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Effects of dissolved oxygen concentration on freshwater fish: A review

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Abstract

Dissolved Oxygen (DO) is one of the most important factors for aquatic animals as especially for those who derive dissolved oxygen from the water. DO levels indicate the quality of water. Many biotic and abiotic factors may influence DO concentration like mixing of different water bodies, upwelling, atmospheric exchange, respiration, photosynthesis, ice cover, pollution and some physical factors like salinity and temperature. The fluctuations in DO levels in water affect fish physiology. In this review, we will focus on the impact of DO on freshwater fish-physiology. A detailed literature survey is given based on DO and freshwater fish swimming, feeding, disease management, survival, respiration, metabolism, growth, reproduction, health parameters, immunity and stress of freshwater fishes.

Keywords: Dissolved oxygen, hypoxia, hyperoxia, fresh water fish, fish physiology

1. Introduction

The term "dissolved oxygen (DO)" refers to gaseous oxygen that has been dissolved in water and is available for the aquatic organism for their oxygen dependency. Fish and other aerobic aquatic creatures require oxygen to survive and reproduce (Caldwell and Hinshaw, 1994) [1]. Oxygen dissolves in water by the process of diffusion from the atmosphere, that has tumbled over falls and rapids movement, or by photosynthesis through aquatic plants (Singh and Kumar, 2014) [2] oxygen is the most vital factor in aquaculture for their maintenance of metabolism and growth (Doudoroff and Shumway, 1970; Kutty, 1981; Davis, 1975) [3, 4, 5]. In developing countries aquaculture plays an important role to feed the undernourished people. In India, 1.2 million tonnes of freshwater fish were consumed annually (Singh and Kumar, 2014) [2]. The requirement of DO differs from species to species in fish. Generally, the DO concentration is measured in mg/L or percent saturation (Wilson, 2010) [6]. 8-8.5 mg/L of DO supports healthy growth rates (Hicks, 2002) [7] lower than 8 mg/L concentration will affect the mature eggs and the larval development (Davis, 1975; Bjornn and Reiser, 1991) [5, 8]. Thus, dependent on habitat, fishes frequently experience fluctuating O₂ availability, which can range from hypoxia (low O₂ availability) to hyperoxia (O₂ supersaturation) (Diaz & Breitburg, 2009)

When the DO concentration gets below 5-6 mg/L in fresh water, then the required level of an aquatic organism it gets in hypoxic condition (Dong *et al.*, 2011) [10]. The Anoxia and hypoxia are known to be a primary cause of stress, poor appetite, slow growth, illness susceptibility, and mortality (Timmons *et al.*, 2001) [11] can create a large reduction in abundance, diversity and harvest of fishes within affected water (Breitburg, 2002) [12]. Mild hypoxia only resulted in a decrease in blood oxygen saturation and pO₂. At all-time points, both acute and chronic moderate and intense hypoxia resulted in a drop in blood pH, pO₂, total oxygen content, plasma Na+ and Cl (Aboagye and Allen, 2018) [13]. Certain species are far more hypoxia tolerant than others, resulting in differences in long-term survival (Poon *et al.*, 2002) [14]. In general fishes avoid the areas where oxygen concentration is below the specific level (Agostinho *et al.*, 2021) [15]. Hypoxia enhanced haemoglobin oxygen affinity, the lowering in temperature will also improve oxygen uptake (Petersen and Steffensen, 2003) [16].

In aquaculture practice DO above the air saturation is considered as hyperoxia. When fishes are subjected to hyperoxia (<200% saturation), no detrimental consequences or anomalous behaviour are observed (Dejours *et al.*, 1977) [17] albeit there are some alterations in the acid balance of the fish blood (Ruyet *et al.*, 2002; Edsall and Smith, 1990; Wilkes *et al.*, 1981) [18. 19-20]

At high ammonia levels (Foss *et al.*, 2003) ^[21] and stocking density (Wilkes *et al.*, 1981) ^[18] there are no negative consequences. Because of enhanced rate of photosynthesis, hyperoxia occurred at about noon or early afternoon (Richards *et al.*, 2009) ^[22].

In some species such as trout and fast-swimming fish, the bladder acts as a storehouse of oxygen for use in the absence of oxygen. when the water is oversaturated (hyperoxia), The bladder becomes overstretched causing buoyancy issues, especially in small fish (Groot *et al.*,1995) [23]. Also, cause chloremia and respiratory acidosis (Heisler, 1993) [24],

oxidative damages (Brauner *et al.*, 2000) ^[25]. Hyperoxia can arise in shallow-water fish due to the photosynthetic activity of phytoplankton, algae, seaweeds, and macrophytes, or in aquaculture due to O₂ supplementation (McArley *et al.*, 2021) ^[26]. When compared to normoxia, hyperoxia had similar but less effective influences, with weight gain and decreasing in growth rate and increasing in feed conversion ratio, but all of these differences were less than hypoxia (Aksakal and Ekinci, 2021) ^[27]. The long-term implications of hyperoxia are still unknown (Polymeropoulos *et al.*, 2019) ^[28].

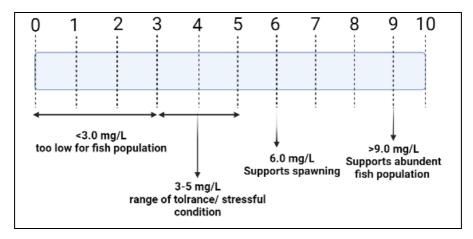


Fig 1: Range of tolerance for dissolved oxygen in fish

2. Factors which affect the concentration of dissolved oxygen in water

2.1 Biotic factors

A sufficient amount of DO is required for optimal water quality to support aerobic living forms (Devis, 1975) ^[5]. But abiotic certain factors like diffusion and aeration, photosynthesis, respiration, and decomposition have an impact on DO concentration (Hargreaves, *et al.*, 2003) ^[29]. Photosynthesis by aquatic plants and algae provides dissolved oxygen to water bodies during the day.

$$6CO_2 + 12H_2O \stackrel{\text{+energy}}{\longrightarrow} C_6H_{12}O_6 + 6O_2 + 6H_2O$$

