FISH ECOPHYSIOLOGY

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Introduction

The earliest known jawless fish (Agnathans) date from the Cambrian period 500–600 million years ago. It is generally agreed among paleontologists that they evolved from sessile, filter-feeding ancestors in shallow fresh or brackish water, not the sea. Their environment was characterized by low salt levels and was probably turbid and at least intermittently oxygen-depleted (hypoxic). They have since spread to virtually all aquatic habitats (**Table 1**), but freshwater is still a stronghold, with a third of all fish species living in rivers, lakes and streams even though such habitats only contain a minute proportion ($<0.01\%$) of the total water on earth. Fish make up the most numerous vertebrate class, both in terms of species' numbers and biomass. They form a remarkably plastic group, exhibiting a diversity of sizes (from 8 mm Philippine gobies, *Mistichythys luzonensis*, to 18 m whale sharks *Rhincodon typicus*), shapes and life histories. Living forms include the numerically dominant teleost bony fish, the elasmobranchs (sharks and rays) and smaller groups such as lungfish, coelocanths (*Latimeria* spp.) and the surviving jawless lampreys and hagfish.

Table 1 Relative proportions of *c.* 30 000 living fish species living in different habitats

Major category	*Subcategory*	*% of total*
Marine fish (58.2%)	Shallow warm water	39.9
	Shallow cold water	5.6
	Deep benthic	6.4
	Deep pelagic	5.0
	Epipelagic	1.3
	Diadromous	0.6
Freshwater fish (41.2%)	Primary inhabitants	33.1
	Secondary inhabitants	8.1

- A third of species are primary inhabitants of freshwater, though freshwater makes up only 0.0093% of the total water of the earth.
- Possibilities of isolation and allopatric speciation are greater in freshwater than in seawater.
- Many marine species have re-invaded freshwater, or are at home in both media.
- Several intertidal and freshwater fish species spend some of their time on land.

After Cohen DM (1970) How many recent fishes are there? *Proceedings of the California Academy of Science* 38: 341–345.

Despite this great diversity, fish are monophyletic, i.e. they have a single origin. All living fish share anatomical and physiological features of their earliest ancestors and are still constrained by them to a greater or lesser extent. Basic fish features include the following:

- Vertebral column with associated myotomal (segmented) muscles. The vertebral column sets fish length and prevents shortening of the animal when muscle contraction powers undulatory swimming.
- Head with food capture apparatus and bilaterally symmetrical sense organs.
- Gills for respiratory exchange, excretion of nitrogenous waste, plus regulation of body fluid ion content and pH.
- Closed vascular system with chambered heart, circulating red blood cells and (in teleost fish) dilute blood plasma (250–600 $\mathrm{mosmol\,kg^{-1}}$, compared with 1000 $\mathrm{mosmol\,kg^{-1}}$ of seawater).
- Elasmobranch fish and coelocanths have similar plasma ionic levels to teleost fish (i.e. much lower than the ionic concentration of seawater), but have high urea and trimethylamine oxide (TMAO) levels that result in total plasma osmolarity being similar to that of seawater (**Figure 1**).

Biotic and Abiotic Factors in Distribution of Marine Fish

Distribution in fish is always controlled by a mixture of biotic and abiotic factors. For example, herbivorous marine fish are limited to shallow water where photosynthesis by microalgae, seagrasses or seaweeds is possible. Carnivorous fish (particularly postlarval and juvenile forms) may also be limited to such areas because they specialize in feeding on herbivorous invertebrates. Young gadoid fish are found living for protection beneath the bells of stinging jellyfish – a resource limited to near-surface waters at specific times of the year. These are all biotic constraints. Abiotic influences are those imposed by physical or chemical factors such as temperature, salinity or oxygen tension, and they are the main focus of this article since they profoundly affect fish physiology and tolerances and therefore

