**Compensatory Growth in Fish: A Review**

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**PREFACE**

Aquaculture, the underwater agriculture, is defined as rearing of fish in a natural or artificially created environment which favors their growth. Among the animal protein producing sectors, aquaculture represents the nascent industry, which is undergoing development and intensification of culture practices globally. From an insignificant industry in 1970’s, aquaculture has undergone a major transformation, competing with marine fishing sector in terms of production. According to the latest FAO (2024) report, 185 mmt of fish were produced at the global of which aquaculture alone produced 94.4 mmt of fish, with a contribution value of 51%. Of the total fish produced, 89% was utilized for direct human consumption. Presently, around 600 aquatic species have been raised in captivity at the global level, but their preferences may vary based on local region, market price and demand. However, because of human evolution and expansion, the demand for fish is increasing day by day and by 2050, the sector needs to double its current production to meet global fish demand. To address the nutritional needs of the expanding fish consumption population, the aquaculture sector must achieve a blue revolution – through the implementation of intensive culture systems to increase the production of fish and marine products. In the 1980s, the sector has initiated intensification with the introduction of quality feed, hatchery-produced seed, aeration devices and other pond and fish health management techniques. The aquaculture sector has many positive aspects such as i) minimal carbon emissions among the food production sectors, ii) an efficient system for producing animal protein (in a world facing protein shortage), iii) the generation of organic products, and iv) the capacity to boost economies in developing nations (where 95% of fishers and farmers reside). Therefore, the wise use of existing natural resources, in aquaculture production systems is crucial to achieve future production targets.

The aquaculture sector, including both marine and freshwater sectors, needs to intensify its culture systems by adopting diversification, eco-friendly hatcheries and farming practices. The current challenge faced by commercial aquaculture systems is the lack of sufficient of high-quality seeds. The sector had developed various seed production technologies like induced breeding protocols, selective breeding programmes, SPF and SPR seed production, etc. to overcome this challenge. However, the above-mentioned seed production technologies are more sophisticated, cost ineffective and time-consuming in terms of standardization. Therefore, the sector needs an alternative seed production technology to eliminate unhealthy seeds during the production process and yield a high-quality seed strain that will attain market size within a short culture duration. In this context, rearing normal fingerling at higher stocking densities with sub-optimal level of feeding and fertilization for 8-12 months leads to the production of stunted fish seed. This stunted seed or yearling (100-150 g) can be stocked in production ponds to achieve more production than normal fish seed. Compared to normal fish seed, stunted fish seed display faster growth, attain marketable size in a shorter period, less vulnerability to diseases, higher survival and better feed utilization patterns. Presently, stunted yearlings have a higher market demand, as they require a shorter culture duration to reach the marketable size.

A distinctive characteristic of stunted fish seed is their compensatory growth (CG) response in grow-out conditions. Upon release into optimal rearing conditions, stunted seeds display CG, which results in a faster growth rate than the normal fingerling. In the CG phase, fish exhibited accelerated growth when favourable conditions were restored after a period of growth depression. CG is characterized by hyperphagia, high growth rate, enhanced feed utilization, higher mitogen production and improved feed conversion efficiency. CG has been widely studied and described in both marine and freshwater fish due to its possible application in aquaculture. CG is an essential topic in aquaculture research because of its potential in feed management and production enhancement. During optimum feeding, stunted fish showed increased appetite which was considered the reason for faster growth and better feed utilization. Therefore, stunted seed which display better CG is highly preferred by aqua-farmers. However, before starting commercial level stunted seed production of any fish species, a suitable candidate species must be identified, and its optimum duration of stunting also needs to be addressed for maximizing the production and profitability. The post-stunting CG response depends on the duration and severity of growth suppression and varies among species. Currently, there is a lack of information on the impact of various stunting durations on compensatory growth, physiological changes and proximate composition of fish species. Therefore, based on field level expertise in this sector, we developed a comprehensive book that explores the effects of stunting on growth, physiological responses and nutritional changes occurring in various fish species during the stunting and post stunting phases. This approach aims to provide a deeper understanding of compensatory growth (CG) in fishes.

**ABSTRACT**

Compensatory growth (CG) is an elevated growth rate often observed in fish that have previously experienced stress and returned to normal conditions. To induce CG responses, fish must undergo a catabolic phase, in which they utilize endogenous energy reserves. In nature, fish encounter starvation due to food limitations, migration and predation which represents the catabolic phase. In the natural environment, fish commonly experience starvation because of constraints on food resources, migration, and predation, which collectively represent the catabolic phase. In aquaculture, the catabolic phase is achieved through stunting practices such as feed-restrictions, environmental manipulation and crowding stress. When fish experience the catabolic phase in captivity, they undergo various behavioural, physiological and biochemical changes to cope with the altered environmental conditions. Behavioural changes include reduced swimming and locomotion activities. Physiological adjustments involve metabolic changes such as reduced circulation of proteins, antibodies, enzymes and other molecular compounds. In biochemical alterations, fish utilize endogenous energy resources, such as lipids and proteins, which affect their overall nutritional composition. However, when stressed fish return to favourable conditions, they exhibit a CG response and rapidly restore their lost body weight, metabolic compounds and endogenous energy reserves. The effectiveness of the CG response can vary significantly depending on several factors, including the specific fish species, duration and severity of the stunting practice, as well as the conditions during the refeeding phase. This phenomenon has been harnessed in aquaculture to produce stunted fish seed. Extensive research on CG responses in fish over the past few decades has yielded inconsistent results, fostering debate over the practical application of CG response in aquaculture. To better understand and potentially leverage this phenomenon in aquaculture practices, it is crucial to critically examine the physiological changes that occur in fish during both stunting and post-stunting phases. This book aims to provide a comprehensive analysis of the actual changes occurring in fish during the stunting and post-stunting phases and explore the potential applications of CG responses in aquaculture, offering insights for more efficient and sustainable fish farming practices.

Keywords: stunting; restricted feeding; stress response; growth; physiological response; nutritional quality.

1. **INTRODUCTION TO COMPENSATORY GROWTH IN FISH**

***Introduction***

In the past two decades, the consumption of healthy and nutritious food has increased significantly, especially intake of fish, which is the cheapest source of nutritious food. In the meantime, from 1961, the average annual food fish consumption (3.2%) surpassed the global population growth (1.6%) and other terrestrial meat consumption (combined - 2.8%), except poultry (4.9%) (FAO, 2018). The expansion of fish consumption patterns, due to an increase of health-conscious consumers, has placed immense pressure on the fish production sectors. However, in recent years, the supply of fish has reduced and fishery resources are in a severe crisis throughout the world (Watson et al., 2014). Aquaculture, a major agricultural sector that redefines fish production, has grown rapidly and contributes to food security through domestic consumption and economic growth through the export trade (Anderson et al., 2017). In 1970, aquaculture contributed only 4% of the total fish production; however, the technological interventions implemented in the aquaculture sector, from the 1980’s to the present, led to a blue revolution and surpassed capture fisheries production (FAO, 2022). Among the major technological interventions, hatcheries, the commercial captive seed production units, have played an important role in achieving the blue revolution in aquaculture through their quality seed supply. However, the poor management practices employed in hatcheries, coupled with the environmental implications imposed by climate change, have placed huge pressure on the production of good quality seeds. On the other hand, the advancement of intensive fish culture practices over the past three decades has necessitated high quality seeds as stocking material for grow-out practices.

***Stunted fish seed***

The stunted fish seed production technique, harvesting of larger size seed than normal fingerling, is considered one of the most suitable techniques, as it yields quality seed rather than the quantity of seed (Nandeesha et al., 2013). Based on the stunting duration, the stunted seed size may vary up to 50-150 g. In general, stunted seeds are produced by inflicting crowding stress (stocking a greater number of seeds in a limited area), restricted feeding (feeding sub-optimal ration to fish) environmental stress (rearing of fish in unfavourable environmental conditions) or a combination of these conditions (Ali et al., 2003). Most farmers have adopted a combination of stocking density and restricted feeding conditions for stunted seed production. Fish farmers are practicing a stocking density of 25000 to 100000 seeds/ha and a sub-optimum level (only to survive) of feeding to stunt the fish seed (Nandeesha et al., 2013). The aim of stunting is to remove weak and sick fry during seed production and to produce healthy larger size fish seed for grow-out culture (Jobling, 2010). In the evolutionary context, stocking of stunted seed in aquaculture practices is becoming more popular, as they possess better survival, disease resistance and can withstand a wide range of environmental fluctuations (Ravi et al., 2012). Contradictory to this, Raina and Sachar (2014) recommended that prolonged feed deprivation, as a stunting practice, should be avoided in aquaculture practices since they produce unhealthy seeds. Additionally, in carps, the early maturation of stunted yearling, in grow-out culture conditions, is considered a major problem, as it negatively affects growth performance and flesh composition (Charan et al., 2012). In contrast, Biswas et al.(2015) suggested that stunted seed production of commercial fish species is a practical solution for addressing existing challenges in the aquaculture industry. However, stunting could be a viable option for fish species that exhibits late maturation (>3+ years). Amid these controversies, what makes the stunted seed more special? Does it enhance the aquaculture production? Can it exhibit accelerated growth compared to normal fish seeds? Can they demonstrate superior survival rates in commercial aquaculture systems compared to normal seeds? The single answer for all these questions is “COMPENSATORY GROWTH”.

***Compensatory growth in fish***

Compensatory growth (CG), an elevated growth rate, is often associated with fish, that have been previously subjected to any stressed conditions and returned to normal conditions (Ali et al.,2003; Jobling, 2010; Won and Borski, 2013). Fish farmers believe that triggering the CG response under captive conditions, using economic feeding strategies and feed deprivation protocols, enhances aquaculture production. This principle is based on the proven fact that feed deprivation for some duration reduces the normal weight gain of fish which is compensated by a shorter duration of the grow-out phase (Mohapatra et al., 2017). Depending on the degree of recovery, three types of compensatory growth, i.e., over, complete and partial growth compensation, have been reported. In over-compensation, several cycles of feed deprivation and re-feeding resulted in a weight gain that exceeded that of fish fed continuously (Hayward et al., 1997). In complete compensation, fish previously subjected to food restriction achieve the same body mass as continuously fed fish (Kim and Lovell, 1995; Tian and Qin, 2003). Whereas, in partial compensation, food-restricted fish exhibit accelerated growth after the resumption of normal feeding but do not achieve the same body mass as continuously fed fish (Paul et al., 1995). To achieve the benefits of CG response under captive conditions, fish must undergo catabolic and anabolic phases. However, it is important to standardize the duration of catabolic and anabolic phases, as they adversely affect the growth and health status of cultured fish.

