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The Physiology of Tropical Fishes

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SERIES EDITORS: William S. Hoar, David J. Randall, Anthony P. Farrell

THE PHYSIOLOGY OF TROPICAL FISHES

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THE PHYSIOLOGY OF TROPICAL FISHES

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PREFACE

The present volume was conceived to cover the most recent advances in the physiology of tropical fishes. The readers can find information about the physiology of tropical fishes in many of the first 20 volumes of the Fish Physiology series. However, *The Physiology of Tropical Fishes* is the first volume to specifically gather information about the large and important group of fishes that live in the tropics. Tropical environments are as diverse as are the groups of fishes living there. Rather than trying to cover all areas of the physiology of tropical fishes, this book brings together the subjects related to their physiological adaptations to tropical environments, which they have shaped during their evolutionary history, and what make tropical fishes an amazing group to study. *The Physiology of Tropical Fishes* hopes to broaden our understanding of what is so special about freshwater and marine tropical habitats that makes tropical fishes one of the most diverse groups of vertebrates in the world. Indeed, subjects such as Growth, Biological Rhythms, Feeding Plasticity and Nutrition, Cardiorespiration, Oxygen Transfer, Nitrogen Excretion, Ionoregulation, Biochemical and Physiological adaptations are all presented and discussed in the light of their specific fitness to tropical environments such as intertidal pools, coral reefs, and the Amazon's different types of waters, all of them typically hypoxic and warm water bodies. These subjects have been developed by top scientists studying specific characteristics of tropical species and also their many interactions with their ever-changing environments. The voyage through this volume brings us the conviction that tropical fishes are barely studied and much more needs to be done before we have a clear picture of the adaptive characteristics that allow them to survive extreme tropical environmental and biological conditions. We are very grateful to all colleagues who contributed to this volume, for their enthusiasm and their dedication to this project. Also, we are grateful to the many reviewers for their constructive comments. We thank Claire Hutchins for her support and the staff of Elsevier for providing the proofreading formats and helping with the final editing of the volume. At last, but not least, we thank the Editors of the Series Fish Physiology, Bill Hoar, David Randall, and Tony Farrell for their invitation and for keeping such an important subject updated for the many generations to come.

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1

TROPICAL ENVIRONMENT

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I. INTRODUCTION

The tropical climate zone occupies *ca.* 40% of the surface of the earth and is located between the Tropics of Cancer (latitude 23.5 °N) and Capricorn (latitude 23.5 °S). The main ecological driving forces within this zone are relatively stable high temperatures and air humidity. Although there are variations in climate within the tropics, 90% of tropical ecosystems are hot and humid, whether permanent or seasonal, and the remaining 10% are hot and dry and include mainly desert-like ecosystems. These variations are determined by altitude, topography, wind patterns, ocean currents, the proportion of land to water masses, geomorphology, vegetation patterns, and more recently by large-scale/man-made environmental changes.

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Various attempts have been made to classify the climates of the earth into climatic regions. Köppen Climate Classification System, proposed by the Köppen in 1936 (Köppen, 1936), is based on five inputs: (i) average temperature of the warmest month; (ii) average temperature of the coldest month; (iii) average thermal amplitude between the coldest and warmest months; (iv) number of months with temperature exceeding 10 °C; and (v) winter summer rains. Two other classifications followed this classification: the classification of Holdridge, which takes into account temperature, evapotranspiration, and annual rainfall, being also known as life zone classification (Holdridge, 1947), and the classification of Thornthwaite, which takes into account moisture and temperature indexes (Thornthwaite, 1948). The "empirical, and somewhat obsolete, albeit fairly efficient" characteristics of the Köppen classification have driven some rejection to this and some other similar classifications (Le Houérou *et al*., 1993). However, the Köppen classification is widely used with a variety of amendments, and based on this system five major climatic groups are recognized in the world, plus a sixth for highland climates. They are: Tropical humid (A); Dry (B); Mild mid-latitude (C); Severe mid-latitude (D); Polar (E); and Highlands (F). These main types are further classified into various subtypes, as reviewed by McKnight (1992). For the purpose of this book and based on Köppen's classification, three broad categories of tropical climates are distinguished: *Af*, tropical humid climate with relatively abundant rainfall every month of the year; *Am*, tropical humid climate with a short dry season; and *Aw*, tropical climate characterized by a longer dry season and prominent, but not extraordinary, wet season (Figure 1.1).

An intricate relationship does exist between soils and water bodies. Under many circumstances water composition and its major characteristics are determined by the surrounding soil that in tropics is highly diverse, and so are the water bodies, as we shall see later on this chapter. In addition, as the anthropogenic pressure increases dramatically on land, more and more aquatic environments are experiencing significant challenges. These water bodies, however, often have an amazingly high ability to neutralize the large quantity of diversified chemical products reaching them (Val *et al*., 2004, in press; van der Oost *et al*., 2003). This chapter aims to depict the major aquatic habitats of tropical fishes, with emphasis on their physical, chemical, and biological characteristics and effects of man-made and global changes on these environments.

Diversity is the keyword defining tropical aquatic ecosystems as they include hundreds of different types of water bodies, with different water composition, and different biological and physical characteristics. In addition, a single water body undergoes significant changes throughout the year, even disappearing, in some cases, during the dry season. Disappearance of water