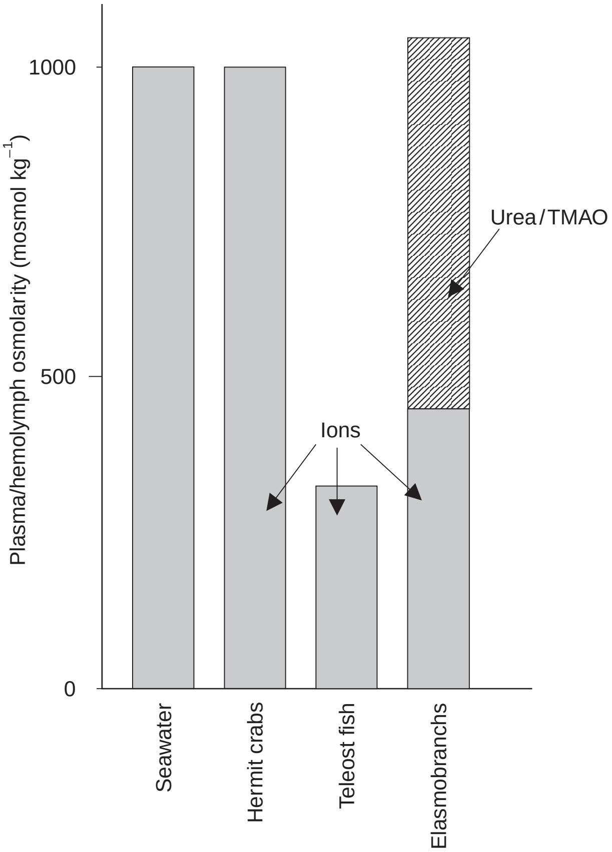

Figure 1 Diagrammatic comparison of relative contributions to total plasma/hemolymph osmolarity of ions and urea/trimethylamine oxide (TMAO) in telecost fish, elasmobranchs and hermit crabs (*Pagurus bernhardus*). Data for seawater given as reference.

distribution. There are other features that are strictly abiotic, in particular physical habitat type (e.g. mud, sand, coral reefs, tangled mangrove roots), but they do not impinge directly on fish physiology, so will not be considered here.

Tolerances and Limits to Distribution

Presence of Water

Limitation to an aqueous habitat is the most fundamental physiological constraint imposed on fish. No elasmobranch or agnathan species can survive out of water, and only a few dozen amphibious teleost species plus the three surviving lungfish species have the ability to live out of water for significant periods. Most of these species are freshwater, so outside the scope of this encyclopedia. Amphibious intertidal fish such as mudskippers (*Periophthalmus* sp.), shannies (*Lipophrys pholis*) or butterfish (*Pholis gunnellus*) are rarely more than a few meters from seawater and are emersed only for a few hours at a time. Eels (*Anguilla* sp.) are catadromous and move between freshwater and seawater, these migrations often involving movement on damp/wet land between water bodies.

When fish are emersed they have problems of respiration, excretion, acid–base balance and locomotion. Fish respiration involves the passage of an incompressible medium (water) over the gills. If an unadapted fish is taken out of water it becomes short of oxygen (hypoxic), accumulates CO_2 (hypercapnia) and cannot excrete H^+ – all because the gills collapse and the animal cannot circulate compressible air over them. It soon dies because the blood becomes acid, not because of lack of oxygen, and usually death will occur long before dehydration becomes a factor. Mudskippers and shannies have strengthened gills with relatively few filaments that are less prone to collapse. They also have scaleless, well-vascularized skins that allow respiratory exchange; the gills are relatively less important for respiration, though they can still take up oxygen from water held within the buccal cavity, and are involved in H^+ regulation. Nitrogen excretion is also a problem for amphibious fish. Most fish excrete nitrogen as NH_3 or $NH_4{}^+$, with 50–70% of excretion being by diffusion across the gills in marine fish. Although $NH_3/NH_4{}^+$ is metabolically inexpensive to produce, it is toxic and therefore cannot be accumulated within the body. Amphibious marine fish such as mudskippers reduce protein breakdown when in air, and also accumulate a proportion of N_2 as urea or trimethylamine oxide (TMAO), both of which are less toxic than ammonia. However, for marine fish, nitrogenous excretion is a fundamental constraint on survival on land; they have to return to the sea to get rid of accumulated nitrogen and metabolites. Basic fish anatomy is unsuitable for terrestrial locomotion, though butterfish and eels 'swim' through three-dimensional habitats, such as pebbles and thick grass, relying on secretion of mucus for lubrication. Shannies and mudskippers have strengthened prop-like pectoral fins that stop them falling over and raise the belly off the ground to some extent. They are propelled in a series of hops by the tail.