Catabolic phase, stunting phase or negative energy period, is essential for inducing CG response in fish (Won and Borski, 2013). Normal fish must experience a catabolic phase, where they spend endogenous energy reserves, which convinces the fish to undergo a CG response once feeding resumes in the anabolic phase. In nature, fish normally encounter starvation due to limitations in food sources, migration and predation all of which act as a catabolic phase (McCue, 2010; Ashouri et al.,2013; Bar, 2014). In aquaculture practices, the catabolic phase is achieved by stunting practices, keeping fish in feed-restricted conditions or environmental manipulations or by imposing crowding stress (Mohapatra et al.,2017). When stunted fish return to normal feeding conditions, the re-alimentation or re-feeding phase, results in hyperphagia, an elevated food consumption rate, leading to better growth performance (Ali et al.,2003). In general, the CG response of fish, under favourable aquaculture conditions, depends on the duration and severity of the imposed stunting practice. Depending on the stress experienced by the fish during the feed deprivation phase, they display the CG response during the satiation phase.

Generally, when the catabolic phase is inflicted under captive conditions, fish undergo various behavioural, physiological and biochemical changes to cope with the changes in environmental conditions. Subsequently, the same stressed fish, when returned to favourable conditions, rapidly restored their lost body weight, metabolic compounds and endogenous energy reserves, which makes stunting a quality seed production technique. However, the changes that occur in fish during the starvation and re-alimentation phases are yet to be unleashed, which creates a dispute on the application of CG responses in aquaculture. This book critically reviews the actual physio-metabolic changes that occur in fish during the feed restriction and re-alimentation phases.

1. **GROWTH PATTERN OF FISH IN STUNTING PHASE**

***Fish growth pattern***

Fish, a poikilothermic aquatic animal, continues to grow with increasing in age. However, farmers rear fish for a certain period, 6-12 months, to produce protein-rich food and obtain economic benefits. Moreover, farmers aim to maximize profits with minimum input and maximum output. Therefore, fish growth is a vital factor in aquaculture practices. Besides many economic reasons, the onset of maturation in fish plays a major role, which slows down the growth rate as vast amounts of energy derived from feed gets diverted to gonadal development (Enberg et al., 2008). Furthermore, nutritional and environmental factors play an important role in the regulation of fish growth (Dutta, 1994). Therefore, fish nutrition, providing balanced supplementary feed under captive conditions, plays a significant role in augmenting aquaculture production.

***Growth of fish in stunting phase***

In contrast, restricted feeding or starvation, a strategy mimicked from nature, is followed in captive conditions to induce nutritional stress. In the absence of supplementary feed, fish breakdown and utilize the energy stored in old molecules and tissues which play a crucial role in inducing CG response (Enberg et al., 2008; Won and Borski, 2013). Ali et al. (2003) mentioned that larger fish may require more extended periods of starvation, to induce the 'nutritional stress,' than smaller fish to provoke a compensatory growth (CG) response.

When fish are subjected to stunting, their metabolic activity and energy expenditure are reduced, which affects their normal growth patterns. However, contrary reports are available for fish subjected to restricted feeding or starvation (Table-01). In many fish, feed restriction or starvation resulted in significant reduction in body weight gain and specific growth rate (Zamal and Ollevier, 1995; Zhu et al., 2003; Zhu et al., 2005; Rahimi et al., 2010; Bavcevic et al., 2010; Chatzifotis et al., 2018). Furthermore, fish growth in the catabolic phase is profoundly influenced by the type of feeding restriction imposed (Jobling et al., 1994). Lingam et al. (2019b) reported that stunting of milkfish for different durations (4, 8 & 12 months) resulted in various sizes of stunted seeds at the end of stunting phase. In the stunting phase, stunted fish seeds grow slower and display significantly reduced body weight gain and specific growth rates compared to their normally fed counterparts. In general, food type and ration size largely affect fish growth in captive conditions (Li et al., 2014). Under normal feeding conditions, excess or remaining energy is stored as an energy reserve, after fulfilment of the metabolic energy demand, leading to body growth. In contrast, the metabolic energy demand of feed restricted fish is satisfied by the minimum available energy (feed), which reduces normal growth of the fish. Furthermore, prolonged activation of the hypothalamus pituitary inter-renal (HPI) axis, as a stress mitigation response, creates a negatively aaffects the energy balance, between energy intake and utilization, which indirectly reduces growth (Morales et al., 2004; Huntingford et al., 2006; Won and Borski, 2013). The lower body weight of the stunted fish compared to their counterparts was due to the suboptimal feeding regime imposed during the stunting phase.

**Table 1 Effect of stunting on the growth performance of fish**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No** | **Type of stunting imposed** | **Species** | **Effects** | **References** |
|  | Feed deprivation (1-3 weeks) | Atlantic Cod  *Gadus morhua* | Significant reduction in the body weight, HSI and condition factor were noticed | Jobling et al. 1994 |
|  | Feed restriction (up to 9 weeks) | Channel catfish*,*  *Ictalurus punctatus* | Significantly reduced body weight and SGR | Kim and Lovell, 1995 |
|  | Starvation (up to 66 days) | African catfish*,*  *Clarias gariepinus* | Significant reduction in body weight, HSI and VSI values | Zamal and Ollevier, 1995 |
|  | Starvation (210 days) | Golden perch *Macquaria ambigua* | HIS and GutSI were significantly reduced | Collins and Anderson, 1995 |
|  | Starvation (10 weeks) | White sturgeon Acipenser *transmontanus* | Significant reduction in body weight, HSI and VSI | Hung et al. 1997 |
|  | 4-week of starvation | Sea bass  *Lates calcarifer* | Significant reduction in body weight and SGR | Tian and Qin, 2003 |
|  | Fasting (up to 14 days) | Rainbow trout*,*  *Oncorhynchus mykiss* | Final body weight, SGR and food intake were significantly reduced | Nikki et al. 2004; Rahimi et al. 2010 |
|  | Starvation (up to 32 days) | Atlantic halibut*,*  *Hippoglossus hippoglossus* | Significant reduction in body weight | Heide et al. 2006 |
|  | 4 weeks of fasting | Nile Tilapia *Oreochromis niloticus* | Body weight and SGR were significantly reduced | Abdel-Tawwab et al. 2006 |
|  | Restricted feeding ration (up to 8 weeks) | Pangasius (*Pangasius bocourti*) | Significant reduction in body weight, SGR, survival and increase in FCR | Jiwyam, 2010 |
|  | Fasting (up to 14 days) | Red porgy  *Pagrus pagrus* | No change in body weight, but significant reduction in body length and SGR were noticed | Caruso et al. 2012 |
|  | Short term cyclic feed deprivation (2 days feed deprivation) | Mozambique tilapia, *Oreochromis mossambicus* | Final body weight, weight gain and SGR were lowered | Gabriel et al. 2018 |
|  | Short term feed starvation (1 & 2 days feed deprivation) | Indian pompano (*Trachinotus mookalee*) | Significant reduction in body weight, SGR and daily feed intake in 2 days starvation | Xavier et al. 2023 |

***Feed utilization of fish in stunting phase***

In aquatic animal-based feed experiments, feed utilization capacity was assessed by measuring the feed conversion ratio, feed efficiency ratio and protein efficiency ratio. It was concluded that fish had better growth capability when they displayed better feed utilization capacity. In most published studies, better FCR, FER and PER values have been associated with better body weight gain in fish. However, if we calculate the feed utilization pattern of fish experiencing restricted feeding, different results can be obtained. The contrary is due to the availability of limited nutrients and changes in fish behaviour under changed environmental conditions such as restricted feeding. In nature, when the resource (energy) is limited, either it should spend well, or the fish should adapt to changing conditions. Here, the fish perform both the tasks simultaneously. Fish in stunting phase, unlike normally fed fish, reduce their locomotion and other energy expensive activities – as adaptive measure - which ultimately reduce their basal metabolic activity and increase their chance of survival. Even though restricted feeding produces little weight gain in fish under limited nutrient availability, proper utilization of nutrients coupled with altered metabolic activities results in better FCR, FER and PER of fish in the stunted phase.

***Survival of fish in stunting phase***

Survival, the existence of life under adverse conditions, is a challenging task for fish, especially under starvation or feed-restricted conditions. The ability of fish to withstand a prolonged period of stunting varies among species, depending on their capacity to utilize endogenous energy reserves and lifestyle adaptation in stunting (Collins and Anderson, 1995). Prolonged stunting had significantly reduced the survival of milkfish (Baliao et al., 1987; Lingam et al., 2019b) and Nile tilapia (Abdel-Tawwab et al., 2006). In contrast, channel catfish (*Ictalurus punctatus*) and traira (*Hoplias malabaricus)* exposed to prolonged feed restriction did not show any significant reduction in survival rate with normally fed fish (Kim and Lovell, 1995; Rios et al., 2002). This discrepancy in outcomes is attributed to the stocking of fish with diverse life stages, encompassing varying sizes, for stunting. Stocking smaller fish leads to significant reduction in survival. Smaller fish (fish fry) lack sufficient endogenous energy reserves, for utilization during stunting, and, consequently, require more energy to meet metabolic demands rendering their survival more challenging. In contrast, larger fish (adult fish) have more stored endogenous energy reserves and their metabolic energy demand can be effectively regulated in the stunting phase, which improves their chances of survival. The stunting duration is another factor that has a significant effect on fish survival during the stunting phase. Short-term stunting can be managed by metabolic changes (Joshi, 1973) whereas prolonged starvation cannot be regulated by metabolic changes and may lead to fish death (Love, 1970; Ali et al., 2003).