The net effect on DO concentrations is usually very low because these same organisms consume comparable amounts of DO through respiration during the night when photosynthesis is not active (Wilson, 2010) [6]. Aerobic respiration obtains energy from energy-rich carbon molecules by oxidising carbon in to CO₂ and reducing oxygen to H₂O to sustain life. As a result, due to respiration needs, dissolved oxygen concentrations will be highest in the mid to late afternoon, when photosynthesis rates are highest, and lowest immediately before the sun rises the next morning when photosynthesis rate at lowest. This pattern of fluctuation is known as the "diurnal oxygen cycle" (Talling, 1957) [30]. In addition to photosynthetic organisms' demands during darkness, other organisms such as aquatic vertebrates and invertebrates, as well as bacterial and fungal communities involved in decomposing dead plants and animals, use oxygen within the system through aerobic respiration (Boyd & Hanson, 2010) [31]. Biological oxygen demand (BOD) is a measure of the potential for DO inside a water body to become low and might became anaerobic due to microbial biodegradation of organic molecules (Ultsch et al., 1978) [32]. When management operations may enhance the available carbon within a system, such as aquatic weed management

with aquatic herbicides, BOD considerations are especially essential. As the plants are decomposed by microbial organisms, they will become a source of BOD in the system. When water body gets enriched with nutrients caused by the nutrients runoff from nearby lands and drainage systems leads increased in algal production, frequently known as algae blooms. As microorganisms decompose these algae blooms, BOD levels will rise dramatically (Francis-Floyd, 2006) [33]. DO level is frequently used to indicate freshwater quality, stream and river health, and the severity of aquatic pollution (Kannel et al., 2007) [34]. A stream with a saturation rating of more than 80% oxygen is regarded to be healthy. Warmwater fish should have a minimum DO concentration of 5 mg/L, while cold water fish should have a minimum DO concentration of 6 mg/L (Doudoroff and Shumway, 1970) [3]. Fish growth, reproduction, physiology, biochemistry, and behaviour can all be affected by low DO levels (Davis, 1975) [5]. Oxygen depletion can occur as a result of sewage plant discharges, abattoir wastes, sawdust, feedlot manure, and food processing plant and paper mill use. These contaminants serve as a food source for bacteria, which use dissolved oxygen to break down these organic molecules, lowering the DO level in the environment. Other factors that contribute to oxygen depletion include the release of anoxic (lack of oxygen) bottom water from dams, the turnover of oxygen-deficient hypolimnetic water, an abundance of aquatic vegetation, and huge algal blooms. Fish swimming at or near the surface gulping air are signs of possible oxygen depletion, as are sudden changes in watercolour to brown, black, or grey, a rotting odour from the water, extended periods of hot, gloomy weather, algae die-offs, and thunderstorms. Poor DO concentrations can lead to the extinction of more vulnerable species in an environment, resulting in a loss of species diversity (Kibria, 2004) [35].

Overpopulation of bacteria and over fertilization of water plants could all contribute to decrease in DO levels in a body of water (Bansal and Jaspal, 2009) [36]. If DO level in a water body falls down below than 4-5.0 mg/L then the aquatic life gets under stress (Dey, 2017) [37]. Even the most tenacious fish would perish if DO drops below 3 mg/L. the requirement of DO for eggs and the immature stages is more than normal DO concentration. However, the amount of DO require by an aquatic organism is determined by its species, physical state, water temperature, contaminants present, and other factors (Mallya, 2007) [38]. Fish are cold-blooded in nature because of that their metabolic rates increases at higher temperatures; hence they consume more oxygen at higher temperature. High DO concentrations can pose issues just as low DO concentrations can. Gas bubble disease in fish and invertebrates can be caused by supersaturated water, however, this is a very unusual event. When DO maintains above 115% - 120% air saturation for an extended period of time, significant death rate occurs (Geist et al., 2013) [39]. At 120 per cent DO saturation, total mortality occurs in young salmon and trout in less than three days. Gas bubble illness affects invertebrates as well. While invertebrates are susceptible to gas bubble sickness, they can typically withstand higher amounts of supersaturation than fish. The bubbles, also known as emboli, obstruct the passage of blood via the blood arteries, resulting in death. External bubbles (emphysema) can form and be visible on fins, skin, and other tissue (Weitkamp and Katz, 1980) [40]. Eutrophication and organic pollution are one of the main factors of water, especially in the heavily populated region (Pollock et al.,

2007) [41].

2.2 Abiotic factors

The total amount of oxygen that can be broken up in the water is depend upon several factors, including water temperature (Rajwa et al., 2014) [42] salinity (Moon et al., 2003) [43] and atmospheric pressure. Higher water temperature cause increase in molecular vibrations, which leads decreasing in the intermolecular spaces between the water molecules. That's why the amount of DO is higher in cold water and low in warm water (Khani et al., 2017) [44]. Altitude makes also difference in DO concentration in water (Paz et al., 2020) [45]. Since the density of atmospheric O_2 for dissolution at higher altitude is low than at sea level (Zaker, 2007) [46]. Oxygen transmission across the air-water interface is facilitated by increased surface area exposed to the atmosphere. The surface area of a water body in contact with the atmosphere is increased through wind-driven waves and ripples, as well as forcing water into droplets by splashing over obstacles or forcing via a fountain (Connell and Miller, 1984) [47]. The surface area to volume ratio is crucial for determining a water body's baseline oxygen status, since aeration is the most prevalent means of adding oxygen to an aquatic system (Singh and Kumar, 2014) [2]. Deepwater bodies with a smaller surface area will have less possibility for O2 dissolution into the water than shallow water bodies with a larger surface area exposed to the atmosphere (Araoye, 2009) [48].