Depth of Water

Four decades ago Jacques Piccard took photographs from the bathyscaphe *Trieste* of tripod fish (Chlorophthalmidae), resting on the bed of an oceanic trench at a depth of over 10 000 m. In doing so he demonstrated that fish could live at all depths, despite their shallow-water origin. Trawling, cameras and submersible observations have confirmed that a diverse ichthyofauna may be found at all depths, in all seas. However, increasing depth may control the sort of fish that are found. Some depth-related constraints are biotic; deep water generally has a restricted energy supply due to absence of light and distance from the productive surface layers. However, there are two major physical problems imposed by depth: increasing pressure and low temperature (particularly at depths greater than 1000 m). In addition, there is an important related chemical problem. In warm surface waters, the sea is practically a saturated solution of calcium carbonate and relatively little energy is needed to maintain calcareous materials (e.g. bone, shells) in solid form. However, solubility rises with increasing pressure and decreasing temperature. In consequence, building and sustaining solid calcareous materials becomes more expensive, particularly at depths beyond 3000 m (below which calcareous sediments are unknown). The problems of pressure and calcium carbonate solubility interact in the physiology of fish buoyancy. A high proportion of shallow-water teleost fish have swim bladders, which develop from gut diverticula. They have sophisticated volume regulatory mechanisms (employing the lactate-secreting gas gland and its associated countercurrent multiplier system), particularly in physoclistous fish in which the swim bladder is isolated from the gut. The original adaptive value of swim bladders probably lay in offsetting the burden of dense scales and armoured skulls, so that shallow-water benthic fish could swim into the water column without undue effort. At depths down to about 1000 m some 75% of fish have swim bladders, but at greater depths pelagic fish usually have no swim bladder or a swim bladder filled with fat; they also show progressively reduced musculature and ossification, plus a very high water content. Lack of ossification has been interpreted as an energy-saving strategy in a food-poor environment where dissolution of calcium carbonate takes place. Loss of swim bladders has been attributed to the metabolic expense at great depth of pumping gas into swim bladders. Interestingly, benthopelagic fish (i.e. those living close to the sea bed) from deep water can possess working swim bladders even at depths of 7000 m; they are also of robust skeleton and musculature. The near-sea bed environment is now known to be much more energy-rich than the water column above, particularly due to the fall of large carrion items. This suggests that benthopelagic fish can 'afford' to expend energy counteracting abiotic depth-related factors on fish form, because of the biotic influence of a good food supply.

Temperature

Fish are almost all ectothermic animals with no significant production or retention of metabolic heat. A few tuna species can keep their locomotory muscles warm, and some big lamnid sharks (e.g. the great white shark, *Carcharodon carcharias*) are partially endothermic with core body temperatures being held at around 25°C in waters of 15°C. However, the body temperature of most fish is directly determined by environmental temperature. Metabolic rate in ectotherms is strongly affected by temperature, with a useful rule of thumb (the Q_{10} relationship) stating that metabolic rate is doubled by an increase of 10°C in environmental temperature. There is a huge literature devoted to the effects of temperature on aspects of the physiology, development and ecology of marine fish. However, despite this wealth of information, the question of whether thermal physiological constraints control fish distribution is difficult to answer, since marine fish are found in all available habitats, from Antarctic ice tunnels at −2.5°C to Saudi reef pools at over 50°C. Antarctic fish usually die at around +5°C, whereas most temperate fish are stressed severely at temperatures above 30°C. Tropical fish reach their thermal limits at about 45°C (also the upper thermal limit for most tropical marine invertebrates).