**3. LENGTH-WEIGHT RELATIONSHIP OF FISH IN STUNTING PHASE**

***Introduction***

The length-weight relationship and condition factor (CF) are two important indicators that are frequently used in aquaculture and fisheries management. The length-weight relationship (LWR) is a mathematical model, W = aLb, used to estimate fish weight based on its length, where W is the total weight, L is the standard length, and a and b are constants (Shrestha et al., 2023). It helps to assess the growth patterns and health condition of fish populations, facilitating comparisons among different fish populations by correlating body weight with length (Soinski et al., 2020). LWRs are essential for fisheries management, stock assessments, and biomass estimation, as they reflect the physiological states influenced by ecological factors (Zlateva, 2017). This relationship aids in understanding the population dynamics and comparing different fish populations across time and space.

***LWR of stunted fish***

The length-weight relationship (LWR) of fish under restricted feeding conditions is a critical aspect of aquaculture, influencing growth performance and overall health. Similarly, CF is a tool used to estimate the well-being of an individual fish, and an optimal CF denotes a good length-weight relationship of fish (Schneider et al., 2000). However, in most cases, stunted fish had lower condition factor. Starvation of brown trout (*Salmo trutta*) and Atlantic cod (*Gadus morhua*) resulted in lower CF (Jobling et al., 1994; Johnsson and Bohlin, 2005). Short-term starvation in rainbow trout (*Oncorhynchus mykiss*) and European eel (*Anguilla anguilla*) induced a change in CF (Vosyliene and Kazlauskiene, 1999; Caruso et al., 2010). On the other side, long-term starvation (80 days) in channel catfish (*Ictalurus punctatus*) significantly reduced the condition factor (Luo et al.*,* 2009). Adjustment of endogenous energy reserves and lack of proper nutrition are the two major factors that affect changes in condition factor of fish during restricted feeding.

Previous studies indicate that restricted feeding can initially lead to decreased growth rates, as seen in juvenile red tilapia, where prolonged feed restriction resulted in lower condition factors and growth metrics (Robisalmi et al., 2021). However, compensatory growth may occur at post-restriction feeding, although studies indicated that this is not always guaranteed, as evidenced by the lack of compensatory growth in red tilapia after re-feeding (Robisalmi et al., 2021). LWR can exhibit both positive and negative allometry, which are influenced by feeding levels and stocking densities. Restricted feeding at 1.0% body weight leads to lower growth, whereas 1.5% promotes better growth in catfish, highlighting the importance of adequate feeding for optimal growth (Afia, 2023). Negative allometric growth was recorded in *Channa striata* larvae, with b values ranging from 2.006 to 2.627, during delayed initial feeding which significantly affected the growth performance and survival rates under restricted feeding conditions (Karthy et al., 2022). Accurate LWR estimations are essential for effective aquaculture management, allowing for better prediction of biomass and feed requirements (Moslen and Miebaka, 2017).

**4. BIOCHEMICAL CHANGES IN FISH BLOOD DURING STUNTING PHASE**

***Introduction***

Starvation and feeding strategies significantly affect the physiological, biochemical and metabolic activities of fish (Falahatkar, 2012). Similar to the changes in growth parameters, physiological changes were also observed in fish during stunting phase.

Under altered environmental conditions, fish undergo behavioural and physiological changes, including blood metabolites, in the stunting phase to withstand energy shortages (Pottinger et al., 2003). Once the stunting effect overcomes the behavioural changes and primary endogenous energy resources stored in tissues, fish think of its secondary endogenous energy resources. In African catfish, food deprivation significantly reduced blood haematocrit values (Zamal and Ollevier, 1995). Similarly, in traira (*Hoplias malabaricus)*, prolonged duration of stunting (150 and 240 days) reduced the red blood cell count (RBC), mean corpuscular volume (MCV) and haematocrit value (Rios et al., 2005). However, very few studies have been conducted on the effects of stunting on haematological changes in fish during the stunting phase. On the other side, many studies have emphasized the stunting effect on serum biochemical components in fish (Table 2).

**Table 2 Effects of stunting on biochemical changes in fish blood**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No** | **Type of stunting imposed** | **Species** | **Effects** | **References** |
|  | Starvation (up to 154 days) | Atlantic Cod  *Gadus morhua* | No changes in the plasma protein but significant reduction in glucose was observed | Black and Love, 1986 |
|  | Fasting (2 months) | Common carp  *Cyprinus carpio* | Glucose and lactate levels in plasma were significantly increased | Blasco et al. 1992 |
|  | Starvation (up to 66 days) | African catfish*,*  *Clarias gariepinus* | Significant reduction in body weight, HSI and VSI values. Significant reduction in haematocrit value | Zamal and Ollevier, 1995 |
|  | Starvation (10 weeks) | White sturgeon Acipenser *transmontanus* | Significantly reduced blood glucose and no change in protein were noticed | Hung et al. 1997 |
|  | Long term feed deprivation (up to 240 days) | Trahira fish  *Hoplias malabaricus* | RBC, haemoglobin and Haematocrit values were significantly lowered | Rios et al. 2002; Rios et al. 2005 |
|  | 4 weeks of fasting | Nile Tilapia *Oreochromis niloticus* | Significantly lower Hb and RBC were noticed | Abdel-Tawwab et al. 2006 |
|  | Starvation and temperature (60 days and 17-26°C) | Meagre*,*  *Argyrosomus regius* | Significant reduction in plasma glucose and blood lipid concentrations | Chatzifotis et al. 2018 |
|  | Restricted feeding and high stocking density (up to 12 months) | Milkfish,  *Chanos chanos* | Significant reduction in serum components including glucose and cortisol were noticed | Lingam et al. 2019a |

***Serum biochemical changes in stunted fish***

Serum biochemical components, total serum protein, albumin and globulin, are primarily needed for efficient metabolism and immune responses in fish (Kumar et al., 2005). Therefore, the assessment of serum biochemical components provides essential information about the health and physiological responses of fish in feed-restricted conditions (Mohapatra et al., 2017). In many cases, among the various serum biochemical components, proteins are the constituents that are first reduced in stress situations. Short-term starvation in Siberian sturgeon did not yield any significant difference in total plasma protein between starved and continuously fed groups (Ashouri et al., 2013). Similarly, in rainbow trout and sturgeon after 72 days of starvation and in milkfish 120 days of feed restriction did not produce any change in plasma protein levels (Furne et al., 2012; Lingam et al., 2019a). In contrary, 5-week of fasting in Atlantic cod (*Gadus morhua*) and an extended period of feed restriction (above 150 days) in milkfish produced significant reductions in plasma protein levels (Kamra, 1966; Lingam et al., 2019a). In fish, plasma protein is used as a fourth energy source, after the exhaustion of endogenous energy reserves such as glycogen, glucose and lipids (Eslamloo et al., 2017). When fish are exposed to chronic stress and prolonged periods of stunting, they require more energy in the later phase which leads to the catabolism of blood proteins, a non-carbohydrate source for gluconeogenesis, thus reducing serum protein levels.

When we look into the plasma proteins albumin and globulin are the two important components present in fish blood. In addition to blood protein catabolism, changes in albumin and globulin levels have been recorded in fish. Previous studies have reported that, among the plasma proteins, albumin gets reduced first followed by globulin in fish during the fasting stage (Navarro and Gutierrez, 1995; Yengkokpam et al., 2012; Azodi et al., 2014; Li et al., 2016). Globulin, an immunoglobin component, plays a crucial role in the innate defense system of fish (Ellis, 1999); thus, the reduction of globulin levels leads to reduced humoral and cellular immunity during the stunting phase. Besides many published results on the effect of stunting on serum biochemical changes in fish, there is still, controversy and lack of information in understanding the effect of stunting on serum components, which needs to be accomplished in the future to provide better health conditions under captivity.

***Stress enzymes in stunted fish***

The health condition of fish in captivity is regulated by various internal and external stress factors, which also affect blood components. Serum cortisol and glucose levels have been used as general indices for primary and secondary stress responses, respectively, in fish (Porchas et al., 2009). Normally, the nutritional status of fish can influence the circulation of stress indicators such as glucose and cortisol, in fish blood (Holloway et al., 1994). Under nutritional stress, fish must identify endogenous substrates for energy mobilization, which is regulated by elevated plasma cortisol and glucose levels (Barcellos et al., 2010). Although, both are stress indicators, contradictory reports are available regarding their circulation in blood during stunting. However, in fish, during starvation, an increase, decrease, or no change in cortisol levels has been observed (Pottinger et al.,2003; Bar, 2014). On the other side, fish maintain steady blood glucose concentrations during prolonged periods of food deprivation (Navarro and Gutierrez, 1995). However, the response of blood glucose and cortisol levels during stunting depends on the species and duration of stunting, especially the length of food deprivation (Peterson and Small, 2004; Caruso et al., 2010; Kulkarni and Barad, 2015). In milkfish, 4-month of food deprivation did not affect glucose levels, however, when the food deprivation period was extended further (8 and 12 months), they displayed increased circulation of cortisol and glucose in their blood (Lingam et al., 2019a).

Under stress conditions, fish activate the HPI axis and increase the production and circulation of cortisol, which modifies energy metabolism (Li et al., 2016). Cortisol plays multiple roles in fish energy metabolism, especially under feed-restricted conditions, through lipolysis (Caruso et al. 2010), proteolysis (Bar, 2014; Philip et al., 2018), and gluconeogenesis (Borowiec et al., 2015). Previous studies in rainbow trout (Heming and Paleczny, 1987; Furne et al., 2012), sturgeon sp. (Hung et al., 1997; Furne et al., 2012), channel catfish (Peterson and Small, 2004) red porgy (Caruso et al., 2012) and milkfish (Lingam et al., 2019a) have either decreased or no change in glucose circulation during short term starvation or in the initial phase of extended stunting. Similarly, the above studies found either elevated cortisol circulation or lipid degradation in the carcass, except for Heming and Paleczey (1987). The study did not analyze either cortisol or carcass lipids which clearly indicates the role of cortisol in lipolysis during stunting. Generally, fish follow the lipostat model, which uses lipids as the primary energy source during feed restriction. Higher circulation of cortisol catalyzes lipolysis, which increases the catabolism of lipids into free fatty acids (FFAs), thus increasing the circulation of FFAs in the bloodstream and inhibiting glucose utilization and release by the liver (Sheridan, 1988; Collins and Anderson, 1995). Once lipids are exhausted, fish must shift to the next energy source, protein, which requires cortisol for breakdown. A sharp increase in cortisol levels and no change in glucose levels were found in European eel and milkfish after 3 months of fasting and 4 months of stunting, respectively, due to lipid exhaustion (Dave et al., 1975; Lingam et al., 2019a). To break down muscle proteins (proteolysis), fish require elevated circulation of cortisol in their blood (Bar, 2014). However, after the depletion of muscle lipids and protein, fish promote gluconeogenesis, using blood proteins as a non-carbohydrate source for energy production i.e. glucose, which also requires cortisol and increases glucose circulation in the blood. Therefore, elevated cortisol and glucose levels have been observed in fish to meet the increased energy demand during the later phase of prolonged stunting.