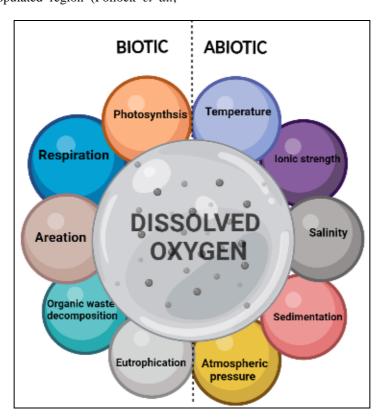


Fig 2: Biotic and abiotic factors affecting dissolved oxygen in water

3. Physiological Changes

3.1 Swimming

It is generally known that fish's aerobic swimming performance is limited by aquatic hypoxia. Hypoxia affects spontaneous swimming activity, with sluggish species slowing down and active species speeding up. Fish can escape hypoxia by actively searching for well-oxygenated areas. Several investigations using swim tunnels and an incremental

technique "critical swimming speed" (Ucrit) have shown that fish in hypoxia has a lower U_{crit} than fish in normoxia. Most of fresh water fish drastically diminished swimming skills when exposed to hypoxia, owing to the high metabolic cost of aerobically propelled swimming as well as the physiological difficulty of hypoxia (Jones, 1971; Herbert and Steffensen, 2005; Smit, 1965; Fu *et al.*, 2011; Hanke and Smith, 2011; Fitzgibbon *et al.*, 2007) [49, 50, 51, 52, 53, 54]. Chronic exposure to hypoxia reduces some of the hypoxia's swimming-limiting effects. Therefore, chronic hypoxia acclimation provides long-term benefits (Ackerly et al., 2018) [55]. Hypoxia tolerance and swimming ability in fish subjected to chronic hypoxia are improved by transient gill remodelling, increased haematocrit, the haemoglobin with stronger O₂ binding affinity, increased anaerobic capacity, and increased cardiac output (Chippari-Gomes *et al.*, 2005; Petersen and Gamperl, 2010; Fu *et al.*, 2011) ^[56, 57, 52]. Larger gill surface area in swamp-dwelling fish, could represent a compensatory technique for the physiological constraints of hypoxia (Chapman and Hulen, 2001) [58]. An individual's anaerobic metabolism can have a considerable impact on performance, particularly at speeds near Ucrit, where aerobic contribution to power performance is often higher (Wilson and Egginton, 1994; Svendsen *et al.*, 2010) [59, 60]. The non-invasive measure of excess post-exercise oxygen consumption (EPOC) can be used to quantify anaerobic activity. EPOC measures an individual's rate of oxygen consumption during the time frame during which excess waste (e.g., lactate) originating from anaerobic metabolism is eliminated from the body (Peake and Farrell, 2004; Svendsen et al., 2010) [61, 60]. Recovery from anaerobic activity requires more oxygen, so recovery from Ucrit can take much longer in hypoxic conditions (Svendsen et al., 2011) [62].

Hypoxia also affects predator-prey interactions, lowering faststart performance in particular species (Domenici et al., 2013) [63]. The effects of hypoxia on aerobic swim performance and sensory information acquisition, as well as the ability of fish enhance aerobic performance through acclimation processes, might affect performance months after first exposure (Ackerly *et al.*, 2018) ^[55]. Hypoxia tolerance was assessed using the aquatic surface respiration (ASR50) and loss of equilibrium (LOE50) values, swimming performance was assessed using the critical swimming speed (U_{crit}), aerobic capacity or space was assessed using the maximum metabolic rate. The hypoxia tolerance drops with decreasing temperature (fish usually showed high hypoxia tolerance due to decreased oxygen demand and environmental oxygen tension at low). Low hypoxia tolerance and poor swimming performance may lead to problem in adoptability (Zhou et al., 2019) [64]. At normal DO concentrations, fish can continue to swim at modest rates. Only at lower DO concentrations, around or below 5 mg/1 and some warm water fishes show limited locomotion. Fish swimming is more linked to DO concentration as compared to dissolved CO2 concentration of aquatic body. Even considerably greater CO₂ concentrations, which have a significant influence on the sustained swimming speeds of coho salmon, Oncorhynchus kisutch, at high levels of DO, are ineffective at very low levels of O2. The acclimatisation of goldfish, Carassius auratus, to O2 shortage has little effect on their maximal speeds at low levels of O₂. In nature, very quick swimming is probably more common than continuous swimming at maximum sustainable speeds (Doudoroff & Shumway, 1970) [3].

The fast-start movement occurs in seconds and is primarily limited by ATP and phosphocreatine in muscle tissues, the lack of a DO influence on maximum speed is simply understood. However, constant acceleration test (U_{cat}) was more susceptible to DO alteration than U_{crit} , with the former showing a substantial decrease at a modest DO level (5 mg/l), but the latter did not. U_{crit} is more likely to be aerobic swimming, whereas U_{cat} is more likely to be anaerobic swimming. The reason for this could be because the

mobilisation, transportation, and use of energy fuels, rather than the availability of oxygen, caused the limiting of Ucrit in some fish species. In species like black barbel catfish Pelteobagrus vachelli (Fu et al., 2009) [65], common carp Cyprinus carpio (Zhang et al., 2010) [66], and Crucian carp (Zhang et al., 2012) [67], this conclusion has been thoroughly demonstrated (a so-called additive metabolic mode compared to a locomotion priority mode in species whose swimming activity can occupy all of their cardio-respiratory capacity; (Fu et al., 2011) [52]. A minor fall in DO may not influence U_{crit} in these types of organisms. U_{crit} was shown to be present in mulloway Argyrosomus japonicus and dark barbel catfish (Pang et al., 2012) [68]. There has been no modification in the current investigation, MO2 active in crucian carp did not decrease at a moderate DO level, indicating that Ucrit was not limited by respiratory capacity in normoxia. Furthermore, instead of a component at the top end of the performance range, U_{cat} consists of two components: an aerobic component of steady swimming supported by aerobic 'red muscle' fibres, and a component at the bottom end of the performance range (Peake, 2008) [69]. Although U_{crit} focuses primarily on anaerobic metabolism, Ucat is governed by both aerobic and anaerobic swimming, with the aerobic components of Ucat relying on oxygen availability rather than substrate transit and use due to its shorter duration. As a result, even little changes in DO will reduce Ucat. It is important to conduct more research into the effects of DO alterations on Ucat and Ucrit in fish with distinct metabolic modes like additive vs. priority mode (Penghan et al., 2014) [70].

3.2 Feeding

The concentration of dissolved oxygen in the water exerts a significant impact on the metabolic rate of fish. Feeding activities and other bodily functions decrease as the concentration of dissolved oxygen drops. As a result, the growth rate slows down and the fish become unable to absorb the nutrients (Tom, 1998; Buentello *et al.*, 2000; Andrews *et al.*, 1973) ^[71, 72, 73]. High DO condition leads to increment in movement and digestion (Dey, 2017) ^[37]. Under hypoxia, both feed intake and growth rate are significantly lower than under normoxia (Chabot, 2003) ^[74]. When water oxygen saturation goes below 70%, salmonids lower their food intake and stop developing (Jobling, 1993) ^[75].