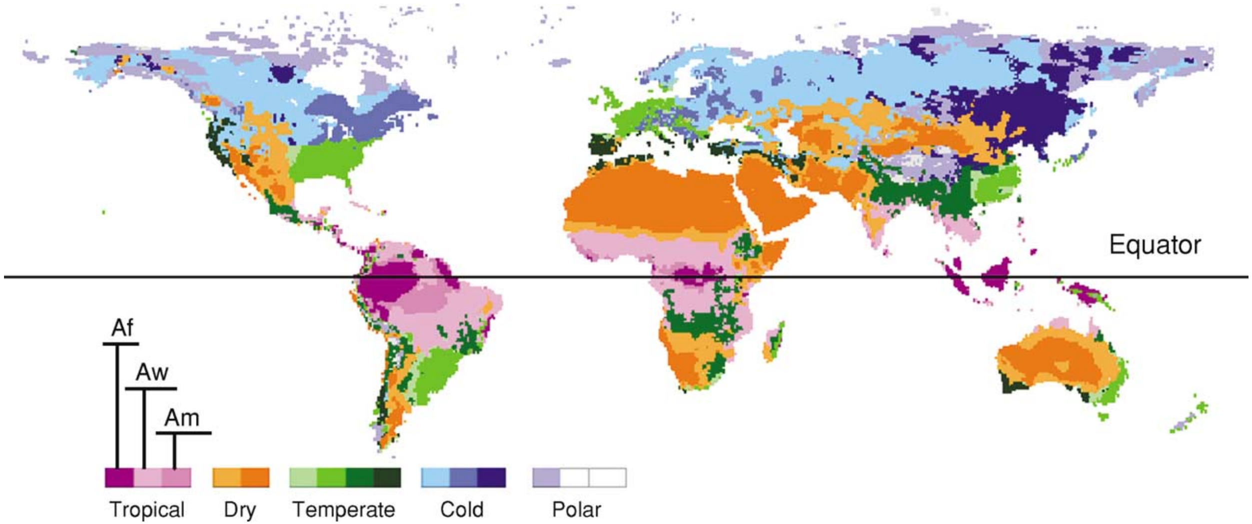

Fig. 1.1 Main types of tropical climates (Köppen's climate classification), including all climates that are controlled by equatorial and tropical air masses; *Af* – tropical moist climates, or **rainforest**, characterized by relatively abundant rainfall every month of the year; *Am* – tropical humid climate, characterized by a short dry season; and *Aw* – wet–dry tropical climate, or **savanna**, which is characterized by a longer dry season and prominent, but not extraordinary, wet season. This last type gets a little cooler during the dry season but will become very hot just before the wet season. Modified from Strahler, A. N., Strahler, A. H., *Elements of Physical Geography*. John Wiley & Sons, 1984.

bodies during the dry season is best exemplified by many shallow lakes in the Amazon (Junk *et al*., 1989; Sioli, 1984; Val and Almeida-Val, 1995), and by the ephemeral lakes in Niger (Verdin, 1996). In many cases, water bodies of the same climatic region or even located close together may have different chemical composition and behave differently. In other words, a water body is a unique ecosystem, without parallel in the world. Each water body can be visualized as a "living tissue" that responds accordingly to each environmental factor. Thus, the biological, chemical, and physical characteristics of the different water systems presented in the following sections are roughly generalizations.

II. TROPICAL MARINE ENVIRONMENTS

The marine environment contains approximately 98% of the water of the planet, with the atmosphere being the smallest water compartment with only 0.001% of the total existing water (Table 1.1). The marine environment is not quiet, stable and uniform as it seems to a casual observer; in fact, it is a moving and changing environment with a large variety of biotopes, inhabited by

Table 1.1
Stocks of Water in the Different Compartments of the Earth

	Volume (1000 km^3)	% of total water	% of total freshwater
Salt water			
Oceans	1 338 000	96.54	
Saline/brackish groundwater	12 780	0.93	
Salt water lakes	85	0.006	
Inland waters			
Glaciers, permanent snow cover	24 064	1.74	68.70
Fresh groundwater	10 530	0.76	30.06
Ground ice, permafrost	300	0.022	0.86
Freshwater lakes	91	0.007	0.26
Soil moisture	16.5	0.001	0.05
Atmospheric water vapor	12.9	0.001	0.04
Marshes, wetlands	11.5	0.001	0.03
Rivers	2.12	0.0002	0.006
Incorporated in biota	1.12	0.0001	0.003
Total water	**1 386 000**	**100**	
Total freshwater	**35 029**		**100**

Source: Shiklomanov (1993).

almost all animal Phyla on the planet (Angel, 1997). In a small area around India, for example, 167 biotopes have been mapped and identified for conservation and sustainable use (Singh, 2003). A marine biotope can be envisioned as an area in which habitat conditions and organic diversity are quite similar. Marine biotopes differ from place to place according to local geology, currents, temperature, depth, light, dissolved gases, transparency, and levels of ions and nutrients, among other parameters.

Basically, these marine biotopes are either pelagic or benthic, in general the environmental quality of conditions for life decreases with closeness to land and the surface of the water, so biotopes are most numerous in inshore waters. The pelagic environment is further divided into (1) neritic zone, a designation for waters over the continental shelf, i.e., from low tide mark up to 100 fathoms (about 200 meters) offshore, and (2) oceanic zone, a designation for all waters beyond the edge of the continental shelf. The area between the lowest and highest tide mark is known as the littoral or intertidal zone and is highly influenced by the supralittoral region (see next section in this chapter for further details). The oceanic zone is further divided into epipelagic, a designation for surface waters away from continental shelf up to about 200 meters in depth; mesopelagic, for waters between 200 and 1000 meters; bathypelagic, for water between 1000 and 4000 meters; and abyssopelagic, for waters roughly below 4000 meters. While the neritic zone biotopes experience seasonal variations in chemical, physical, and biological parameters, the oceanic biotopes are relatively less productive but are much more stable environments with a wide range of living conditions (Lagler *et al*., 1977). These differences are the major determinants of the fish fauna inhabiting each of these biotopes (see Chapter 11, this volume).

Temperature is a major driving force controlling the distribution of marine fish fauna. It can be as high as 55 °C in small intertidal pools during the summer but is normally between 26 and 32 °C in the superficial water of tropical marine environments (see Levinton, 1982, for relationship between temperature of ocean water surface and latitude). Indeed, temperature differences between water surface and deeper water layers are not uniform among the different climatic zones (Figure 1.2). In the tropics, a stable thermocline develops between 100 and 300 meters depth that restricts plankton biomass to the upper warm layers of water and consequently reduces the amount of food for fish living below the photic zone.