**5. IMMUNE AND ANTI-OXIDANT DEFENCE CHANGES IN FISH DURING STUNTING PHASE**

***Introduction***

Immunity is a significant physiological defense mechanism in fish, to evade pathogen infection, and fish have a strong tolerance to dietary restriction. However, it also has negative effects on the immune function of fish (Martin et al., 2010; Kiron, 2012). Additionally, the response of the immune system to stress depends on the intensity and duration of the stress (Tort, 2011). In general, the production of antibodies, proteins and other immune-related metabolites consumes vast amounts of energy (Tort, 2011). However, the availability of lower energy in the catabolic phase devastates the defense mechanisms of fish.

***Respiratory burst activity in stunted fish***

Respiratory burst activity, the production of free radical oxidative compounds by monocytes and neutrophils, is an imperative cellular immune defense mechanism against pathogens in fish (Anderson and Siwicki, 1995). Feed restriction experiments conducted in Senegalese sole (Salas-Leiton et al., 2010), European sea bass and blackspot sea bream (Caruso et al., 2011) and milkfish (Lingam et al., 2019a) found significantly lower respiratory burst activity. Generally, the raised neuroendocrine factor, cortisol, as a stress response during food restriction could reduce respiratory burst activity (Huntingford et al., 2006; Tort, 2011). Additionally, in the stunting phase fish spend less energy on the production of immune compounds, as a physiological adaptation, leading to immunosuppression.

***SOD and CAT activities in stunted fish***

Superoxide dismutase (SOD) and Catalase (CAT) are important antioxidant defense systems in fish that maintain physiological homeostasis by hunting the reactive oxygen species (ROS) which prevent oxidative stress impairment (Shin et al. 2010). An imbalance between the oxidation process and anti-oxidant defense creates oxidative stress, which can damage tissues and affect biomolecules (Furne et al., 2009). Therefore, a slight change in the oxidative defense system, under the pro-oxidant conditions suchas nutritional deficiency, reduces the growth and immunity of fish (Morales et al., 2004). Usually, SOD and CAT activities are affected by extrinsic factors such as, food availability, presence of toxins and pathogens and environmental conditions (Felton, 1995). During the stunting phase, fish consume antioxidants (lipids) that are stored in their tissues leading to ROS production which creates oxidative stress (Gomi and Matsuo, 1998). Elevated production of ROS compounds during lipid hydrolysis, if not neutralized, impairs the redox status of the cell, leading to oxidative stress (Guderley et al., 2003; Pal and Maitra, 2018). On the other hand, as an adaptive mechanism to overcome oxidative stress, fish trigger the production of the anti-oxidant enzymes, SOD and CAT, which have been observed in Atlantic cod (Guderley et al., 2003), sea bream (Pascual et al., 2003), common dentex (Morales et al., 2004), salmon (Nakano et al., 2014) and milkfish (Lingam et al., 2019a). However, when the fish were exposed to extended period of feed restriction, they displayed elevated SOD and CAT activities in the initial phase, which decreased in the later phase. Under feed-restricted conditions, the activation of the antioxidant defense system depends on the availability of fat reserves in tissues. In the late phase of extended stunting, exhaustion of fat reserves leads to lower production of ROS compounds which also reduces SOD and CAT activities.

***Lysozyme activity in stunted fish***

Lysozyme, a non-specific innate immunity index, is a lytic peptide found in marine and freshwater fish that prevents the invasion of bacterial pathogens (Jiang et al., 2008). In general, under stress conditions, lysozyme activity depends on fish species, sex, size and environmental conditions. Also, the activity varies based on the tissue or organ in which the assay has been performed (Bowden, 2008). For example, sea bass starved for 31 days displayed significantly higher lysozyme activity in mucus and lower activity in kidney tissue (Caruso et al., 2011). In the same study, a similar pattern of lysozyme activity was observed in the mucus and plasma samples of blackspot sea bream, confirming the diverse activities of lysozymes in different tissues.

***MPO activity in stunted fish***

The innate immune system of fish plays a crucial role in microbial pathogen defence, which is suppressed at sub-optimal feeding frequencies (Li et al., 2014). Myeloperoxidae, a cell-based immune response in fish, produces bactericidal compounds (ClO-) from halide ions and H2O2 in the blood cells (Whyte, 2007). In some cases, damage to the antioxidant system, especially catalase activity, is compensated by MPO activity which neutralizes H2O2, a toxic oxidative compound, produced by the action of superoxide dismutase (Vera-Jimenez et al., 2013). Maintaining fish under prolonged periods of restricted feeding during stutned seed production leads to immuno-suppression (Ellis, 1999). Feed restriction in chinook salmon (fed at 40% and 60% satiation levels) and lower feeding frequency in blunt snout bream (1 and 2 times/day) significantly increased MPO activity (Alcorn et al., 2003; Li et al., 2014). Furthermore, Tort (2011) reported that stressor intensity and duration regulate the immune system. In shorter feed restrictions, elevated MPO activity has been noticed in fish. Under acute stress, the utilization of antioxidant compounds (lipids), as energy sources, leads to the production of free radicals and H2O2. MPO activity was increased to protect cells from these elevated oxidative compounds. In contrast, in the later phase of prolonged feed restriction, MPO activity is reduced due to elevated cortisol levels, which inhibits cellular immunity in fish. It has been well established that increased corisol levels decrease immune activity, especially myeloperoxidase activity, in fish (Palic et al., 2005; Sadhu et al., 2014).

Magnadottir (2006) stated that the synthesis of humoral components and immune cell production and maturation i.e. monocytes, leukocytes and neutrophils, demand more energy (nutrients); however, the lower availability of nutrients under restricted feeding, leads to immunosuppression in fish which adversely affects the proper functioning of the immune system. However, research on the substantial effects of feed deprivation on immunological responses in fish is limitted (Yengkokpam et al., 2016; Eslamloo et al., 2017). The below table also depicts the effect of stunting on the immune and anti-oxidant denfence system in fish (Table 3)

**Table 3 Effect of stunting on immune and anti-oxidant defence**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No** | **Type of stunting imposed** | **Species** | **Effects** | **References** |
|  | Fasting (up to 14 days) | Red porgy  *Pagrus pagrus* | Singificant increase in cortisol and no change in glucose were recorded. In kidney, lysozyme activity was significantly lowered | Caruso et al. 2012 |
|  | Periodic feed deprivation (up to 10 weeks) | Rohu  *Labeo rohita* | Lysozyme and albumin content were reduced. SOD and CAT activities were increased | Yengkokpamet al. 2012; Yengkokpamet al. 2013 |
|  | Restricted feeding and high stocking density (up to 12 months) | Milkfish,  *Chanos chanos* | A significant reduction in NBT, CAT, SOD, MPO and lysozyme were noticed | Lingam et al. 2019a |

**6. DIGESTIVE ENZYME CHANGES IN FISH DURING STUNTING PHASE**

***Introduction***

Biotic and abiotic factors influence growth under any conditions; however, in fish, ingestion and digestive capacity determine the maximum growth (Belanger et al., 2002). Digestion of ingested food in teleost fish is carried out by digestive enzymes secreted in the digestive tract. Generally, feeding practices followed in aquaculture activities significantly affect the activity of intestinal enzymes in the fish (Krogdahl and Bakke-McKellep, 2005). Therefore, in any feeding trial, examination of digestive enzyme activity is highly recommended because it is a reliable indicator of fish's digestive status and nutritional condition (Bolasina et al., 2007).

Macronutrients such as carbohydrates, proteins and lipids are digested and absorbed by the major digestive enzymes in fish: amylase, protease and lipase, respectively. Like mammalian amylase, fish amylases hydrolyse complex polysaccharides into simple monosaccharides, helping extract energy from the fish diet's excess carbohydrates (Krogdahl et al., 2005). Carbohydrate utilisation patterns vary significantly among fish species, and it has been found that warm water and herbivorous fish digest carbohydrates more efficiently than cold water and carnivorous fish (Wilson, 1994). Protein, a macronutrient composed of amino acids, is an expensive nutrient in the fish diet and is absorbed by protease enzymes that break down protein peptides into freely absorbable amino acids. Fresh and saltwater fish, especially carnivore fish, require high protein levels in their diets. However, proteolytic production was recorded higher in the gut of herbivores and omnivores than in the carnivorous fish due to their higher effective duration of proteolysis and exposure of fish diet to protease enzymes (Sire and Vernier, 1992). Lipid, energy supplementary nutrients in fish diets, plays a crucial role in the growth and survival of developing fish with the aid of lipases that emulsify complex fats into simple fatty acids and monoglycerides. Unlike mammals, many fish display higher lipase activity in the proximal and distal parts of the intestine; however, lipase activity progressively decreases in the distal part of the intestine (Tocher, 2012). Therefore, the effect of stunting on digestive organs and their enzyme activities is species-specific, and some studies have documented the impact of stunting on intestinal organs and digestive enzyme activities in fish (Table 4).