For non-aerated freshwater catfish ponds, a link between feeding rate and dissolved oxygen was observed (Tucker *et al.*, 1979) ^[76]. Minimum dissolved oxygen concentrations were about 1-0, 1-7, and 3-7 mg/litre at maximum feeding rates of 78, 56, and 34 kg/ha day, respectively. Another study used overnight DO prediction models to provide emergency aeration to catfish ponds stocked at six densities and fed from 0 to 224 kg/ha day (Cole and Boyd, 1986) ^[77]. At larger feeding rates, the ponds' aeration requirements increased. There were significant relationship between low dissolved oxygen and feeding rate (Boyd *et al.*, 1979) ^[78].

3.3 Disease management

The availability of dissolved oxygen is the most important, as it is influenced by temperature, water source, and biological demand (i.e., high concentrations of bacteria and decaying matter). The water's pH should be consistent and just below 7. The level of waste products should be kept low, with special attention paid to the presence of excessive carbon dioxide, which is poisonous to most fish, and a build-up of ammonia, which can cause the pH to rise above 7.5 (Cawley, 1983) [79].

When DO levels are low and ammonia concentrations are high that may cause mortality from disease breakout (Chitmanat, 2013) [80]. Reduced respiration rates, diminished reproductive activity, forced habitat shifts, and ultimately reduced fish population sizes are all detrimental effects of a lack of oxygen on fish and other lake biota (Garside, 1959; Pollock *et al.*, 2007) [81,41].

Environmental stress, such as hypoxia, can damage fish immune systems, making them more prone to disease (Wedemeyer *et al.*, 1976) ^[82]. Hypoxia makes certain endemic diseases more harmful (Mellergaard and Nielsen, 1995) ^[83]. Fish sensitivity to low dissolved oxygen concentrations varies by species, life stage (eggs, larvae, adults), and life processes (feeding, growth, and reproduction) as well as different types of activity (resting, swimming, digesting, etc.). Young fish are most sensitive at the time of hatching, resulting in significant losses when dissolved oxygen levels are decreased to 2–3 mg/l for many days. In the lack of oxygen, newly hatched larvae can survive for one hour, while free-swimming larvae can only survive for a few minutes (Alabaster and Lloyd, 1980) ^[84].

While sub-optimal dissolved oxygen levels are not instantly fatal, they can stress fish and cause delayed mortality. A high level of dissolved oxygen is essential for the fish to quickly recuperate from the stress of catching and handling (Rottmann et al., 1992) [85]. Handling stress, poor water quality, fast temperature fluctuations, high stocking density, and inadequate nutrition are all risk factors that can contribute to the spread of viral infections. In intensive aquaculture systems, which are typically highly stocked with fish, these conditions may exist (Akoll & Mwanja, 2012) [86]. Due to overcrowding or chemical pollutant exposure, fish face stress that aggregated due to decreased DO. The situation supports indigenous diseases spread in the aquatic body (Hershberger et al, 1999; Carls et al, 1998) [87, 88]. The DO level in pond water is important because it is directly associated with disease outbreaks (Null et al., 2017; Domenici et al., 2017; Gallage et al., 2016, 2017) [89, 90, 91, 92]. Fish development and productivity will be reduced as a result of disease outbreaks due to hypoxia, (Lovell, 1998; Shoemaker et al., 2000) [93, 94]. Adverse water quality in terms of anthropogenic activities or adverse environmental conditions including hypoxia may damage the immune system, resulting in diminished resistance to pathogen infections (Di Marco et al., 2008) [95]. The majority of bacteria are opportunistic pathogens. As a result, environmental stresses such as high temperature, low dissolved oxygen, high ammonia content, and others are primarily responsible for the initiation and severity of bacterial infections (Plumb et al., 1976; Walters and Plumb, 1980) [96, 97]. Low levels of dissolved oxygen inhibit nitrifying bacteria's capacity to convert ammonia and nitrite, it's critical to keep an eye on dissolved oxygen levels. A strong water quality management programme will help to prevent disease, boost growth, and eliminate the need for chemical treatments (Francis-Floyd et al., 2009) [98].

3.4 Survival

The most essential water quality variable in fish culture is dissolved oxygen content (DO). If dissolved oxygen concentration is continuously declining, then in aquatic animals' growth will be hampered, they will become prone to infectious disease, finally fish will perish out. The smaller fish consumes dissolved oxygen at a higher rate than the larger fish, which explains why the larger fish perished faster

(Nimesh et al., 2012) [99]. Size-dependent mortality, like oxygen deprivation, happens naturally but can be altered by human actions (Lorenzen, 1996; Sogard, 1997; Gislason et al., 2010) [100, 101, 102]. Total dissolved gas (TDG) caused by the rapid overflow of water from the dam may threaten the survival of fish. The increasing TDG level can decrease the tolerance of juvenile fish. Large juvenile fish has weaker tolerance to TDG supersaturated water than small juvenile fish. TDG supersaturation can cause abnormal behaviours in fish like loss of balance, loss of ability to swim and faster breathing (Fan et al., 2020) [103]. The temperature has a twofold effect: it decreases the solubility of oxygen while also raising the metabolic requirement for oxygen in ectotherms (Portner & Knust, 2007; Holt and Jorgensen, 2015) [104, 105]. There is limited work has been done hypoxia influence on reproduction, but it can be hampered by excessive degrees of hypoxia (Wu et al., 2003; Landry et al., 2007; Chabot and Claireaux, 2008) [106, 107, 108]. Demersal fish populations are declining due to a lack of oxygen and overfishing (Diaz and Rosenberg, 2008) [109]. Because the minimal oxygen available is dedicated to maintenance rather than somatic growth, low oxygen saturation in water is a proximate factor causing reduced asymptotic maximal size (Pauly, 1981; 2010; Van Dam and Pauly, 1995; Chabot and Claireaux, 2008) [110, 111, 112,

3.5 Respiration

For optimal fish production, proper oxygen management is critical. The maintenance of healthy fish and bacteria that break down the waste produced by the fish, and the fulfilment of the biological oxygen demand (BOD) in the culture system all necessitate the presence of oxygen. Fish respiration can be hampered by low dissolved oxygen levels, as well as ammonia and nitrite toxicity (Mallya, 2007) [113]. In hypoxic environments, species specialised for aerial and surface film respiration dominated the fish assemblage. Other animals found in hypoxic environments have developed hypoxia-specific behavioural and morphological adaptations. The banded pygmy sunfish (*Elassoma zonatum Jordan*) and pirate perch are both solitary species with low activity levels (Robison and Buchanan, 1988) [114]. Which results in lower respiration rates (Killgore and Hoover, 2001) [115].