Temperature and salinity are independent variables. Between the Tropics of Cancer and Capricorn, salinity decreases towards the Equator while temperature increases, reaching the highest values at the Equator (see Thurman, 1996). This variation is dependent on the balance of evaporation and

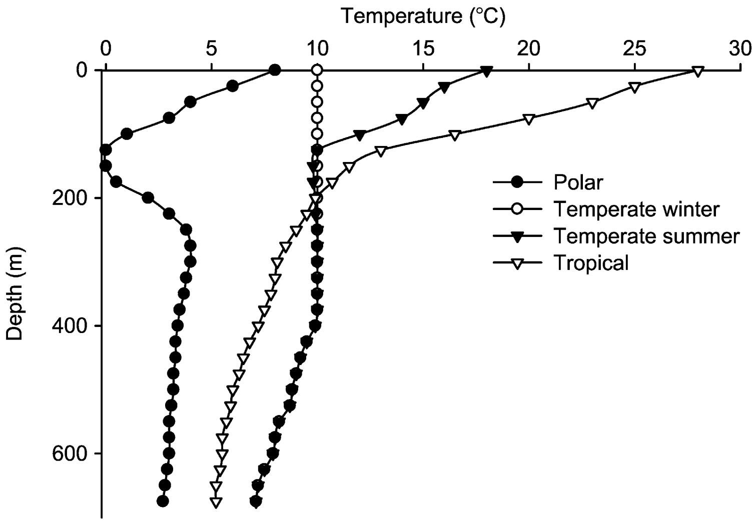

Fig. 1.2 Schematic representation of temperature profiles *versus* ocean depth in different climatic zones of the world. Notice that the deep and bottom waters of all latitudes are uniformly cold. Well-developed thermoclines are at low and mid-summer latitudes. Data compiled from several sources. See text for details.

precipitation that, in some instances, are dependent on atmospheric circulation. In general, surface water salinity is higher than deep water salinity due to evaporation. Below the surface, a halocline is formed where rapid changes in salinity are related to water depth. Near the Equator the halocline extends down to 1000 meters depth. Salinity is, on average, 35.5 ppm in the Pacific Ocean, 35.5 ppm in the Atlantic Ocean and near 40 ppm in the Red Sea. However, salinity can vary and be as high as 90 ppm in the Araruama Lagoon, at Rio de Janeiro, or even as high as 155 ppm in small tide pools subjected to intense evaporation. On the other hand, it can be as low as 8 ppm in the Baltic sea due to precipitation and river discharges (Soares-Gomes and Figueiredo, 2002).

Light is also a key factor that shapes marine biotopes as photosynthesis is entirely dependent on this physical parameter. Generally, three light zones can be distinguished: (1) photic zone, from water surface down to about 100 meters, where light is enough for photosynthesis, i.e., more than 5% of sunlight is available; (2) dysphotic zone, between *ca.* 100 and 200 meters, where light is weak for photosynthesis, less than 5% of the sunlight; and (3) aphotic zone, where no light is available at all. These major marine environmental characteristics determine the nature of the organic interactions in these environments.

A. Neritic Zone

1. Supralittoral

Supralittoral zone is the spray zone, extremely variable and very difficult to inhabit, requiring considerable specialized adaptations of animals. The few fish species inhabiting this habitat include, among others, mainly gobies, eels and clingfishes (Bone *et al.*, 1995).

2. Intertidal

The intertidal environment, also known as littoral zone, is characterized by extreme conditions occurring during short periods of time, aggravated by intermittent drying periods that require from the inhabiting fishes extreme ability to overcome temperature, ionic and respiratory disturbances (see Chapter 11). The intertidal zone is, in fact, a demanding environment where the animals are knocked by waves and isolated in pools and mudflats. The most commonly known intertidal fishes are the mudskippers and the blennies that are truly amphibious because they emerge from water to graze on mud or rock in or above the splash zone (Bone *et al.*, 1995). Many intertidal fishes move in from and out to the sublittoral zone, e.g., species of stingrays (Dasyatidae), flounders (Bothidae and Pleuronectidae), soles (Soleidae), bonefish (*Albula*), eels (*Anguilla*), morays (Muraenidae), clingfish (Gobiesocidae), sculpins (Cottidae), searobins (Triglidae), snailfish and lumpfish (Cyclopteridae), midshipmen (*Porichthys*), blennies (Blenniidae), gobies (Gobiidae), pipefish and seashore (Syngnathidae), and cusk-eels (Ophidiidae) (see Bone *et al.*, 1995). There have been a number of reviews on the biology of intertidal fishes (Bone *et al.*, 1995; Graham, 1970; Horn *et al.*, 1998; Horn and Gibson, 1988) and their ecophysiology (Berschick *et al.*, 1987; Bridges, 1993).

3. Sublittoral

The conditions for fish life are still good in the inner littoral zone, where seasonal variations are near maximum and light conditions support high productivity, in turn supporting a highly diverse group of fishes. In addition to the groups found in the littoral zone, the sublittoral zone also includes species of surfperch (Embiotocidae), skates (Rajidae), sharks (Squalidae), bonefish (Albulidae), croackers, kingfish and drums (Sciaenidae), hakes and pollocks (Gadiidae), rockfish (Scorpaenidae), wrasses (Labridae), butterflyfish and angelfish (Chaetodontidae), parrotfish (Scaridae), filefish and triggerfish (Balistidae), trunkfish (Ostraciidae), puffers (Tetraodontidae), porcupinefish (Diodontidae), and kelpfish (*Gibbonsia*) that migrate back and forth to outer littoral zone and to Coral Reefs, to which fish diversity from this sublittoral zone is somehow related.