**Table 4 Effect of stunting on digestive enzyme activity**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No** | **Type of stunting imposed** | **Species** | **Effects** | **References** |
|  | 40 days of fasting | Atlantic salmon  *Salmo salar* | Intestinal mass and enzymes activities were significantly reduced | Krogdahl and Bakke-McKellep, 2005 |
|  | Starvation (up to 72 days) | Sturgeon  *Acipenser naccarii* and Rainbow trout *Oncorhynchus mykiss* | Amylase, protease and lipase activities were significantly reduced at the end of starvation | Furne et al. 2008 |
|  | Periodic feed deprivation (up to 10 weeks) | Rohu  *Labeo rohita* | Amylase and lipase activities were significanlty reduced. | Yengkokpamet al. 2013 |
|  | Restricted feeding and high stocking density (up to 12 months) | Milkfish,  *Chanos chanos* | Significant reduction in major digestive enzyme activties | Lingam et al. 2019b |

***Digestive enzyme activity in stunted fish***

In the stunting phase, fish display a rapid decrease in major digestive enzyme activities (Krogdahl and Bakke-McKellep, 2005). Like other animals, the digestive enzyme activity of fish varied based on their anatomical structure, physiological condition and behavioural differences seen among the different fish. For example, starvation in Japanese flounder significantly reduced lipase activity (Bolasina et al.,2006). In the case of sturgeon and rainbow trout, 72 days of feed restriction did not minimise amylase activity but significantly affected protease and lipase activities (Furne et al., 2008). In contrast, periodic feed deprivation in rohu did not affect lipase activity but significantly increased protease and amylase activities (Yengkokpama et al., 2013). Similarly, Atlantic cod starved for 10 to 25 days displayed similar protease activities, trypsin and chymotrypsin, in the intestine (Gildberg, 2004). The above examples reveal that feeding restriction or starvation effects are enzyme-specific and species dependent.

In general, feed restriction in fish substantively affects the digestive organs. Under starvation conditions, digestive enzyme activity in fish is altered by changes in gut tissue, morphology and cell number (Krogdahl and Bakke-McKellep, 2005). Fish experiencing feed restriction secrete reduced digestive enzymes in the gut, affecting the digestive system's efficient functioning (Windell, 1966). When fish are starved or receive poor quality feed, this can result in decreased gastrointestinal tract function (GIT). In this place, metabolically more active tissue is present (Abolfathi et al., 2012). In plaice (*Pleuronectus platessa*), 35 days of starvation significantly affected the normal functioning of gastrointestinal tissues (Jobling, 1980). Starvation significantly reduced digestive enzyme activity in tambaqui (*Colossoma macropomum*) (Kohla et al., 1992), roach (*Rutilus rutilus caspicus*) (Abolfathi et al., 2012), catla (*Catla catla*) (Pal and Maitra, 2018) and rohu (*Labeo rohita*) (Dar et al., 2018).

The duration of stunting and the type of feed used are other major factors that influence digestive enzyme activity in the stunting phase. Short-term starvation for 25 days in Atlantic cod did not reduce protease activity (Gildberg, 2004). Similarly, milkfish stunted for 4 months showed no change in protease activity. However, the same fish stunted for 8 to 12 months, significantly reduced protease activity (Lingam et al. 2019b). During short-term feed restriction, fish adjust their metabolic activity to cope with situations that may not significantly affect the digestive organ function. The same fish under extended feed restriction may reach the metabolic fatigue stage and display various tissue level changes such as reduction in intestine length and diameter, pyloric ceaca and intestinal microvilli, which directly affect the proper digestion of food by decreasing digestive enzyme activities (Windell, 1966; Gas and Noailliac-Depeyre, 1976). Comparably, under prolonged starvation, the digestive enzyme activities of salmon (Greene, 1926), bluegill sunfish (Windel, 1966) and brown trout (Elliot, 1972) are affected by gut tissue atrophy, which decreases villi and cells. On the other hand, a study conducted by Lingam et al. (2019b) in milkfish reported that amylase activity was not influenced by the duration of stunting and explained that the use of a carbohydrate-rich diet, de-oiled rice bran with 66% carbohydrate, was the reason for stable amylase activity throughout the study. The results of their study proved that fish could adjust their specific digestive enzyme activity based on the nutritional value of the supplementary diet provided in the restricted feeding phase to extract maximum energy from the diet.

**7. NUTRITIONAL QUALITY CHANGES IN FISH DURING STUNTING PHASE**

***Introduction***

In recent years, consumer preferences for fish selection have shifted towards criteria based on their nutritional value, such as fat deposition, protein content, muscle texture and flavour rather than external characteristics such as appearance and size (Fauconneau and Laroche, 1996; Sahu et al., 2000). However, the growth of the aquaculture production sector with the help of antibiotic drugs and chemicals is deeply concerned with the quality of the produced fish. Among the various intrinsic parameters, carcass chemical composition and fat content play a major role in determining fish quality.

The relationship between changes in biochemical components and starvation in fish was first established in the late 60’s (Love, 1970). In fish, biochemical changes in the carcass have been assessed to study the energy metabolism rate and determine the reserved energy utilization pattern during starvation (Jobling, 1980). In the absence of supplementary energy, fish display biochemical response, after behavioural and physiological response, by consuming the reserved energy stored in the tissues, which leads to nutritional depletion in the carcass (Pinder et al., 1992; De Coen and Janssen, 1997). In general, carcass quality of fish is controlled by a set of inherent factors (chemical composition, fat content, texture, *etc*.), however, the inherent factors are highly influenced by some of the external factors (feeding, environmental conditions, handling stress, *etc*.) (Johnston, 1999). Therefore, it is recommended to study the carcass composition of fish, under any experimental conditons, to determine their nutritional condition, which provides a better understanding of the biochemical response of fish to a particular situation. Most of the previous studies have also targeted the effects of stunting on the nutritional composition of fish, and they suggest that the nutritional utilization pattern of fish varies among species. Some studies conducted in fish reveals the relationship between nutritional composition and stunting effects which are listed in the Table 5.

**Table 5 Effect of stunting on carcass quality of fish**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No** | **Type of stunting imposed** | **Species** | **Effects** | **References** |
|  | Starvation (up to 154 days) | Atlantic Cod  *Gadus morhua* | Decrease in lipid, protein and glycogen and increase in moisture content were noticed | Black and Love, 1986 |
|  | Starvation (up to 66 days) | African catfish*,*  *Clarias gariepinus* | Significant decrease in moisture and saturated fatty acid and increase in moisture and ash content | Zamal and Ollevier, 1995 |
|  | Starvation (210 days) | Golden perch *Macquaria ambigua* | Reduction in lipid, protein and glycogen were noticed | Collins and Anderson, 1995 |
|  | Starvation (10 weeks) | White sturgeon Acipenser *transmontanus* | Significant increase in moisture and decrease in lipid and protein contents were found | Hung et al. 1997 |
|  | Feed deprivation (2 & 4 weeks) | Gibel carp,  *Carassius auratus gibelio* | Lipid and lean body mass was significantly lowered | Xie et al. 2001 |
|  | 4-week of starvation | Sea bass  *Lates calcarifer* | Significant reduction in moisture, lipid and protein | Tian and Qin, 2003 |
|  | 4 weeks of fasting | Nile Tilapia *Oreochromis niloticus* | Significantly lower fat and higher ash contents were recorded | Abdel-Tawwab et al. 2006 |
|  | Starvation (up to 80 days) | Channel catfish*,*  *Ictalurus punctatus* | Body fat content and saturated fatty acids were significantly reduced | Luo et al. 2009 |
|  | Starved for 5 weeks | Atlantic halibut*,*  *Hippoglossus hippoglossus* | Flesh with harder texture has been noticed | Foss et al. 2009 |
|  | Starvation (up to 72 days) | Sturgeon  *Acipenser naccarii* and Rainbow trout *Oncorhynchus mykiss* | Significant reduction of glycogen, protein, and lipid were recorded in white muscle | Furne et al. 2012 |
|  | Starvation and temperature (60 days and 17-26°C) | Meagre*,*  *Argyrosomus regius* | Significant reduction in muscle lipid and protein and increase of moisture were noticed | Chatzifotis et al. 2018 |
|  | Short term cyclic feed deprivation (2 days feed deprivation) | Mozambique tilapia, *Oreochromis mossambicus* | Crude fat and protein contents were significanllty reduced | Gabriel et al. 2018 |
|  | Restricted feeding and high stocking density (up to 12 months) | Milkfish,  *Chanos chanos* | Significant reduction in carcass lipid and protein and increase of moisture were recorded | Lingam et al. 2019b |
|  | Fasting (2 months) | Common carp  *Cyprinus carpio* | Dry matter and fat were significantly reduced. Ash content was increased | Debbarma et al., 2019 |
|  | Short term feed starvation (1 & 2 days feed deprivation) | Indian pompano (*Trachinotus mookalee*) | Increased moisture and lower lipid contents were recorded. | Xavier et al., 2023 |

***Water content***

Proximate analysis broadly classifies biochemical components of fish carcasses into two major categories: water and dry matter. Water content, the percentage of water present in the carcasses, of the fish samples were measured by the weight loss method using a hot air oven. The dry matter content, consisting of nutritional components such as crude protein, lipid and ash, was analyzed based on the interest in nutrients. The inverse relationship between water and dry matter contents, clearly indicated the relative importance of water content in proximate analysis. Therefore, the nutritional composition of fish can be understood based on water content (Love, 1970).

Starvation in fish leads to the utilization of deposited lipids, through lipid oxidation, which yields water and carbon dioxide, thereby elevating the moisture level in the carcass tissues (Sargent et al., 1989). However, contrary reports are available regarding the moisture content of fish during starvation conditions. In golden perch, prolonged feed deprivation, for 210 days, did not increase the moisture content (Collins and Anderson, 1995). In contrast, 66 days of starvation in African catfish significantly elevated the water content (Zamal and Ollevier, 1995). In the fasting phase, fish undergo tissue hydration and absorb large amounts of water, which, coupled with the utilization of reserved dry matter, fat and protein, for metabolic activities, ultimately increases the water content of the carcass (Weatherley and Gill, 1987). Quinton and Blake (1990) reported a significant increase in moisture content of rainbow trout during starvation.