Many fishes are exposed to seasonal temperature fluctuations in their natural environment, rise in environmental temperature causes an increase in metabolism in teleosts, as seen by oxygen intake (Fry and Hart, 1948; Beamish, 1964; Heath and Hughes, 1973) [116, 117, 118]. This increased oxygen demand creates additional demands on the respiratory and cardiovascular systems, which are partially addressed by increased ventilation volume and heart output (Hughes and Roberts, 1970; Stevens et al., 1972; Watters and Smith, 1973) [119, 120, 121]. Any variation in O₂ concentration is likely to cause respiratory or cardiovascular compensations in fish. These difficulties, which include variations in respiratory rhythm (opercular rate), are adaptive and do not indicate any impairment of ecologically important functions. Incipient respiratory compensation may give idea of the dissolved O₂ requirements of fish (Doudoroff and Shumway, 1970)^[3].

During aquatic hypoxia, fish can maintain oxygen intake by increasing gill ventilation. Increases in breathing rate and stroke volume (Smith & Jones, 1982) [122]. Because marked bradycardia is countered by an increase in stroke volume, cardiac output is maintained during hypoxia. Systemic resistance increases, increasing both dorsal and ventral aortic

blood pressure (Short et al., 19979) [123]. Pulse pressure rises dramatically as a result of the increased heart-stroke volume and lower heart rate. The levels of dopamine, adrenaline, and noradrenaline in the blood of sandy dogfish Scyliorhinus canicula also increases in response to hypoxia (Butler et al., 1978) [124]. Both arterial and venous blood oxygen contents decrease (Holeton & Randall, 1967) [125]. (Soivio et al., 1980) [126] found that erythrocytic ATP levels are lowered, resulting in a significant increase in haemoglobin oxygen affinity. Hypoxia increases the number of circulating erythrocytes, which expand in some fish, resulting in a significant increase in haematocrit. In sandy dogfish (S. canicula), however, no rise in haematocrit has been seen in response to hypoxia (Butler et al., 1979) [124]. Hypoxia cause increased activity in vagal cholinergic fibres innervating the heart leads decrease in heart rate (Randall, 1982) [127]. The afferent arm of this reflex originates from receptors that respond to hypoxia and are found on the first gill arch in the region of the various vessels (Daxboeck & Holeton, 1978) [128]. When water flow through the gills increases in proportion to oxygen absorption, and in hypoxia, it is raised to sustain oxygen supply (Smith & Jones, 1981) [122].

3.6 Metabolism

The concentration of oxygen in the rearing environment has a significant impact on the metabolic rate of fish (Tom, 1998) ^[71]. Metabolism transforms meals or stored energy into the energy required to carry out daily tasks. This process eventually necessitates the use of oxygen, which must be obtained from the environment (Nelson, 2016) ^[129]. Fish have evolved respiratory and circulatory systems to perform this role over a wide range of ambient oxygen levels, from above air saturation to levels below which oxygen-demanding activities cannot be sustained and death occurs (Chabot *et al.*, 2016) ^[130]. Hypoxia has been shown to have an impact on a variety of physiological systems in fish, including metabolism as a result, a reduction in feeding and growth (Chabot & Dutil, 1999) ^[131].

Only a stable essential level of O_2 can be ecologically important, below which metabolic rates sustained by fish in natural situations is still unknown or limited studies has been done (Doudoroff and Shumway, 1970) ^[3]. In limited DO fish groups had lower protein and lipid content in their bodies because of metabolism requires more energy to cope with hypoxic stress. Lipid and protein may be employed as an energy metabolic substrate to adapt to low DO conditions and sustain overall metabolism, resulting in a decrease in lipid and protein content. Normal DO groups had more protein and fat content, which could be linked to lower energy requirements for feed absorption and other physiological processes. Fish with normal DO levels appear to be able to lower the proportions of metabolic energy and energy loss, saving more energy for growth and lipogenesis (Duan *et al.*, 2011) [132].

When a fish is under hypoxia stress its aerobic metabolism is suppressed, whereas anaerobic metabolism is boosted and metabolism of steroid hormones is slowed. Cell cycle arrest occurs in liver cells, genes involved in cell development are down-regulated in aerobic metabolism, while genes involved in anaerobic metabolism are up-regulated. Uncoupling proteins 2 and 3 are upregulated and may help to reduce mitochondrial activity (Randall *et al.*, 2006) [133]. Hypoxiatolerant animals have long been thought to be able to extend their length of survival under extreme hypoxic conditions by lowering their basal metabolic rate, which restricts the level of

activation of O_2 -independent ATP generation pathways (Richards, 2009) [134].

3.7 Growth

Dissolved oxygen had a substantial effect on fish growth, and low oxygen levels combined with reduced feed intake led to decreased growth and changes in to stress response (Lakani *et al.*, 2013) ^[135]. Low DO has a negative impact on fish growth and feed intake (Abdel-Tawwab *et al.*, 2015) ^[136]. Growth rates reduced and became progressively less as the dissolved-oxygen concentrations decreased (Carter, 2005) ^[137]. Fish metabolism and growth are dependent on the availability of ambient oxygen. The growth rate of fish is fastest at high dissolved oxygen and the growth rate of fish is slowest at low dissolved oxygen. It is clearly shown that the different level affects fish growth (Tsadik and Kutty, 1987) ^[138].