The coral reefs constitute a distinct formation occurring in warm tropical seas that link sublittoral and littoral zones. By far, the major fish diversity living in shallow seas is found associated with coral reefs and atolls, which is the paragon of a rich marine community (Cornell and Karlson, 2000), including many small fishes. Coral reefs are mainly found in the Indian and Western Pacific oceans, in the Caribbean and around the West Indies. Coral reefs provide a wide diversity of habitats due to their physical structure and spatial coral arrangements. Despite that, there is a striking difference in the number of coral reef fish species in different regions from the richest central Indo-West Pacific reefs of the Philippines with more than 2000 species to the less rich reefs around Florida, which house between 500 and 700 fish species (Figure 1.3) (Sale, 1993). Recently, an elegant analysis of speciation of reef fishes shows how dispersal from a major center of origin can simultaneously account for both large-scale gradients in species richness and structure of local communities (Mora *et al*., 2003). In addition, these authors succeeded in showing that the Indo-Pacific Region stands out as the major center of endemism in the Indian and Pacific Ocean and that the number of fish species decreases from the center (lower latitude) to the borders (high latitude, 30 °N, 30 °S), something that has been already demonstrated for other biological groups.

An analysis of coral reef assemblages is likely to be influenced by both coral diversity and substratum complexity; many studies have provided evidences that fish abundance and species richness are correlated with coral cover, availability of shelter, structural complexity, and biological characteristics, such as territoriality (Caley and John, 1996; Letourneur, 2000; McCormick, 1994; Munday, 2000; Nanami and Nishihira, 2003; Steele, 1999). Corals show nocturnal hypoxia and the effects of hypoxia on one of its inhabitants, *Gobiodon histrio*, has been described (Nilsson *et al*., 2004; see Chapter 12). As coral reefs may be continuously distributed over a large area, widely spaced, and patchily distributed, there is increasing attention on the relationship of connectivity and species diversity and richness (Mora and Sale, 2002; Nanami and Nishihira, 2003), as this information is relevant for environmental management and conservation.

The outer sublittoral zone is comparatively less productive and, therefore, conditions for fish life vary seasonally. Light, ranging from blue to violet, reaches the bottom of this zone, further limiting its productivity. Fish community is poor and includes species of haddock, cod, hake, halibut, chimaera, hagfish and eel. Beyond this point is the abyssal zone, an essentially stable, dark and cold zone even within the tropical oceans (Lagler *et al*., 1977; Lowe McConnell, 1987), and includes an almost unknown fish community (see Fish Physiology, Volume 16).

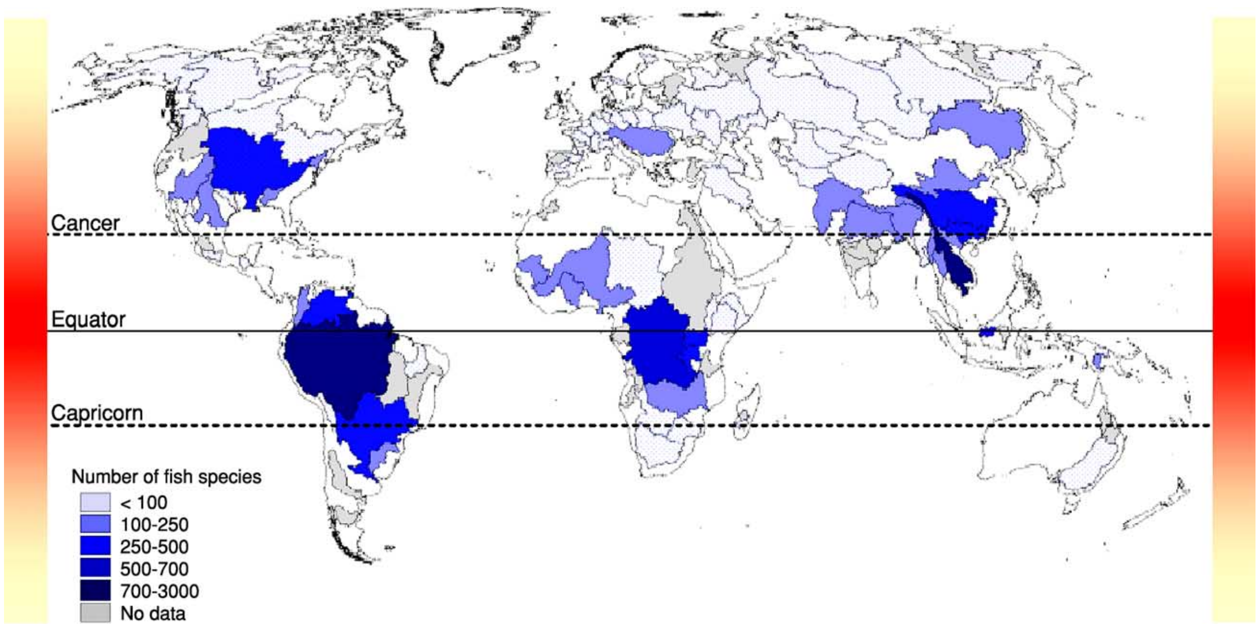

Fig. 1.3 Freshwater fish species diversity over the world showing the hotspots where fish species occur at high densities: hotspots are closer to the Equator, and the most-diversity site is located in the Amazon region (see text for further details). Modified from the map compiled by the World Conservation Monitoring United Nations Environmental Programme (UNEP-WCMC), (www.iucn.org).

B. Oceanic Zone

The open ocean covers nearly two-thirds of the world's surface and is the habitat of some 2500 fish species; half of them are pelagic. The Oceanic zone is relatively uniform; seasonal fluctuations affect only some areas, although conditions change with depth (Lowe McConnell, 1987). It is much less productive than the Neritic zone and Estuaries. As above mentioned, this zone is divided into (1) epipelagic, (2) mesopelagic and (3) bathypelagic zones. They refer, in fact, to the different stratum layers of the oceans that differ in depth and light availability, and so in biomass productivity.

