few are untouched by human activity whether as destructive discharges of waste water or modifications of the bank-side environment.

1.2.3.1 Hyposaline

During the tidal cycle, an estuary may contain dilute sea water but in contrast there are other marine aquatic habitats where the salinity is always below that of sea water. Sometimes these are referred to as brackish water systems. There are several large and partially enclosed bodies of brackish water including the Baltic Sea, the Caspian Sea, and the White Sea, as well as many smaller examples. The fauna is reflective of organisms of marine origin and in some ways resembles the fauna of estuaries, but in each case there are critical and specific differences.

The Baltic is generally shallow, lacks a tidal cycle, receives a substantial freshwater input from rivers and the salinity is about 8 ppt or about 25% sea water. The fauna contains marine organisms tolerant of dilute sea water as well as freshwater animals tolerant of moderate salinity. Thus pike and cod may be found together in certain locations. However, marine animals intolerant of dilute sea water are generally absent, e.g. elasmobranches and cephalopods.

The Black Sea has minimal connection to the Mediterranean, is much deeper then the Baltic Sea, and the salinity ranges from 17–21 ppt (about 60% sea water). Since there is virtually no vertical mixing, the deeper water is depleted of oxygen and the majority of biological production occurs in localized shallows. The Black Sea has been significantly exposed to over-fishing, input of pollutants, and the introduction of alien species.

1.2.3.2 Hypersaline Sea Water

Hypersaline environments occur in locations such as coastal marine embayments where there is little tidal action or mixing, the temperatures are high, and rate of evaporation exceeds inflow of freshwater. Salinity in the Suez Canal is commonly over 40 ppt, and in salt marshes near Cedar Key, Florida salinities can be as high as 70 ppt (approximately 200% sea water). Other examples include the Curacao Lakes in the West Indies and locations near the Crimean Peninsula in the Black Sea. A few species of fishes including flounders, mullet, and sailfin molly may establish populations in hypersaline environments up to about 200% sea water. Higher salinities are populated only specialist crustaceans such as brine shrimp.

1.2.3.3 Inland Hypersaline Lakes

Fresh waters make up about 2.4% of the water on earth and most is captured as ice at the poles (Table 1.1). Approximately 0.01% of fresh water exists in lakes and rivers and almost a similar amount is present as salt lakes. Inland salt lakes occur worldwide in arid and semi-arid basins and are formed where the input from inland drainage systems is balanced by outputs. They may contain water permanently or intermittently. Salts dissolved in the freshwater inputs are concentrated in the lake by evaporation, and the ionic content of salt lakes is variable depending on location and season. Whilst the ionic content of normal freshwater lakes seldom exceeds 3 g L^{-1}, in salt lakes the salinity may range between 3–300 g L^{-1} (50–270 ppt) depending on climatic conditions. Most of the inland salt water is held in the Caspian Sea and other large lakes including the Aral Sea, Lake Balkhash, and Great Salt Lake, although there are many smaller lakes as well. The salinity of the Caspian Sea is relatively low (up to about 13 ppt or one-third sea water) and supports a variety of moderately euryhaline species including sturgeons, mullets, carp, bream, roach, and trout. Lake Balkhash in central Asia is over 300 m above sea level. Its salinity is similar to that of the Caspian Sea, parts of the lake freeze during winter and like the Aral Sea, there is much disturbance from economic activities.

The alkaline lakes of the African Rift Valley are fed by geothermal hot spring vents containing relatively high concentrations of sodium bicarbonate and carbonate. Approximate values for the major ions are Na^+, 350 mmol L^{-1}; Cl^-, 110 mmol L^{-1}; alkalinity, 380 mmol L^{-1}; osmolality, 580 mOsm kg^{-1}; pH 10.0. Parts of this inhospitably alkaline environment support populations of a uniquely adapted fishes, the Magadi tilapia (*Oreochromis alcalicus grahami Trewavas*). They occur in shallow lagoons that have temperatures of about 37 °C and feed on abundant mats of blue-green algae. This species has several unique adaptations including the ability to produce urea as a nitrogenous end product (see Chapter 3).

1.3 Physical and Chemical Properties of Water

Most of the water on the planet is in liquid form but it is also present in smaller amounts as a solid and as a gas. Indeed water is the only common substance to exist in the natural environment in all three physical states: ice, water, and water vapour. Modern life, including terrestrial organisms, remains tied to water. Most cells contain 70–90% water and are themselves surrounded by water.

A single water molecule is made up of an oxygen atom covalently bound to two hydrogen atoms in a V-shaped configuration. It is a polar molecule since the oxygen atom retains a partial negative charge attracting up to four positively charged hydrogen atoms of neighbouring water molecules (Fig. 1.1). These relatively weak hydrogen bonds are easily broken and at any instant, only about 15% of water at 37 °C is in this configuration but even so, compared to other liquids, water is significantly structured and cohesive. Hydrogen bonding accounts for a number of important properties of water such as the surface tension, in that water behaves as though it was covered by an invisible film. This allows certain specialized animals to walk on the water surface or for a glass to be slightly overfilled.

Application of heat to a body of water at first increases its temperature by only a small amount since much of the energy is used to break hydrogen bonds. Thus water has a high specific heat, compared to other liquids, since a relatively large amount of energy is required for a small increase in temperature. Similarly as

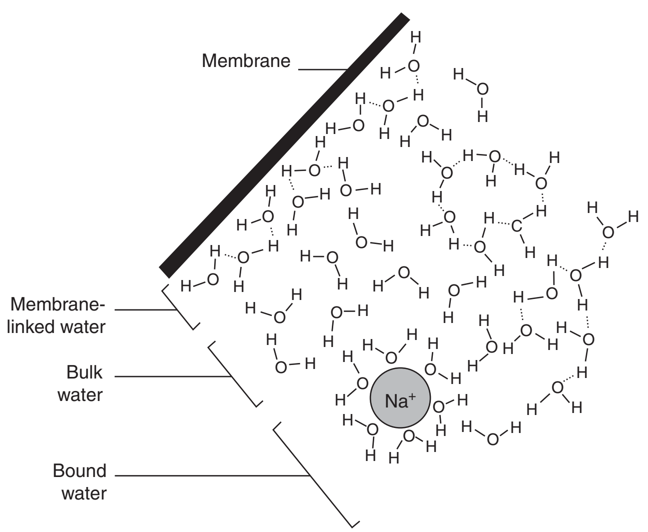

Fig. 1.1 Diagrammatic representation of the structure of bulk water, bound water, and membrane-linked water in a cell (dotted lines are hydrogen bonds). From Willmer *et al.* (2004), with permission from John Wiley & Sons.