***Lipid and Fatty acid***

Fish bodies are composed of two major components, lipids and lean body mass (LBM). In the past decades, from 1970 to the 1990’s, many studies have been conducted to determine the energy utilization of fish during fasting. Successively, in a review paper published by Ali et al. (2003) concluded that, under feed deprivation fish displayed changes in the carcass quality, especially lipid content. After conducting extensive studies in many fish, Jobling, an early researcher who worked mainly on energy utilization and compensatory growth in fish, found that fish expend lipids, as their primary reserve energy source, during starvation or stress. It was found that, Plaice (*Pleuronectes platessa*) can cope with 35 days of starvation by using stored lipids to satisfy their energy requirements (Jobling, 1980). In subsequent years, studies on rainbow trout, black rockfish and milk fish confirmed a similar pattern of lipid utilization under starvation or feed restriction (Quinton and Blake, 1990; Oh et al., 2008; Lingam et al., 2019b).

Alongside, it has been found that fish store biochemical components, especially nutrients, in different body components that vary among species (Love, 1970). The liver, muscle and viscera are the energy storage sites in fish. Successively, scientist noticed that active fish accumulate its fat in muscle and less-active fish deposit in their liver (Robinson and Mead, 1973). Fish exhibit a strong selection pattern for the utilization of stored lipids in the absence of exogenous supplementary feeding. Initially, the liver and visceral fats were consumed by the fish, and later, exhaustion of these fats convinced them to exploit the muscle reserve, which is the last stage of reserved lipid utilization during starvation in fish. Very few studies have been conducted on the utilization patterns of reserved nutrients in fish. In Arctic charr, eight weeks of starvation leads to the consumption of liver and visceral fats, which significantly decreases their liver and viscera size compared to their body mass (Miglavs and Jobling, 1989). Similarly, in Golden perch, a 210-day period of starvation was insufficient to induce the utilization of muscle reserves and depletion of reserved nutrients exclusively in the liver and visceral sites was observed (Collins and Anderson, 1995).

Consequently, lipolysis observed in the fasting phase, which utilizes stored lipids through fatty acid oxidation, leads to the reduction of fatty acid content in fish. However, the choice of fatty acids used, to supply energy, to fish during starvation varies between species (Satoh et al., 1984). Previous studies have found that fish prefer to use saturated and mono-unsaturated fatty acids rather than poly-unsaturated fatty acids during starvation. In common carp (*Cyprinus carpio*), African catfish (*Clarias gariepinus*) and Nile tilapia (*Oreochromis niloticus*) stunting has significantly reduced either saturated or mono-unsaturated fatty acids (Murata and Higashi, 1980; Zamal and Ollevier, 1995; Yang et al., 2015). Interestingly, the above-mentioned studies did not find any reduction in the PUFA content of fish during stunting, which shows the physiological importance of PUFA in fish. PUFA play an important role in membrane fluidity, cell function, phospholipid formation, prostaglandin synthesis and other physio-metabolic activities in fish (Bell et al., 1986) which may hinder their utilization during the fasting phase.

***Protein***

What happens when fish completely consume their reserved lipids? How can metabolic activity be managed under extended restricted feeding conditions? A simple solution is to identify the alternative energy sources. At this point, proteins come into action and play an important role in fish. Proteins are exploited when reserved lipids are sufficiently depleted (Weatherley and Gill, 1987). In protein preferring carnivorous fish, the absence of a supplementary protein source in captivity leads to the consumption of reserved protein, ultimately reducing carcass protein content (Jobling, 1980). Fish undergo protein synthesis under optimal feeding conditions and deposit proteins in their tissues; however, this is not possible under restricted feeding conditions, because of the higher energy requirements for protein synthesis (McMillan and Houlihan, 1989). Kulkarni and Barad (2015) reported reduced protein synthesis under feed-deprived conditions, which also affects protein deposition in the carcass.

Once the reserved fat reaches its critical limit, fish spend protein following the lipostat model of energy utilization, which leads to an elevated rate of protein degradation (Jobling and Johansen, 1999). In most fish, the duration of feed deprivation determines protein exploitation because protein is a secondary energy source in which consumption starts when the fish reaches its threshold point of reserved lipids. Thereafter, fish uses proteins to produce carbohydrate compounds, for metabolic energy purposes, through gluconeogenesis (Love, 1980). For example, in juvenile roach and milkfish fry, 36 days of starvation and 120 days of feed restriction, respectively, did not produce any change in carcass protein values (Mendez and Wieser, 1993; Lingam et al., 2019b). Whereas, 66 days of starvation in catfish (*C. gariepinus*), four-week feed deprivation in hybrid tilapia (*O. mossambicus*× *O. niloticus*), 14 days of feed restriction in black rockfish (*Sebastes schlegeli*) and 60 days of cyclic feeding in Mozambique tilapia (*O. mossambicus*) had significantly reduced carcass protein content (Zamal and Ollevier, 1995; Wang et al., 2000; Oh et al., 2008; Gabriel et al., 2018).

***Carbohydrates***

Fish, basically a dietary protein lover, poorly utilize dietary carbohydrates, therefore, they play a minor role during fasting. Generally, most fish prefer either lipids or proteins as endogenous energy reserves to supply energy during fasting. Whereas, in some fish such as Common carp (*Cyprinus Carpio*), Northern pike (*Esox lucius*) and Snake head (*Ophiocephalus maculatus*) starvation leads to the utilization of stored carbohydrates (Nagai and Ikeda, 1971; Ince and Thorpe, 1976; Woo and Cheung, 1980).

During starvation, along with lipid and protein, glycogen, a polysaccharide carbohydrate, is mobilized as an energy substrate to regulate glucose homeostasis in fish (Furne et al., 2012). Generally, glycogen is stored in either the liver or muscle; however, liver glycogen is the primary substrate in many fish during fasting. Feed deprivation or starvation in common carp (*Cyprinus Carpio*), channel catfish (*Ictalurus punctatus*), brycon fish (*Brycon cephalus*), snakehead (*Channa punctatus*) and Siberian sturgeon (*Acipenser baerii*) was reduced liver glycogen content (Blasco et al., 1992; Gaylord and Gatlin, 2000; Figueiredo-Garutti et al., 2002; Namrata et al., 2011; Liang et al. ,2017).

***Ash content***

In fish, non-edible portions of bones, scales and skin contribute to the ash content, which is an inorganic incombustible residual (Wilkins, 1967). The depletion of lipids and proteins during feed deprivation leads to an increase in the fish ash content. In herring, feed deprivation and carcass ash content are directly related (Wilkins, 1967). Similarly, in African catfish starvation significantly increased carcass ash content (Zamal and Ollevier, 1995).

**8. GROWTH OF STUNTED FISH IN POST-STUNTING PHASE**

***CG in stunted fish during re-alimentation phase***

Stunted fish show an elevated growth pattern in the refeeding phase, called compensatory growth, which has been observed and reported in various marine and freshwater fish, such as *Gadus morha* (Jobling et al., 1994), *Lates calcarifer* (Tian and Qin, 2003), *Salmo trutta* (Johnsson and Bohlin, 2005), *Pangassius bocourti* (Jiwyam, 2010), *Anguila Anguilla* (Caruso et al., 2010), *Onchorhynchus mykiss* (Rahimi et al., 2010), *Paralichtys olivaecus* (Cho et al., 2012), *Labeo rohita* (Biju, 2014), *Oreochromis niloticus* (Limbue and Jumanne, 2014), *Chanos chanos* (2019b), *Heros severus* (de Oliveria et al., 2020) and *Salmo salar* (Hvas et al., 2022). However, various factors influence the CG response of stunted fish during the re-alimentation phase such as fish size, food availability, environmental factors, duration of restricted feeding, seasonal variations and age of maturity. Furthermore, the CG response manipulates patterns of feed utilization and physiological activity in fish. In the post-stunting phase, Nile tilapia, which expressed a CG response, showed higher feed conversion efficiency (FCE) and protein efficiency ratio (PER) and lower feed conversion ratio (FCR) than continuously fed fish (Limbue and Jumanne, 2014). Similarly, a higher FCE was achieved in yellow catfish, subjected to intense feed deprivation, during the re-alimentation phase (Ruan et al., 2015).

Among various factors, the duration and severity of the catabolic phase determine the degree of compensation in the re-alimentation phase (Jobling et al., 1993). Belanger et al. (2002) suggested that the catabolic phase should be cranked up to its threshold limit in fish to spark the CG response in the anabolic phase. Based on the stress experienced in the catabolic phase, stunted fish exhibit either partial or complete growth recovery in the re-alimentation phase and in rare cases, display over-growth compensation. The duration of the catabolic phase, which induces nutritional stress to stimulate CG response, may vary among species. In an odd scenario, three weeks of feed deprivation in the Atlantic Charr was not enough to trigger CG (Jobling et al., 1993), but the same fish exhibited a CG response after six months of cyclic feed restriction (Jobling et al., 1994). Das et al. (2016) recommended that stunting of rohu for more than 6 months may leads to poor growth performance in grow out phase. Moreover, the rate of recovery depends on the re-feeding strategies employed during the anabolic phase (Llameg and Serrano, 2014).

***SGR and feed utilization pattern of stunted fish in re-alimentation phase***

In general, CG is distinguished by an elevated SGR and better FCE during the re-feeding stage (Ali et al., 2003; Won and Borski, 2013). Additionally, the specific growth rate was used as an indicator to evaluate the growth performance of the fish (Kohla et al., 1992). Typically, the SGR value of fish is not constant throughout their lifetime, as it decreases with increasing fish size (Jobling, 1994; Ali et al., 2003). Furthermore, a study by Jobling (2010) comparing the same age group of stunted and normal fish revealed that stunted fish reached a smaller size than normally fed fish at the end of the stunting phase, which subsequently led to higher SGR in stunted fish during the initial phase of re-alimentation. However, a prolonged period of feed deprivation hinders the fish from compensating for its body weight during re-alimentation phase (Turano et al., 2007). In contrast, short-term starvation (up to a few months) or feed restriction shows a limited response in the re-feeding phase (Caruso et al., 2011). In the stunting phase, fish should reach a stage where they completely exploit their expendable energy reserves to open the gateway for physiological changes that induce the compensatory growth response in the re-alimentation phase (Won and Borski, 2013).