Some fish species are particularly sensitive to oxygen saturation, and increasing DO to 100% enhances their growth rate. In tropical freshwater fish, 5 mg per litre (80% saturation) is indicated as the minimum and most effective dose (Mallya, 2007) [38]. Fish development and feed utilisation were harmed by low DO levels. A lack of oxygen available for fish growth may reduce the growth observed under low DO conditions. Fish development and feed efficiency were affected by DO availability, according to (Bergheim et al., 2006; Duan et al., 2011) [139, 132], When fed at a high enough DO in water, fishes were always showed good feed efficiency. according to (Abdel-Tawwab et al., 2014) [140] Low DO levels significantly reduced the development of *Nile* tilapia, Fish appetite and digestibility were both reduced in low DO circumstances, resulting in low feed intake and growth (Tran-Duy et al., 2012; Gan et al., 2013) [141, 142]. As a result, under typical DO conditions, significant growth was mostly owing to increased feed consumption and nutrient digestibility. Spotted wolfish, Anarhichas minor (Foss et al., 2002) [143], Nile tilapia, O. niloticus (Tran-Duy et al., 2008, 2012; Abdel-Tawwab et al., 2014) [144, 141, 140], striped bass, Morone saxatilis (Brandt et al, 2009) [145] Atlantic halibut, Hippoglossus (Thorarensen et al., 2010) [146]; Japanese flounder, Paralichthys olivaceus (Duan et al., 2011) [132] and grass carp, Ctenopharyngodon idella (Gan et al., 2013) [142] Under hypoxic conditions, all of these fish had lower feed intake and growth.

Smaller fish at a low-calorie diet and developed faster than larger fish at normal DO (Tran-Duy *et al.*, 2008; Abdel-Tawwab *et al.*, 2010) [144, 147]. Larger fish were found to tolerate low DO better than smaller fish. Small ones are substantially less hypoxia-tolerant than larger ones (Almeida-Val *et al.*, 2000; Sloman *et al.*, 2006) [148, 149]. As big body has lower metabolic rate and body size affect a fish's ability to take up oxygen under hypoxic situations (Nilsson and Ostlund-Nilsson, 2008) [150].

3.8 Reproduction

The most significant abiotic elements impacting aquatic species breeding efficiency are temperature (T) and dissolved oxygen (DO). Maintaining the best combination of temperature and DO will aid in improving breeding efficiency and ensuring the largest quantity and quality of fingerlings are produced (Qiang *et al.*, 2019) ^[151]. Dissolved oxygen concentrations in freshwater streams must be enough for fish viability. To oxygenate the blood and meet their metabolic demands, fish have evolved highly efficient physiological processes for acquiring and utilising oxygen in the water.

Reduced amounts of dissolved oxygen, can affect the growth and development of eggs, and fry, as well as the swimming, eating, and reproductive abilities of juveniles and adults (Tang *et al.*, 2020) ^[152]. By modifying embryo incubation durations, decreasing fry size, increasing the chance of predation, and decreasing feeding activity, such changes can have an impact on fitness and survival. Low dissolved oxygen concentrations can be fatal for fish under extreme circumstances (Carter, 2005) ^[137].

Hypoxia can affect courtship behaviours, mate choice, and reproductive efforts in fish. It can cause major reproductive impairments by inhibiting testicular and ovarian development, affecting sperm and egg production and quality, reducing fertilisation and hatching success, and affecting larva survival as well as the quality of fitness of juveniles (Spence et al., 1996) [153]. In many fish species, hypoxia has been demonstrated to delay embryonic growth and hatching. Under hypoxia, fish embryos lose their usual synchronisation, and defects in spinal and vascular development are prevalent (Wu, 2019) [154]. Hypoxia has been shown to affect fish endocrine systems, slowing gonadal development and lowering spawning, fertilisation, and larval growth success (Zhou et al., 2001; Wu et al., 2003) [155, 106]. Zebrafish exposed to hypoxia (0.5-0.8 mg/L) produced just 9 eggs per fish after the first day, compared to 52 eggs per fish in the control group (Zhou et al., 2001) [155]. Fertilized zebrafish eggs hatch 48 to 60 hours after fertilisation in normoxia, with 93.8 per cent of the eggs hatching. Fertilized eggs took 96 to 260 hours to hatch in hypoxia, with only 4.9 per cent hatching and the rest dying. Fertilized eggs growing in hypoxia were pale, indicating that they lacked pigment. Growth was slowed, and there were numerous anomalies (Randall and Yang, 2003)^[156].

Fish embryonic and larval stages are especially vulnerable to low dissolved oxygen levels (Chapman, 1986) [157]. When dissolved oxygen levels are below saturation (but over a critical level), embryos can survive, although development is often disrupted. When dissolved oxygen levels were below saturation throughout development, embryos were found to be smaller than normal, and hatching was either delayed or preterm (Bjornn and Reiser, 1991; Wu *et al.*, 2002; Zhou *et al.*, 2001) [158, 159, 155]. (Jones and Reynolds, 1999) [160] observed that low DO did not affect hatching success or the size of the young; nevertheless, hatching began one day later on average in hypoxic environments. Similarly, (Lissaker *et al.*, 2003) [161] observed no link between decreased DO and increased filial cannibalism.

Fish won't spawn at hypoxic condition. There were no eggs laid at 1.0 mg/L DO, and there were fewer laid at 2.0 mg/L DO than at control levels of 5.9–9.9 mg/L DO (Brungs, 1971) [162]. The time it took for the eggs to hatch varied with temperature and DO concentrations, with the latter increasing as the former decreased. All of the fry died within 6-13 days at 2.0 mg/L, while only 6% of the fry survived 30 days at 3.0 mg/L. Approximately 18% of the fry that survived the 4.0 mg/L treatment had spine curvatures. When it comes to fry survival, fish exposed to 5.0 mg/L DO were comparable to controls. At 2.0 mg/L, fry length was drastically reduced. With lowering DO, the number of spawning attempts per female dropped (Brungs 1971) [162].

3.9 Immunity

Fish can adjust to low dissolved oxygen levels in water by boosting blood flow and red blood cell concentration. By this way fish can increase the oxygen-carrying capacity of the blood per unit volume and in the long run, by releasing excess blood cells from the spleen (Svobodova and colleagues, 1993) [163]. Hypoxia significantly affects the physiological and immune responses of fish, making them more vulnerable to disease. It leads to a functioning acute inflammatory response to bacterial stimulation, and mildly down regulated gene expression (FTH1, HIF1A, and NR3C1) (Abdel-Tawwab *et al.*, 2019; Schafer *et al.*, 2021) [164, 165].