1. Epipelagic Zone

This zone is an euphotic zone, where photosynthesis takes place. Despite the warm water and higher solar irradiance, the primary productivity of tropical oceans ranges from 18 to 50 g.cm^{-2}.year^{-1} while its temperate counterparts ranges from 70 to 120 g.cm^{-2}.year^{-1} (reviewed by Lourenço and Marquez Junior, 2002), a significantly higher primary productivity. In fact, primary productivity tends to increase from the latitude 0, the Equator, towards higher latitudes, with values more or less homogeneous up to the Tropics of Cancer and Capricorn and then peaking between this point and 60 °N and 60 °S (Field *et al.*, 1998). Inspecting the maps generated by the global CO_2 survey, JGOFS (Joint Global Ocean Flux Study) it becomes evident that the warm equatorial Pacific Ocean is the largest continuous and natural source of CO_2 to atmosphere while, in contrast, the cold North Atlantic, North Pacific and the Southern Ocean are important CO_2 sinks, i.e., the ocean regions where large amounts of CO_2 are physically absorbed and biologically assimilated (Takahashi *et al.*, 1999). Fish life depends ultimately on primary production by algae at the base of the food web, a condition met in tropical oceans, although at a relatively low level, throughout the year as a consequence of the constant temperature and solar incidence. The epipelagic fish fauna is richer in warm compared to cold regions (Bone *et al.*, 1995) and includes many species that feed on the neritic zone. The epipelagic fauna include mackerels, tuna (migrate to cold water during reproduction), sharks, marlin and others.

2. Mesopelagic Zone

Inhabitants of the mesopelagic zone, also known as the twilight zone, depend on the plankton and other corpses dropping from the epipelagic zone. Many fish species living in this zone migrate upwards at night to feed in the upper zone, sinking again before dawn. They are adapted to dark, to save energy as food is scarce, and to pressure, since pressure increases by one atmosphere with every 10 meters of depth. In general, as depth increases, size,

Table 1.2
Diversity of Fish of the Brazilian Coast

Order	Families	Species	POZ*	Occurrence
Anguilliformes	4	5	M (60%)	E – M – M/B
Clupeiformes	2	2	M (100%)	M
Osmeriformes	4	6	B (57%)	M – B – M/B
Stomiiformes	8	19	M (76%)	M – B – M/B
Aulopiformes	5	11	M (54%)	E/M – M – M/B – E/M/B
Myctophiformes	2	38	M (95%)	M – B
Lampridiformes	3	4	E (67%)	E – E/M
Polymixiiformes	1	1	M (100%)	M
Gadiformes	6	10	M (60%)	E/M – M – M/B
Batrachoidiformes	1	1	E/M (100%)	E/M
Lophiiformes	3	3	M (60%)	E/M – M – M/B
Beloniformes	2	2	E (100%)	E
Beryciformes	3	3	M (50%)	E – M – M/B
Zeiformes	3	3	M (60%)	E – E/M – M
Gasterosteiformes	2	2	E (67%)	E – E/M
Scorpaeniformes	3	7	M (57%)	E/M – M
Perciformes	27	59	E/M (59%)	E – E/M – M
Pleuronectiformes	1	1	E/M (100%)	E/M
Tetraodontiformes	4	6	E (71%)	E – E/M
Total diversity observed and total percentage of each occupied zone				
TOTAL	84	183	-	E (16%) E/M (30%) M (40%) M/B (9%) B (5%)

*Abbreviations: POZ, Predominantly occupied zone (E = Epipelagic; M = Mesopelagic; B = Bathypelagic; E/M and M/B = transition zones).

Source: Compiled from Figueiredo *et al.* (2002).

abundance and fish diversity decreases. Fish diversity of the mesopelagic zone of tropical oceans is poorly known. Studying the fishes of the southern Atlantic, between Cabo de São Tomé (22 °S) and Arroio do Chuí (34 °S), within 200 nautical miles of the Brazilian coast, and using pelagic trawling, Figueiredo *et al.* (2002) collected a total of 28 357 specimens belonging to 185 species, 84 Families and 19 Orders (Table 1.2). Despite the gear type used, 86% of the sampled families had representatives inhabiting the epi and/or mesopelagic zone and only 14% inhabiting the meso and/or bathypelagic zones.

3. Bathypelagic Zone

Inhabitants of this zone depend entirely on the food gravitating from the zones above. Animals are adapted to high pressure, to darkness, to food limitations, and to energy economy. Most animals are bioluminescent. Fishes are greatly reduced in number and diversity. Interestingly, all the five strictly bathypelagic species collected in the Brazilian coast (*Bathylagus bericoides*, *Dolichopteryx anascopa*, *D. binocularis*, *Chauliodus sloani*, *C. atlanticus* and *Ceratoscopelus warmingii*) have large geographic distribution. All collected specimens were small in size and have bioluminescent organs (Figueiredo *et al*., 2002).

C. Estuaries

An estuary is an area of interaction between oceanic salt water and freshwater from a stream. The estuary definition proposed by Cameron and Pritchard (1963) stating that an estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which seawater is measurably diluted with fresh water derived from land drainage, is the most common and widely used. However, by restricting estuaries to semi-enclosed water bodies, the authors do not recognize the salinity gradient caused by the interaction of both types of waters that extends away from the land masses. In other words, Cameron and Pritchard's definition fails to consider the drainage of the Amazon and the Mississippi rivers as estuaries. Functionally, an estuary can be envisaged as an ecotone (Lagler *et al*., 1977) and so it includes the boundaries of the salinity gradient in both the upstream and open ocean. The world's great estuaries are situated in the tropics: the Amazon, Orinoco, Congo, Zambezi, Niger, Ganges and Mekong; all very large rivers draining enormous geographical regions. The Amazon River discharges 20% of all freshwater entering the oceans of the world (see Sioli, 1984), with a flow of 0.2 Sv (1 Sv $= 10^6\ m^3/s$) that accounts in large part for the sea surface salinity in the west tropical Atlantic Ocean (Masson and Delecluse, 2001). Tropical estuarine environments include, indeed, seasonally flowing streams and lacustrine water bodies intermittently connected to sea. Chemical, physical and biological conditions of these tropical estuaries are far from uniform, and greatly influence the estuarine life, including fish fauna. In general, estuaries are characterized by extreme changes in salinity, tidal and stream-current turbulence, turbidity and siltation. No other water systems undergo extreme seasonal fluctuations as observed in tropical estuaries. In addition, estuaries bordered by cities (13 out of 16 largest cities in the world are on the coast) and industries may also experience extremes of pollution. Roughly, tropical estuaries can be divided in four categories: (a) open estuaries; (b) estuarine coastal waters; (c) coastal lakes; and (d) blind estuaries.