From an aquaculture perspective, feed, the major operational cost input, plays an important role in determining the economic success of fish farming. When exposed to quality feed, stunted fish exhibit accelerated growth in the post-stunting phase, which must be highlighted to improve feed utilization (Llameg and Serrano, 2014). However, the higher feed intake of stunted fish in the re-alimentation phase, the hyperphagic response, may force the farmer to dump more feed into the fishpond. Fortunately, the same fish spend most of their energy for accumulating the lean body mass and a modest level of energy on metabolism and locomotion (Jobling et al., 1994; Ali et al., 2003), thereby displaying better feed utilization patterns than continuously fed fish. The hyperphagic response of stunted fish reduces FCR and increases FCE in many fish (Kohla et al., 1992; Koppe et al., 1993; Broekhuizen et al., 1994; Turano et al., 2007).

***Compensatory growth in milkfish - a case study***

Lingam et al. (2019b) studied the CG response of normal and different duration stunted milkfish at field conditions for 540 days. Milkfish were stunted for 4, 8 and 12 months and at the end of the catabolic phase stunted fish displayed lower body weights than their normal counterparts. In the anabolic phase, when the stunted fish were released into optimal rearing conditions, the three groups of stunted fish expressed CG responses (Fig. 1A-C) at different levels. Remarkably, the study observed three types of CG response in a single experiment using milkfish, which clearly indicated that the duration of stunting determines the degree of CG in the anabolic phase. Fig-1A and 1C show the partial growth compensation of stunted fish compared to normal milkfish at the same age. Similarly, Fig. 2B and 2C show the partial growth compensation of milkfish between the different stunted group durations. This clearly signifies that stunting of milkfish for 4 and 12 months may not induce complete CG in the anabolic phase, as the duration is either insufficient or severe to encourage complete CG. On the other hand, Fig. 1B shows the complete growth compensation of 8 month stunted milfish compared to their normal counterparts. Interestingly, the study recorded over-growth compensation when comparing 4 and 8 month stunted milkfish (Fig. 2A), which further implies that a catabolic phase of 8 months would beneficially trigger the CG response in milkfish. Similarly, optimizing the duration of the catabolic phases for different species would constructively affect aquaculture production in the future.

**….**  Stunting phase

Post-stunting phase

**(A) C\*T4**

**….**  Stunting phase

Post-stunting phase

**(B) C\*T8**

**….**  Stunting phase

Post-stunting phase

**(C) C\*T12**

C-normally fed fish; T4-4 months stunted; T8-8 months stunted; T12-12 months stunted. In each graph, the intervals highlighted with different alphabets indicate that values are significantly differ at p<0.05.

**Figure 1 Comparison of CG response of normally fed and different duration stunted milkfish**

**….**  Stunting phase

Post-stunting phase

**(A) T4\*T8**

**….**  Stunting phase

Post-stunting phase

**(B) T4\*T12**

**….**  Stunting phase

Post-stunting phase

**(C) T8\*T12**

T4-4 months stunted; T8-8 months stunted; T12-12 months stunted. In each graph, the intervals highlighted with different alphabets indicate that values are significantly differ at p<0.05.

**Figure 2 Comparison of CG response of different durations stunted milkfish**

**9. LENGTH-WEIGHT RELATIONSHIP OF STUNTED FISH IN POST-STUNTING PHASE**

***Introduction***

The length-weight relationship of fish varies among the different with respect to their inherited body shape and size. It also varies within a species according to culture conditions, robustness of fish and food availability. The relationship between length and weight was used to assess the health condition of the fish. Some factors like food availability, sex, maturation, spawning season and water conditions are known to influence the length-weight relationship of fish. Fish exhibit three different categories of growth viz., isometric growth, negative allometric growth and positive allometric growth. The fish that shows isometric growth refers that there is no change in body weight with respect to increase in length. Lean fishes are known to show negative allometric growth whereas fat fishes exhibit positive allometric growth (increase in weight at faster rate in relation to its increase in length).

Similarly, based on the length and weight relationship of fish b (slope value) can be calculated and this value represents the type of growth pattern in fish. When the slop value is 3, it indicates isometric growth. When the value of b is greater than 3, the fish growth pattern is indicated as allometric either positive allometric (b = > 3) or negative allometric (b = < 3) if the value of b is less than 3 (Levent et al., 2007). The variation in length weight relationship can be found using condition factor, K. The condition factor K can be determined using the formula K = W\* 100/ L3 Where, W = Weight of the fish (g and L = Total length of the fish (cm).

***LWR of stunted fish in re-alimentation phase***

In general, the b value (slope) and CF (condition factors) of fish were estimated during the length-weight relationship studies. The condition factor of a fish also shows its physical and biological conditions which can therefore be used as an indicator of general fish condition. Most of the fish displayed a slope value closer to 3.0, an isometric growth pattern, in which the fish maintained a constant proportion of weight to its length increment (Schneider et al., 2000; Ak et al. 2009). However, restoration of exploited endogenous energy reserves in stunted fish during the re-alimentation phase causes morphometric changes, which in turn renews the altered condition factor. Moreover, CF signifies the available energy reserves in fish and any change in CF directly influences the overall nutritional composition of farmed fish (Ali et al., 2004; Caruso et al., 2012). Once endogenous energy reserves are rebuilt, it inhibits the CG response in stunted fish during post-stunting (Jobling, 2002) . Therefore, CF has been used as a predictive tool to determine the CG response of stunted fish. The starved gilthead sea bream could only compensate for its body weight and failed to restore its length (Bavcevic et al., 2010). The red porgy displayed restoration of CF in the post-stunting phase, after a considerable reduction in CF during the starvation phase (Caruso et al., 2012).

Álvarez and Nicieza (2005) found that brown trout (*Salmo trutta L.)* showed partial compensation for body weight but no compensation in length. Similarly, gilthead sea bream (*Sparus aurata*) compensated for weight, but not length (Bavčević et al., 2010).

Feed and feed ingredients are a major cost of intensive aquaculture. By understanding the length-weight relationship of stunted fish during the refeeding phase, optimization of growth and feed utilization can be performed. Further studies could help to assess the long-term effects of refeeding on fish health and growth.

**10. BIOCHEMICAL CHANGES IN STUNTED FISH BLOOD DURING POST-STUNTING PHASE**

***Introduction***

Under normal circumstances, the physiological behaviour of fish changes with age. In contrast, in the compensatory growth phase, metabolic activities of fish are triggered resulting in fish with better haematological, immunological and digestive profiles than those of normal fish.

Like other animals, fish blood, a specialized body fluid, plays a major role in fish physiology by supplying oxygen and nutrients to the cells and carrying away the metabolic waste produced by the cell. It is comprised of liquid (plasma) and solid (cell) components. The liquid portion was further subdivided into water, protein and salts, whereas the solid portion comprised of blood cells, RBC, WBC and platelets. Interestingly, in fish, more studies have been carried out in either plasma or serum, as they can be preserved for a certain duration (3-6 months) at low temperatures (-20 to -40°C).

***Serum biochemical changes in post-stutned fish***

Serum, a portion of the plasma, is a yellow colour fluid that lacks clotting factors, prothrombin and fibrinogen. Generally, serum components are measured in fish to their know the health conditions. Fish require serum proteins, such as albumin and globulin to perform immunological activities more efficiently (Kumar et al., 2005; Yengkokpam et al., 2016). Blood protein content in fish ranges from 2-8 g/dl, however, it varies from species to species based on their pathological and physiological conditions (Georgiev and Kamenov, 1980). On the other hand, stunted fish in the re-alimentation phase can rapidly regain lost blood metabolites (Weatherley and Gill, 1987), which subsequently increases their serum protein content. Dentx fish, *Dentex dentex,* starved for five-weeks displayed significantly higher total serum protein in the refeeding phase (Perez-Jimenez et al., 2012). Biju (2014) reported successful restoration of total serum protein and increased circulation of protein in the blood of stunted rohu yearlings under optimal culture conditions.

In fish, serum albumin and globulin proteins are involved in various physio-metabolic activities; therefore, their levels in the blood are used as biomarkers to assess fish health and immune conditions (Kovyrshina and Rudneva, 2012; Yengkokpam et al., 2016). Rohu stunted for about 6-month and kept under starved conditions (1, 2 and 3 days per week) displayed increased circulation of serum albumin and globulin than the normally fed fish (Yengkokpam et al., 2012; Biju, 2014). Blunt snout bream, *Megalobrama amblycephala*, experienced hypoxic stress and fed with different feeding rations exhibited variation in total serum protein and globulin content in post-hypoxic conditions (Li et al.,2016). In milkfish, 8-month of crowding and feed restriction led to improved circulation of total serum protein, albumin and globulin during the re-feeding phase (Lingam et al.2019a). The presence of globulin, an antibody protein, in the blood indicates the efficient functioning of the immune system and is being a part of the serum protein. In fish, increased innate immunity is correlated with elevated levels of serum proteins (Magnadottir, 2010).

***Stress enzymes in stunted fish during re-alimentation phase***

Glucose, a major sugar source in blood, is the main energy source for cells that regulate feed intake in fish (Carter et al.,2001). During the re-alimentation phase, the rate of feed intake and hyperphagia significantly influences the compensatory growth response. Studies have found an inverse relationship between blood glucose levels, food intake and growth efficiency in red piranha and rainbow trout (Bellamy, 1968; Boujard et al., 2000). Additionally, the duration of the catabolic phase and species-specific metabolic responses of stunted fish also influence the restoration of blood glucose levels during the re-feeding phase (Caruso et al., 2010). Persian sturgeon starved for different durations (1, 2, 3 and 4 weeks) displayed increased plasma glucose levels in the re-alimentation phase (Yarmohammadi et al., 2012).