Individual heterogeneity in disease susceptibility in fish has been connected to fish species (Yuasa *et al.*, 1999; Evans *et al.*, 2000) [166, 167], genetic diversity, and immune response (Suanyuk *et al.*, 2008; Mian *et al.*, 2009; Zamri-Saad *et al.*, 2010; Sarder *et al.*, 2001) [168, 169, 170, 171]. Fish immunity was found to be stronger in larger fish than in smaller fish, showing that bacterial infection and innate immunity in farmed fish may be influenced by fish weight or age. Similarly, individual fish coping techniques may have an impact on the fish susceptibility to infection (MacKenzie *et al.*, 2009; Huntingford *et al.*, 2010) [172, 173].

Hypoxia, or lack of oxygen saturation, is one of the most serious stressors in intensive aquaculture. The impact of hypoxic conditions (3.2 mg/L DO) grown in RAS on their health and immunological system. In fish, low dissolved oxygen (DO) causes primary, secondary, and tertiary stress reactions. Furthermore, the duration and intensity of hypoxic conditions, as well as the animal's susceptibility to low oxygen saturation, determine the result of the triggered reaction (Schafer *et al.*, 2021) [165].

3.10 Stress

In fish, hypoxia causes primary, secondary, and tertiary stress responses (Bernier and Craig, 2005; Welker *et al.*, 2007; Bernier *et al.*, 2012; Segner *et al.*, 2012) [174, 175, 176, 177]. Fish in captivity are constantly exposed to recurrent and chronic stressors (e.g., confinement, crowding, handling, and changing water quality, including hypoxia) from which they have no method of escaping. As a result, fish must adapt to any of these husbandry stressors. As a result, the DO level should be kept near saturation to improve fish development and feed intake, as well as growth, development, disease resistance, behaviour, and reproduction (Mallya, 2007; Thorarensen *et al.*, 2010) [38, 146].

Two hormonal systems, that produce corticosteroids (primarily cortisol) and catecholamines (adrenaline and noradrenaline and their precursor dopamine) which controls the stress response (Reid *et al.*, 1998) [178]. These components work together to regulate secondary stress response, factors that affect the delivery of vital resources such as energy and oxygen to important parts of the body, as well as the hydromineral balance and the immune system (Seibel *et al.*, 2021) [179]. If a fish survives a stressor, it returns to normal state by homeostatic balance. The long-term effects of repeated or protracted stress exposures are maladaptive, compromising other vital life functions (growth, development, disease resistance, behaviour, and reproduction), because of high energy cost generates stress response (Schreck and Tort, 2016) [180].

Acute stress from capture, handling, transport, forced exercise, hypoxia, osmotic and temperature shocks, or social stressors, as well as exposure to water pollutants like acid water containing aluminium, has been shown to cause a rapid rise in muscle and plasma lactate, as well as a drop in blood pH and oxygen content. These alterations were typically accompanied by a significant increase in ventilation, branchial

blood flow, gas exchange, and blood glucose levels, as well as enormous catecholamines (CA) release from the chromaffin cells (Barton and Iwama, 1991; Brown, 1993; Mazeaud and Mazeaud, 1981; Pickering *et al.*, 1987; Randall and Perry, 1992; Witters *et al.*, 1991) [181, 182, 183, 184, 185, 186].

Acute hypoxia generated a release of epinephrine over norepinephrine (Perry and Reid, 1994) [187], with the reduction of arterial oxygen content/ saturation (rather than PO₂) being a key trigger inducing catecholamines to release. Gill injury can also reduce arterial oxygen content, which may contribute to catecholamines release in response to stress (Duthie and Hughes, 1987) [188]. The fact that when hyperoxic and normoxic rainbow trout were made acidotic by hypercapnia concentration, blood pH decreased more in the hyperoxic than in the normoxic fish, whereas CA levels increased only in the normoxic animals, who had a lower arterial oxygen content, suggests that acidosis is insufficient to induce CA to release (Perry et al., 1989) [189]. However, it is unclear whether rapid CA release during acute stress is only mediated by the stressor's effects on arterial oxygen levels, or if it might also be induced by the perception of external sensory cues.

The immunological response of fish is to boost innate function when the stressor is acute and a short-term response is stimulated (Tort, 2011) [190]. Acute stress causes an increase in the number of circulating leukocytes (Barcellos et al., 2004) [191]. This is due to the sympathetic nervous system's activation and the production of catecholamines, which mobilise both erythrocytes and leukocytes (Nardocci et al., 2014) [192]. When a stressor is long-term, the immune system is inhibited, which raises the risk of infection (Niklasson et al., 2011) [193]. The negative effects of stress on the immune response are thought to be mediated mainly by the suppressive effects of glucocorticoids (i.e., cortisol) and are a result of a failure to adjust to chronic stresses (Nardocci et al., 2014) [192]. This could happen because coping with the stressor has an allostatic cost that interferes with the immunological response that is required.

3.11 Behaviour

Fish constantly expend energy on perfusion, typically on ventilation, and frequently on movement during the process of oxygen acquisition. These expenditures, as well as the risk of predation, will change depending on the amount of oxygen available and the sort of behavioural response demonstrated. The four primary behavioural reactions to diminishing external availability of dissolved oxygen are (1) changes in activity, (2) increased use of air-breathing, (3) increased use of aquatic surface respiration, and (4) vertical or horizontal habitat alterations. Fish should select the response combination that reduces the expense of supplying their oxygen demands (Kramer, 1987) [194].

Hypoxia effects on fish behaviour like schooling which is beneficial for their survival could have cause substantial ecological consequences (Domenici *et al.*, 2017) [195]. It also impacts on anti-predator behaviour and fish escape responses, as well as its modulation by ASR and schooling behaviour (Domenici *et al.*, 2017) [195]. When oxygen levels drop, fish prey's metabolism and growth slow down, as well as their overall health. This may have an adverse effect on their locomotor and sensory abilities (Ackerly *et al.*, 2018) [55]. Hypoxia can alter the circumstances of fish predators (growth and metabolism). It can affect the preys escape performance and predators attack performance (Lefrancois *et al.*, 2005) [196]. This could lead to a reduction in the number of predator-

prey encounters. Terrestrial predators, on the other hand, could be able to take advantage of fish prey's reduced performance in hypoxia, improving their chances of catching a meal (Domenici *et al.*, 2017) [195].