The position and breadth of a species' thermal niche is determined by a variety of factors. At the biochemical level, fish must have enzymes with appropriate thermal optima. Cell membranes are effectively liquid crystals that must remain fluid if the cell is to survive. Maintaining fluidity over the full environmental temperature range requires modulation of the fatty acid composition of membrane lipids (homeoviscous adaptation). In many fish these characteristics can vary geographically and seasonally, but within overall limits which are species specific. These limits do constrain fish distribution. In the northern hemisphere capelin (*Mallotus villosus*) do not penetrate much further south than the 5°C summer surface isotherm, whereas the corresponding limit for cod (*Gadus morhua*) is about 20°C. In marked contrast, deep-water fish living at very stable low temperatures (*c.* 2°C) can have extremely wide distributions despite limited thermal tolerance. For example, the orange roughy (*Hoplostethus atlanticus*) living at 800–1200 m has been fished off New Zealand, Namibia and northern Europe.

A specialized warm-water example of thermal constraints on distribution is provided by flying fish (Exocoetidae). Flying fish take off through or from the sea surface at very high speed (15–30 body lengths s^{-1}). This in turn demands extremely high rates of tail beat (*c.* 50 beats s^{-1}). Calculations demonstrate that take-off is unlikely to be possible at water temperatures below 20°C, and surface water of this temperature approximates to the northern and southern limits of this essentially tropical group.

Physiologically, fish need greater gill areas per unit mass at high temperature because their respiratory requirements are greater and because the solubility of oxygen decreases with rising temperature, so less environmental oxygen is available. At the ecological level, high temperatures imply high metabolic rates and elevated food consumption. A typical tropical fish needs roughly six times the oxygen to support resting metabolism as does a typical polar fish. High temperature, high activity lifestyles can only be sustained in energy-rich environments. However, it should not automatically be assumed that low-temperature environments (e.g. the deep sea, polar waters) are inexpensive to live in. Low temperature is associated with high viscocity so swimming demands proportionally more energy, as does pumping of blood around the body. Antarctic fish in particular tend to show viscocity-related modifications; they (and some deep-water bathypelagic fish) generally have low hematocrits (i.e. have relatively few red blood corpuscles) so that effective blood viscocity is reduced. Icefish (Channichthyidae) provide extreme examples of this, having no red blood corpuscles or hemoglobin and possessing wide-bore blood vessels through which viscous plasma flows more easily. The trade-off is that they are sluggish fish with extremely low endurance, demonstrating again that lifestyle can be constrained by temperature.

Oceanic seawater of salinity 34‰ (osmolarity 1000 mosmol kg^{-1}) freezes at about −1.9°C. Elasmobranch fish are at little risk of freezing because their blood has a similar osmolarity (**Figure 1**). Because teleost fish have relatively dilute body fluids (300–600 mosmol kg^{-1}) they are potentially liable to freezing at temperatures of −0.6 to −1.0°C, when seawater is still fluid. Lower temperatures than this occur in the winter in the Arctic and throughout the year in the Antarctic. This contrasts with the situation for freshwater fish in which freezing cannot take place unless the water around them is itself frozen. Intertidal pools can become even colder, unfrozen high salinity water beneath ice sheets reaching −3 to −8°C. High latitude marine fish show various adaptations to deal with freezing risk. Anadromous arctic charr (*Salvelinus alpinus*) migrate from the sea to freshwater in the winter, whereas other arctic fish migrate to low latitudes or deep water. There appears to be a fundamental constraint on the distribution of resident intertidal fish, which are absent from northern Norway, Russia and Canada throughout the year – presumably because they cannot compete effectively in deeper water in winter, are too small to migrate significant distances southwards, and cannot avoid freezing.

Antarctic fish and permanent surface-water residents of the winter Arctic all exhibit physiological adaptations that permit freezing avoidance even when pack ice is present. All have relatively high blood osmolarities, depressing their potential freezing points, and most can produce so-called antifreezes: peptides or glycopeptides. These molecules do not actually stop ice formation in body fluids, instead they adsorb onto the crystal surfaces of minute ice nuclei and prevent these nuclei from growing or propagating. In icefish these mechanisms are effective to −2.5°C, allowing them to live in ice tunnels in Antarctic ice shelves. Several arctic species overwinter in deep water which is colder than their potential blood freezing point, but does not contain ice nuclei that can initiate freezing. This supercooled state is precarious and there are records of schools of capelin (for instance) straying into shallow water containing ice during cold weather and freezing instantly.