1. Open Estuaries

All medium and large tropical rivers draining into the oceans form open estuaries and among them are all well-known tropical estuaries referred to above. They are never isolated from the sea and experience all the major environmental estuarine oscillations. These river-mouth estuaries exhibit layering, with freshwater overlaying the salt water beneath, that can extend for long distances, as observed for the Amazon River (the "Pororoca"). The water layers may have distinct ichthyofauna and may serve as a route for diadromous fishes or even as a route for casual freshwater invasion, as occur with elasmobranches that can be found in the middle Amazon River, near Manaus (Santos and Val, 1998; Thorson, 1974).

2. Estuarine Coastal Waters

The effects of Amazon drainage into the Atlantic are felt up to 400 km from the mouth, a distance that depends on several variables, including tidal cycles and seasonal changes in river water level. Similar situations occur with many other large and small rivers, such as the Orinoco (Venezuela), Ganges (India), Paraná (Brazil), and in general it is difficult to establish the boundaries of such environments. The shallow nature of these tropical waters and their lowered salinities, in conjunction with high turbidities, make them only partly estuarine from a fish fauna perspective (Baran, 2000; Blaber, 2002; Blaber *et al.*, 1990; Pauly, 1985).

3. Coastal Lakes

Coastal lakes, also known as coastal lagoons, are lacustrine bodies behind tropical shorelines. They are relatively large water bodies, which is what makes them unique. They undergo high seasonal fluctuation that in the end determines the form and regularity of the lake–sea connection. Four main subtypes have been recognized: isolated lakes; percolation lakes, silled lakes and lagoonal inlets. Their fish fauna is mixed, marine and estuarine, depending on the salinity.

4. Blind Estuaries

Blind estuaries are small water bodies, both in length and catchment, regularly formed by a sandbank across the sea mouth. When it is closed, freshwater enters from the river and fills the system. The salinity is dependent on tidal regimes, freshwater inflow, sandbank draining rates and wind. In general, blind estuaries are exploited for local subsistence.

Undoubtedly tropical estuaries are highly complex and variable aquatic ecosystems. They are among the most productive ecosystems, contributing effectively to maintain marine life. In addition, estuaries are the nursery grounds for many important fisheries, which often depend on one of its components that are the mangroves. Mangroves are composed of salt-tolerant trees and shrub that grow in shallow warm water; their muddy waters are rich in nutrients and serve as shelter for many types of marine organisms. A recent study has shown that mangroves in the Caribbean are unexpectedly important for neighboring coral reefs as well (Mumby *et al*., 2004). Mangroves dominate the border of almost all known tropical estuaries, covering a quarter of the world's tropical coastline (Blaber, 2002; Wolanki, 1992).

III. TROPICAL FRESHWATER ENVIRONMENTS

Freshwater environments are many times smaller than the oceans both in area and in volume of water even though they are equivalent in terms of habitat diversity. They represent only 0.8% of total habitats in the Earth while marine environments represent 70.8% (Table 1.1). High and constant temperatures through the year and an almost absent seasonal variation in day length contrast tropical freshwater environments with their temperate counterparts. Water and land are distributed unevenly over the globe and so are freshwater bodies over the land and this is unrelated to population spread or economic development. In contrast to marine environments, freshwater bodies are many and vary in size, shape, depth and location. Thus, extensive water–terrestrial transition zones, so-called ecotones, are formed and play a central role in freshwater life. Ecotones, in fact, constitute habitats for some fish species, at least during part of their life (Agostinho and Zalewski, 1995). Indeed, external and internal processes influence the energy flow between the two interacting systems, the function of the ecotone, and, therefore, life and landscape interaction (Bugenyi, 2001; Johnson *et al*., 2001). Freshwater bodies are broadly divided in two groups of environments: (a) standing water and (b) flowing water environments – lentic and lotic environments, respectively. Basically, lakes, reservoirs and wetlands are lentic, and rivers and streams are lotic environments. Two other types of freshwater bodies deserve some attention as habitats for tropical fishes: springs and caves.

A. Lakes and Ponds

Tropical lakes are far less numerous than temperate lakes because glacial lakes are rare in the tropics. Tropical lakes vary in size, from minute ponds to lakes with gigantic proportions, such as Lake Victoria, with a surface area of 68 635 km^2. However, the great majority of them are relatively small water bodies – only 88 lakes in the world have a surface area larger than 1000 km^2 and just 19 are larger than 10 000 km^2, six of them are located in the tropics: four in Africa (Victoria, Nyasa, Chad and Turkana), one in South America (Maracaibo) and one in Australia (Lake Eyre). Some tropical lakes are located in high mountains and most have tectonic origin, for example Lake Titicaca, which is 3812 m above sea level in South America, or Lake Victoria, located at

1136 m and Lake Tanganyika, at 773 m above sea level in Africa (Babkin, 2003). Table 1.3 shows the morphological characteristics of the major tropical lakes.