Fish appears to be able to safely avoid fatal levels of DO in natural (Doudoroff and Shumway, 1970) [3]. Fish might be seen swimming fast in a circular manner with a wide mouth gape in other circumstances when the DO level was at its lowest. As DO is restored to a normoxic level, this tendency faded to normal swimming activity (Bowyer *et al.*, 2014) [197]. This behaviour could be related to gill adaptation to hypoxia, which includes decreased gas diffusion distance and increased total respiratory surface (Saroglia *et al.*, 2000) [198].

4. Consequences of Fluctuations in Dissolved Oxygen

In aquatic habitats, changes in oxygen levels are common; as a result, organisms, including fish, have evolved a diverse range of adaptations to both anoxia/hypoxia and hyperoxia. Reactive oxygen species cause oxidative damage to cellular components, affect glutathione status, and cause antioxidant ant enzymes to respond to fluctuating oxygen supply in fish. Antioxidant enzymes are increased in anticipation of oxidative stress in anoxia- and hypoxia-tolerant species during low-oxygen states, enhancing their antioxidant capability for dealing with possible oxidative damage upon restoration to normoxia. The glutathione system appears to play an important adaptive role in hyperoxic environments. Most stressful situations result in a rapid increase in lipid peroxidation products, which are then quickly detoxified by low- and high-molecular-weight antioxidants (Lushchak & Bagnyukova, 2006) [199]. It should be noted that both an excess and a deficiency of O₂ cause oxidative stress. HIF-1 is made up of a constitutively expressed HIF-1ß subunit and an O₂-regulated HIF-1 subunit. Prolyl hydroxylase domain (PHD) proteins use oxygen as a substrate to hydroxylate HIF-1 on proline 402 and/or 564. Proline hydroxylation allows binding to the "von Hippel-Lindau" protein (VHL), which recruits a ubiquitin ligase and promotes HIF-1 proteasomal degradation (Kaelin et al., 2008) [200]. HIF-1α has been shown to be activated faster by intermittent hypoxia than by continuous hypoxia, though through different mechanisms (Peers et al., 2007) [201]. Intermittent hypoxia induces ROS production by NADPH oxidase, activating phospholipase (PLC)y, which generates inositol 1,4,5-triphosphate (IP3) and diacylglycerol, thereby mobilizing intracellular Ca²⁺. Calcium activates calcium-calmodulin kinase (CamK), protein kinase C and finally mTOR, which facilitates HIF-1α synthesis and inhibits PHD2-dependent degradation.

When a cell has given the treatment of hyperoxic conditions results in an exponential release of ROS. Studies revealed that the inhibition of mitochondrial complexes I & II by hyperoxia leads releasing of ROS through ETC predominantly in early phase and in late phase with more ROS being released by NAD(P)H oxidase. Mitochondrial ROS initiates a calcium (Ca²⁺) signal, that translocates Rac1 (a small GTPase) to the plasma membrane, where it activates NAD(P)H oxidase (Brueckl et al., 2006) [202]. Hyperoxia increases in ROS affects a large number of intracellular signal transduction proteins, including protein kinases, channels, transcription factors, receptors and members of the apoptosis pathway (Gore et al., 2010) [203]. Molecular responses to hyperoxia are the redox-activated transcription factors, nuclear factor, erythroid 2 related factor 2 (Nrf2), nuclear factor kappa B (NF-KB) and activator protein-1 (AP-1) (Wright and Dennery, 2009) [204].

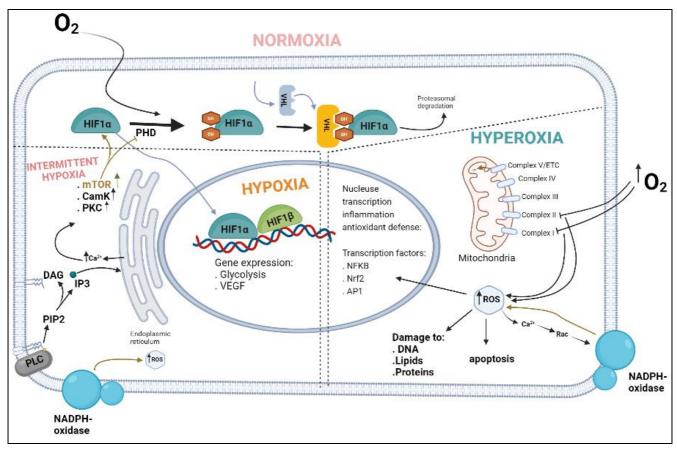


Fig 3: Cellular response to different oxygen condition, Abbreviations: activator protein 1 (AP1), calcium (Ca2+), Ca2+/calmodulin dependent protein kinase (CamK), diacyl glycerol (DAG), electron transport chain (ETC), hypoxia-inducible factor (HIF), inositol 1,4,5-triphosphate (IP3), mammalian target of rapamycin (mTOR), nicotine amide adenine dinucleotide phosphate (NADPH), nuclear factor 'kappa-light-chain-enhancer' of activated B-cells (NFKB), nuclear factor erythroid 2-related factor 2 (Nrf2), oxygen (O₂), prolyl hydroxylase domain protein (PHD), phosphatidyl inositol (4,5)-bisphosphate (PIP2), phospholipase C (PLC), protein kinase C (PKC), Rac, small GTPase;, reactive oxygen species (ROS), von Hippel-Lindau protein (VHL).

5. Conclusion

In this review we provide a concise overview on the influence of higher and the lower concentration of dissolved oxygen on freshwater fish. Dissolved oxygen is a critical premise for the healthy growth of aquatic organisms, particularly in aquaculture. Therefore, an accurate concentration of dissolved oxygen is very important for the survival of fishes. The fluctuations in DO are mainly caused by biotic and abiotic factors like respiration, photosynthesis, organic decomposition, aeration, temperature, salinity atmospheric pressure etc. Increasing and decreasing in these factors make hypoxic and hyperoxic conditions in aquatic ecosystem. These conditions cause drastic consequences in fish physiology. Somewhere the anthropogenic activities for the development of mankind is the root cause of variation in DO concentration. To prevent these aquatic animals, get under hypoxic and hyperoxic condition some preventive measures should have taken like enhancement in the surface area of an aquatic body for aeration, minimize in biological oxygen demand, controlling weeds, lowering in nutrient inputs. So, these practices can make an aquatic body healthier for the survival of fish.

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