Salinity

The great majority of marine fish species live under very stable salinity conditions (34–35‰; osmolarity *c.* 1000 mosmol kg^{-1}). This medium, though stable, is much more concentrated than the freshwater or brackish media encountered by ancestral fish. As a result, the osmotic and ionic physiology of marine teleost fish is very different from that of freshwater fish, and relatively few species can live in both media (mainly anadromous and catadromous fish such as salmonids and eels). Elasmobranch fish (sharks, skates and rays) are adapted to seawater by virtue of high blood urea levels that make the blood slightly hyperosmotic to seawater so that they have little or no osmotic problem. Although this group does have a few brackish water species, it is generally limited to fully marine habitats and will not be discussed further.

Briefly, marine teleost fish have to drink seawater to replace water lost osmotically (mainly across the gills) because the blood is much more dilute than seawater (**Figure 2**). To gain access to the water taken into the foregut, salt pumps (actually ATP-ase enzymes embedded in cell membranes) sited on the intestinal wall pump salts from gut fluid to blood

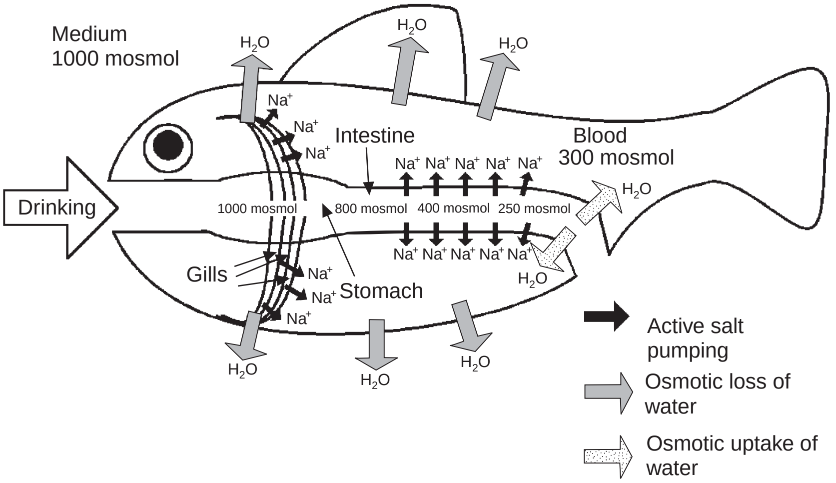

Figure 2 Diagrammatic representation of osmotic and ionic regulation in a marine teleost fish.

until (in the posterior parts of the gut) the osmolarity of the gut fluid is below that of the blood, so that water flows into the blood osmotically. The combination of drinking seawater and active desalting of the gut fluid results in much salt uptake, augmented by diffusion from the salty external medium. To counteract this, salt pumps located mainly in 'chloride cells' on the gills actively pump salt outwards.

In the bulk of the world's oceans, salinity does not constrain distribution. Difficulties only occur at the seas' margins, in estuaries, lagoons and pools where salinities can be much higher or lower. Generally, there appears to be an upper limit of survivable salinity for fish of around 80–90‰, with one or two specialists (such as the killifish *Fundulus heteroclitus*) tolerating up to 128‰. Impressive though this performance is, it is much poorer than that exhibited by many invertebrates, particularly crustaceans, some of which can tolerate up to 300‰ (e.g. the brine shrimp, *Artemia*). Fish are constrained by what is known as the 'osmorespiratory compromise'. Fish gills are necessarily large in surface area to support gaseous exchange. Gill epithelia are also thin to permit ready diffusion. Unfortunately, these two characteristics also favor rapid osmotic loss of water that has to be replaced by drinking, plus salt diffusion that must be opposed by salt pumps. There comes a point where the balance breaks down; killifish are unusual in that they tolerate a 30% rise in plasma osmolarity at 128‰, most fish would succumb.