Roughly, tropical and temperate lakes are not different in total annual solar irradiance but they do differ in minimum annual irradiance (Lewis Jr, 1996). Changes in solar irradiance induce gradients in water temperature that further lead to water column mixing. Light controls photosynthesis that is further moderated by temperature and nutrient supply and these are different between both temperate and tropical lakes and among Tropical lakes. Clearly, mean temperature decreases from the Equator up to the Tropics of Cancer and Capricorn though there is no difference in the annual maximum temperature and, thus, temperate and tropical lakes are differentiated mainly by minimum rather than by maximum temperatures. Seasonal changes in temperature are associated with water mixing and stratification that are clearly present in temperate lakes but by no means absent in tropical lakes. Deep tropical lakes stratify and tend to mix predictably at a particular time of the year (Lewis, 1987). In contrast, floodplain lakes are destabilized annually by hydraulic forces as observed for some lakes of the Amazon. In this case, floodplain lakes are annually inundated by lateral overflows of rivers. Wind may also affect stratification and water mixing in tropical lakes more readily than in their temperate counterparts; this more dynamic process has been related to the efficiency of recycling nutrients and the productivity of tropical lakes compared with temperate lakes (Lewis, 1987).

Continuously high temperature throughout the water column and continuously high solar irradiance make the basic conditions for a high rate of annual photosynthesis in tropical lakes. This often results in hyperoxia during the day and hypoxia during the night. The chemical and biological demand for oxygen is high in tropical lakes. Together these conditions result in a hypoxic or even anoxic hypolimnion that has consequences for oxygen concentrations all through the water column, and dramatically affects biogeochemical cycles of carbon, nitrogen and phosphorus. Because chemical weathering of phosphorus is more efficient at higher temperatures and because denitrification is higher in tropical waters, tropical lakes experience low nitrogen:phosphorus ratios in the hypolimnion, and not rarely, a nitrogen deficit takes place throughout the water column when deep waters mix with surface waters. Thus, the deficit of nitrogen is more critical for tropical lakes than the amount of phosphorus (Lewis Jr, 2000).

The hypolimnion of tropical lakes is more prone to anoxia and chemical stratification than temperate lakes, due to the reduced oxygen solubility at high temperatures and to the increased oxygen consumption by a variety of biological and chemical processes. Oxygen scarcity is widespread in tropical freshwater, particularly in floodplain lakes, inundated forests and permanent

Table 1.3
Morphological Characteristics of Major Tropical Lakes

Lake	Country	Major characteristics	Depth maximum (m)	Volume (km^3)	Surface area (km^2)	Watershed area (km^2)	Residence time (years)	Annual fish catch (ton/year)
Chad	Chad, Cameroon, Niger, Nigeria	Known for its yield of natural soda, an activity that contributes to keeping the lake water fresh	10.5	72	1540	24 264	NA	135 500
Eyre	Australia	A great salt lake of tectonic origin. The vast catchment area is only marginally desert and as such is very responsive to even slight variations of rainfall	5.7	30.1	9690	1 140 000	NA	NA
Maracaibo	Venezuela	Largest lake of South America, semi-arid in the north and has an average rainfall of 127 cm in the south	60	280	13 010	NA	NA	NA
Nyasa	Mozambique, Malawi and Tanzania	Most southerly of the great African Rift Valley lakes, consisting of a single basin	706	8400	6400	6593	NA	21 000

Tanganyika	Tanzania, Zaire, Zambia and Burundi	Second largest of the African lakes; second deepest (next to L. Baikal) and the longest lake of the world. Its very ancient origin is only rivalled by such old lakes as Baikal	1430	17 800	32 890	263 000	NA	518 400
Titicaca	Bolivia and Peru	Largest lake in South America, highest elevation large lake in the world, one of the oldest lakes in the world	281	893	8372	58 000	1343	6327
Turkana	Ethiopia and Kenya	Tertiary volcanic rocks are found in the south and along most of the western side of the lake, while a later lava flow (Pleistocene) forms a barrier in the southern end of the lake	109	203.6	6750	130 860	12.5	15 000
Victoria	Kenya, Tanzania and Uganda	Second largest freshwater lake by surface area; one of the oldest lakes in the world	84	2750	68 800	184 000	23	120 000

Abbreviations: MY, million years; NA, data not available.
Source: Borre *et al*. (2001); ILEC (2004).

swamps (Carter and Beadle, 1930; Chapman *et al.*, 1999; Junk, 1996; Kramer *et al.*, 1978; Townsend, 1996; Val and Almeida-Val, 1995). In many of these habitats, dissolved oxygen exists only in the first few millimeters of the top of water column with levels close to zero or even zero below this water layer (Figure 1.4). In floodplain lakes of the Amazon, this oxygen is the sole source for many fish species that have evolved an extraordinary set of adaptations to explore this zone of the water column (Junk *et al.*, 1983; Val, 1995; see Chapters 6 and 7). Habitat diversity, structure and function of river floodplains of the Amazon have been reviewed elsewhere (Junk, 1997).

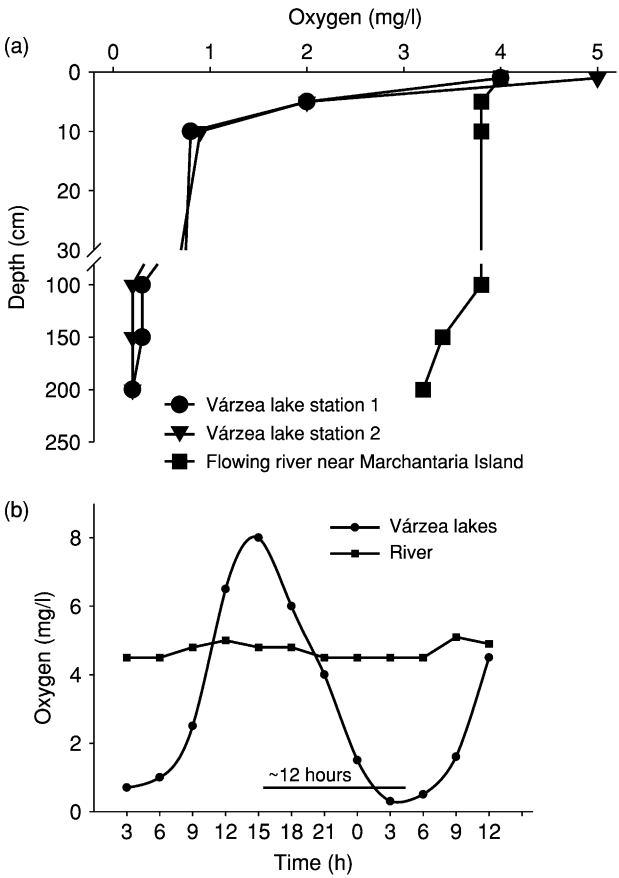

Fig. 1.4 Changes in dissolved oxygen in water bodies of the Amazon: (a) diurnal changes in oxygen levels according to water depth in a *várzea* lake; (b) comparison of dissolved oxygen during 24 hours in a *várzea* lake and in the river.