The majority of marine fish have blood osmolarities of around 300 mosmol kg^{-1}, equivalent to about 10‰. If unadapted marine fish are placed in media less concentrated than this, they die because of blood dilution caused by osmotic uptake of water and diffusional loss of salts. To survive in dilute media, euryhaline fish of marine origin have to stop drinking the medium and pump salts inwards at the gills, effectively reversing the osmotic physiology exhibited in seawater. Many fish of this type acclimate slowly over a period of days to dilute media, since profound microanatomical and biochemical changes have to take place; migratory salmonids fall into this category. Some fish that forage regularly into brackish water (flounders (*Pleuronectes flesus*), mullets (*Mugilidae*), ròvolos (*Eleginops* sp.)) respond more quickly, and a few species such as the shanny are capable of reacting to extreme salinity changes in a matter of minutes. Shannies inhabit the intertidal zone and may be found in crevices that are fed by freshwater runoff when the tide falls. They exhibit the constrained features of such highly euryhaline fish, i.e. small size, thickened gills and a low skin permeability to salts and water, that slow changes in blood concentration and reduce the energetic costs of regulation. Most marine fish that are regularly exposed to low salinity are benthic and slow moving, another consequence of the osmorespiratory compromise.

Oxygen tension

Fish in general, and marine fish in particular are intolerant of oxygen-depleted (hypoxic) conditions. Many freshwater habitats are hypoxic and fish have multiple hemoglobins to deal with this situation and extract oxygen from hypoxic water. Broadly speaking, marine habitats are mostly close to equilibration with the atmosphere (air-saturated; normoxic), so oxygen tension poses no constraints and most fish have few or single hemoglobins. Pollution incidents have often revealed the sensitivity of marine fish to hypoxia, with diatom bloom formation sometimes resulting in massive fish kills at night when plant respiration has dramatically reduced water column oxygen tension (P_{O_2}). In general marine fish avoid hypoxic areas rather than tolerating them, though large schools of clupeoids (e.g. herring, *Clupea harengus*) create their own hypoxic environments in the heart of the shoals. Shannies will even leave nocturnally hypoxic intertidal pools and respire in air, particularly in summer when their respiratory demands are high. Marine fish unable to avoid transient hypoxic conditions (e.g. sole, *Solea solea* in shallow organic-rich water) usually respond by reduced activity, depressed basal metabolic rate and activation of anaerobic metabolism. This is a short-term response and is supplemented by behavioral responses such as burst-swimming to the surface where higher oxygen tensions prevail.

pH

Fish have a plasma pH of 7.4–8.1. Unlike higher vertebrates they have limited internal buffering mechanisms and the viscocity of water means that ventilatory pH control is much less effective than in air-breathers. Excretion rather than respiration controls fish acid–base balance. In many freshwater habitats, whether natural or affected by acid rain, environmental pH poses considerable physiological costs and constraints. This is not the case for marine fish because the sea is a slightly alkaline environment (pH 7.8–8.0) that has enormous buffering capacity for H^+ and CO_2 and poses no problems whatsoever. Only in rock pools are great pH fluctuations known (7.2 at night; 10.6 by day), and even here there are no documented problems for rock pool fish.

Optima

Optimal abiotic environmental conditions for fish species have been studied from two perspectives. First, there are now numerous commercially valuable marine fish species in culture, principally for human food, but increasingly in tropical countries for the aquarist trade. An extensive literature reporting on the ideal conditions for survival, rapid growth and effective reproduction has arisen. Much of the work done has involved multifactorial experimental approaches (e.g. combinations of temperature, salinity and oxygen tension) and these have often revealed changes in optima at different stages of the life history. Rearing densities are high and have biotic effects on optimal rearing conditions, but these in turn can create constraining abiotic problems (e.g. NH_4 and nitrite accumulation) that do not arise in nature. Such studies have revealed constraints on where economic acquaculture can be performed. For example, halibut (*Hippoglossus hippoglossus*) farming is practiced only in cold areas of northern Europe (e.g. Norway, Scotland) because *Hippoglossus* is a deep-water species intolerant of elevated temperature. Conversely, turbot (*Scophthalmus maximus*) farming, once tried in such areas, proved to be uneconomic because extra (expensive) heat was needed to secure fast growth; production is now centered in France and Spain.

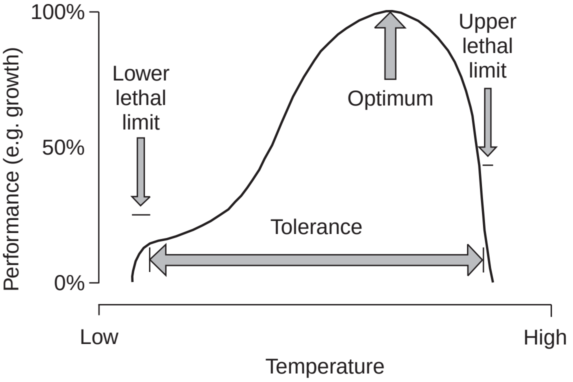

Figure 3 Diagram to illustrate tolerance range, optimum performance and lethal limits (using temperature as an example).

Secondly, abiotic optima have been considered from a biogeographical perspective, almost exclusively in thermal terms (**Figure 3**). This is linked with the constraints on distribution already discussed, but is presently a rather poorly developed research area, ripe for development. For temperature, there is evidence that fish seek out preferred (assumed optimal) temperature regimes, though much of this work has been conducted on freshwater species. Widely distributed marine species have been assumed to have optima either in the center of distribution, or close to the warmer limits, but some work on fish living at the edge of distributions show no evidence of maladaptation or of particular population instability. Difficulties lie in deciding what optimal performance means, and in disentangling biotic and abiotic influences. Fish in temperate zones usually grow more quickly in the warmer areas of their distribution. They may reproduce at an earlier age, often at smaller size. How much of this is due to biotic influences (e.g. quantity and quality of food supply, trophic structure of the local ecosystem) is usually unclear. Optimal performance essentially involves maximizing contribution to the gene pool; establishing the ecophysiological conditions that deliver this is still a challenge.

See also

Antarctic Fish. Deep-sea Fishes. Eels. Fish Larvae. Intertidal Fishes. Salmonids.

Further Reading

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FISH FARMING

See **MARICULTURE DISEASES AND HEALTH; MARICULTURE OF AQUARIUM FISHES; MARICULTURE OF MEDITERRANEAN SPECIES; MARICULTURE OVERVIEW; MARICULTURE, ENVIRONMENTAL, ECONOMIC AND SOCIAL IMPACTS OF**

FISH FEEDING AND FORAGING

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Introduction

There are approximately 24 600 species of fish of which 58% or 14 268 live in the sea. The sea covers about 71% of the surface area of the earth and has an average depth of around 3800 m, so that the total volume of the marine environment is about $1370 \times 10^6\,\mathrm{km}^3$. Much of this volume, removed from the influence of the sun's rays, is an inhospitable place to live, being dark, cold, and very low in available food. With such a volume for living, it is no surprise to learn that there are some 15 basic ways in which fish can gain food from the environment (**Table 1**). Because the open ocean and the deep ocean have low productivity compared with the shallow seas, most of the fish diversity is found in waters less than 200 m deep with the highest concentrations being found in tropical waters over coral reefs. The fish in these areas also have the greatest diversity of ways of making a living. Coral reefs and other inshore areas also have the most complex linking between fish with long food chains.

Modes of Feeding in Fishes

During the course of evolution, fish in the marine environment have developed a diverse array of behavioral, morphological, and physiological adaptations to cope with the food they most commonly eat. Although fish feeding habits can be classified into a relatively few groups, the diversity within each group is significant. The different modes of feeding are shown in **Table 1** together with a selection of illustrative species. With this table in mind, it becomes possible to examine in more detail the principles of behavioral adaptations used to cope with different conditions.

Feeding mode can be classified by the type of food eaten. A species adopting a particular type of food, say that of a piscivore, will develop a body form and a set of foraging tactics suiting it to the particular types of prey taken and the habitat in which the piscivore lives. For an example, a whiting