Seasonal variations in dissolved oxygen are observed for tropical shallow lakes but they are not as extreme as those described for temperate lakes. Extreme variations in dissolved oxygen do occur in tropical lakes but they tend to occur in much shorter periods of time, e.g., 24 hours. At floodplain lakes, dissolved oxygen can drop from oversaturated levels at noon to values close to zero at night (Junk *et al*., 1983; Val, 1996). After periods of nutrient unloading, the situation may be worsened, as an extensive cover of aquatic plants, most of them macrophytes, is developed limiting irradiance of the water column and further limiting the already weak photosynthesis capacity. Subsequently, such aquatic plant biomass increases oxygen demand due to organic decomposition. Under these situations, stratification develops resulting in hypoxic or even anoxic conditions in the hypolimnion. When the thermocline is disrupted by the end of the day or by winds, water layers mix and hypoxic conditions occur even in the water surface layer. Hydrogen sulfide is displaced throughout the water column when bottom water mixes into the water column above; this poses an extra challenge to fish (Affonso *et al*., 2002; Brauner *et al*., 1995). Adaptations of tropical fishes to hypoxia occur at all levels of their biological organization and will be discussed elsewhere in this volume (Chapters 6, 7 and 10).

Shallow lakes have small stock of water per unit of area but not necessarily a corresponding reduction of water fluxes and therefore are sensitive to water surface processes (Talling, 2001). This contrasts to deep tropical lakes. Lake Tanganyika is the second largest tropical lake and houses a great species richness primarily accounted for by endemic fishes. Its high productivity, interestingly, comes mainly from off-shore, open-water food web, which is biologically poor. The reduced temperature gradient between water surface and water bottom (1470 m) assure wind-driven mixing in bringing nutrients for primary production from the deep water layers. However, it seems that increased air and surface-water temperatures enhance the water density differences, reducing the effectiveness of water mixing with already mapped clear effects on primary production and fish yields.

Many tropical shallow lakes are located in arid and semi-arid zones over dryland. They are large and fill erratically and then recede and dry until the next major inflow, so that water levels may fluctuate widely often in accord with fluctuations in salinity. With increasing aridity, dryland lakes experience increased spatio-temporal variability of rainfall, i.e., in semi-arid and subhumid regions rain falls on a seasonal basis while within arid zones rain falls unpredictably and episodically. As a large amount of water evaporates from these types of water bodies, leaving behind salts carried in, many of them experience increases in salinity above the limit, now widely accepted as 3 g/l, to be considered as freshwater lakes. Salinities of these so-called salt lakes may vary from 3 up to 300 g/l on a seasonal basis, depending on inflows and rainfall. However, a number of factors give rise to salinization and are related to anthropogenic effects such as excessive clearance of natural vegetation, overuse of water for irrigation, and changes in the nature of groundwater/surface water interaction. Despite the causes of increases and changes in salinity, it demands significant physiological adjustments of the biological communities inhabiting these environments to maintain ionic homeostasis (see Chapter 9, and Timms, 2001; Williams, 2000; Williams *et al.*, 1998).

Salt lakes may be highly alkaline; for example, the soda lakes of East Africa. The water of Lake Magadi in the Kenyan rift valley is highly alkaline (pH10) and highly buffered ($CO_2 = 180\,\text{mmol}^{-1}$). Water with these characteristics would rapidly kill most teleost fishes as they are unable to excrete ammonia under these conditions, with the exception of the Lake Magadi tilapia, *Alcolapia grahami* (Randall *et al.*, 1989; Wood *et al.*, 1989). Recently, a review of cichlids inhabiting Lake Magadi and Lake Natron, another representative example of a rift valley soda lake in East Africa, indicates the presence of four species of tilapiines cichlids (Turner *et al.*, 2001), possibly all having the same ability to excrete nitrogen as urea at high rates (Narahara *et al.*, 1996) or an unknown system to avoid neurotoxicity caused by increased body levels of ammonia.

In an opposite situation, though not less challenging, are the acidic ion poor lakes and *igapós* of the Amazon. These water bodies are rich in dissolved organic carbon (DOC), very low in ions (resembling distilled water), acidic (pH 3–3.5) and often hypoxic (Furch and Junk, 1997; Matsuo and Val, 2003). However, fish fauna inhabiting these waters are relatively rich. Rio Negro harbors more than 1000 fish species (Ragazzo, 2002; Val and Almeida-Val, 1995) that are able to maintain ion homeostasis under the dominant environmental conditions (see Chapter 9, this volume and Gonzalez *et al.*, 1998; Gonzalez *et al.*, 2002; Matsuo and Val, 2002; Wilson *et al.*, 1999; Wood *et al.*, 1998). This fish diversity contrasts with that found in alkaline salt lakes that harbor a reduced number of fish species, which initially suggests that acidic conditions present fewer challenges than alkaline conditions, although this has yet to be proven. The presence of specific compounds in the blackwaters of Rio Negro, such as humic and fulvic acids, may provide additional protection against the dominant ion-poor acidic condition of these environments. Many intermediary water conditions and characteristics appear in areas where different types of primary water mix, for example in open lakes formed along the confluence of black and white waters of the Amazon.

Volcanic lakes contrast with these water bodies. Two types of volcanic lakes can be distinguished: (a) volcanic crater lakes with steep-sided walls that are, in general, deep lakes; and (b) volcanic barrier lakes, formed by the blockage of steep-sided river valleys by volcanic lava flows that provide