In fish, cortisol, a major corticosteriod secreted by inter-renal cells in the head kidney of fish under HPI activation, plays a major physiological role and is involved in energy mobilization, carbohydrate and hydromineral balance and glucose and plasma protein syntheses (Goss and Wood, 1988). Unlike mammalian cortisol, the unusual structure of fish cortisol affects carbohydrate, protein and lipid metabolism, significantly influencing fish growth and reproduction (Mommsen et al.,1999). Therefore, in the re-alimentation phase to exhibit better growth compensation, stunted fish try to maintain either low or optimal levels of cortisol circulation in the blood. On the other side, similar to glucose restoration, species-specific metabolic responses and stunting duration affect cortisol circulation in re-alimented fish (Caruso et al.,2010). A 20 days fasted goby (*Gillichthys mirabilis*) took 7-days to restore its elevated cortisol level in the re-feeding phase (Kelley et al.,2001). Based on the intensity of stunting, stunted fish take time to restore their cortisol circulation, which predominantly influences CG response. In our previous study (Lingam et al.,2019a), we noticed a prolonged duration (90 days) of cortisol restoration in the 12-months stunted group which in turn reduced the CG response of that particular group during the re-feeding phase.

**11. IMMUNE AND ANTI-OXIDANT RESPONSES OF STUNTED FISH IN POST-STUNTING PHASE**

***Introduction***

Similar to other vertebrates, the fish immune and anti-oxidant systems play pivotal roles in maintaining health conditions. Reactive oxygen species (ROS), an unstable oxygen compound, are considered an important component in fish defence mechanisms as they contain potent bactericidal compound that kill invading pathogens. On the other hand, free radicals which are unstable compounds produced either from normal metabolism or ROS breakdown due to exposure with foreign materials, may act as potent oxidants that need to be neutralized by the anti-oxidant system (Cross et al., 1987; Biller-Takahashi et al., 2015; Biller-Takahashi and Takahashi, 2018). Therefore in fish, the imbalance between the immune system, production of ROS, and the anti-oxidant system, decomposition of free radicals, leads to oxidative stress. To avoid this situation, fish must maintain both the immune and anti-oxidant systems at optimal levels. Innate and acquired are the two components of the fish immune system. Phagocytosis, the engulfing of foreign particles or cells by phagocytes, is an innate immune process that interconnects the immune and anti-oxidant systems in fish because of ROS production (Biller- Takahashi and Takahashi, 2018).

***Respiratory burst activity in post-stunted fish***

Respiratory burst activity is the rapid production of reactive oxygen species by various cells, whcih increases the ability of phagocytes to kill pathogens (Sharp and Secombes, 1993). Following the recognition of pathogens, fish phagocytes, along with other cells, produce reactive oxygen derivatives, such as superoxide anions (O2-), hydrogen peroxide (H2O2) and hydroxyl radicals, which lead to intense consumption of oxygen, known as respiratory burst (Anderson and Siwicki, 1995; Biller-Takahashi et al., 2013; Biller- Takahashi and Takahashi, 2018). Therefore, an elevated respiratory burst activity in fish signifies the increased pathogen killing capacity of phagocytes, which denotes the better immune status of fish. When the stunted rohu returned from stunting to the re-alimentation phase, they displayed significantly higher respiratory burst activity than the normal rohu (Biju, 2014). Similarly, the same fish when starved for 3-week expressed higher respiratory burst activity in the re-feeding phase (Yengkokpam et al.,2016). Mohapatra et al.(2017) reported a similar pattern of enhanced respiratory activity in the re-alimentation phase in sea bream challenged with *Edwardsiella tarda.* An organism displays phenotypic flexibility, a reversible change in either behaviour, morphology and physiology or collectively all, when it encounters a changed environmental condition (Piersma and Drent, 2003). Under stressed conditions, due to phenotypic flexibility fish may either increase or decrease certain physiological traits to mitigate stress. For instance, reduction in ROS production by fish is a phenotypic flexibility response to feed restriction or starvation conditions. Therefore, once starved fish receive feed, they regain their ROS production. Reinstating altered physiological traits, after stocking in favourable environmental conditions by triggering phenotypic flexibility, plays a major role in CG based aquaculture practices. On the other side, damage to phenotypic flexibility, due to severe stress or extreme stunting practices, can create permanent impairment of that particular trait. Respiratory burst activity is the first-line defence mechanism in fish; therefore, its phenotypic flexibility trait needs to be optimally exploited in the catabolic phase to produce physiologically healthy stunted fish seeds that can easily recover from their altered physiological status due to stunting to combat the various emerging issues in aquaculture practices.

***SOD and Catalase activities in post-stunted fish***

Oxidative stress, an imbalance between ROS compounds and antioxidants, leads to protein, lipids and DNA damage. In fish, ROS compounds are silenced by two important oxidative enzymes, superoxide dismutase and catalase, which help to maintain physiological homeostasis (Shin et al., 2010). The superoxide anion (O2-), ROS compound, is oxidized to hydrogen peroxide (H2O2) by SOD enzyme. Following dismutation, H2O2, a toxic oxidative compound, is further neutralized into oxygen and water by catalase (Vera-Jimenez et al., 2013). The disappearance of oxidative stress during the re-feeding phase successfully restored anti-oxidant enzymes in fish. Supporting this statement, common dentex and catla displayed significantly lower SOD and CAT enzyme activities during the re-feeding phase (Morales et al., 2004; Pal and Maitra, 2018). The change from endogenous to exogenous energy reduces the production of oxidative compounds from stored lipids and significantly affects the activity of anti-oxidant enzymes. During starvation, ROS from blood cells and oxidative compounds from energy metabolism need to be neutralized, whereas in re-feeding, the reduction in oxidative compound production subsequently lowers anti-oxidant enzyme activities. For example, blunt snout bream fed an optimal feeding ration displayed lower SOD and CAT activities than the feed restricted groups (Li et al.,2014). Another study in rohu found increased SOD and CAT activities in 2 & 3 days starved groups, due to oxidative stress, compared to regularly fed fish (Yengkokpam et al.,2013). Therefore, the availability of a lower quantity of oxidative compounds under the optimal feeding, re-alimentation phase, could be the major reason for the reduction in anti-oxidant enzymes during the CG phase.

***Lysozyme activity in post-stunted fish***

Fish possess an innate immune system that defends them against the microbial pathogen invasion. Among the various innate immune parameters, lysozyme, a cell wall breaking enzyme of humoral immune response, is commonly used to determine the immune status of fish in various nutrition-based research experiments, as it has potential antibacterial and antiviral properties and is distributed along the skin mucus, gills, digestive tract and blood (Alexander and Ingram, 1992; Jiang et al., 2008; Kiron, 2012). In captive conditions, such as aquaculture practices, where fish are held in a limited area of access for a considerable duration, fish health conditions completely depend on what fish consumes or what kind of feed is used for rearing. The shift from the anabolic to the catabolic phase upon commencement of feeding increases nutrient availability, which improves the immune response of re-alimented fish compared to that of starved fish. In many cases, the re-alimented fish displayed a better immunological profile than normally fed fish. A study in rohu revealed that, supplementing protein rich diet to the 3-week starved rohu singnificanlty improves its lysozyme activity in re-alimentation phase (Yengkokpam et al., 2016). Contrary to this, a 14-day starved red porgy displayed a recovering trend of lysozyme activity from starvation in the re-feeding phase, but did not show any significant improvement than the normally fed fish (Caruso et al., 2012).

***Myeloperoxidase activity in post-stunted fish***

Myeloperoxidase in fish, a non-specific immunity possessed by neutrophils, kills bacteria by halogenating the cell walls of the pathogen in the presence of halide and hydrogen peroxidase (Alcorn et al., 2003; Uribe et al., 2011). Elevated activity of myeloperoxidase in fish is widely regarded as a strong immune response (Sakai, 1999). A study conducted by Biju (2014) found a better immune response in stunted rohu yearlings, with increased myeloperoxidase activity, when reared under normal pond conditions (post-stunting) than in normal yearlings. In contrast, blunt snout bream juveniles show reduced MPO activity after hypoxia (oxygen-deficient stress condition) (Li et al., 2016). Similarly, milkfish stunted for 4 months did not show any improvement in lysosome and MPO activities in the post-stunting phase (Lingam et al.*,* 2019a). The same study reported immune fatigue in the post-stunting phase, when fish were stunted for a longer duration (12 months). Likewise, when *Penaeus vannamei* was starved for short duration, its immunity was successfully restored, however, long-term starved shrimp were unable to restore their immunity (Lin et al., 2012).

Stunned fish exhibit a better immune response when fed with an appropriate feed and an optimal feeding regime, which resulted in a better health condition (Kiron, 2012). Costas et al. (2011) stated that fish, subjected to stressful conditions, had a better immune profile than normal fish. In the re-alimentation phase, the availability of better nutrition in the form of highly nutritious supplementary feed aids in the proper functioning of the immune system (Kiron, 2012). Basically, feed quality and quantity affect the innate and specific immune responses of fish (Magnadottir, 2006). Similarly, the commencement of optimal feeding for stunted fish improves the energy availability for physiological processes leading to increased immune cells and production of cellular components. Therefore, dietary modulation such as feed restriction, could beneficially affect the immune system of fish during grow-out practices. Although various studies have been conducted out on the immune response of fish during re-alimentation, further studies must be done to get a better understanding of the compensatory growth effect on the fish immune system (Eslamloo et al., 2017; Philip et al., 2018).

A growing body of literature recommend that the immune and antioxidant responses of post-stunted fish play a crucial role in their recovery and overall physiological well-being. Recent research reveals that stunted fish exhibit remarkable phenotypic flexibility, allowing them to restore immune functions such as respiratory burst activity, superoxide dismutase (SOD), catalase (CAT), lysozyme, and myeloperoxidase (MPO) activities during the re-alimentation phase. These responses are primarily influenced by the shift from the catabolic to the anabolic state upon resumption of feeding, which enhances pathogen defense mechanisms, restores oxidative balance, and improves overall immune function. While short-term stunting followed by optimal feeding can enhance immune resilience, prolonged stunting may lead to immune fatigue and reduced recovery potential. The findings highlight the importance of dietary modulation and appropriate feeding strategies in aquaculture to optimize the health and immune status of stunted fish. Future research should focus on understanding the long-term implications of compensatory growth on immune function and identifying optimal feeding protocols that ensure the sustainable and efficient recovery of post-stunted fish in commercial aquaculture practices.

**12. DIGESTIVE ENZYME ACTIVITIES OF STUNTED FISH IN POST-STUNTING PHASE**

***Introduction***

Digestion, a key metabolic process, controls the nutrients available for all biological functions and is controlled by digestive enzymes (Gisbert et al., 2009; Abolfathi et al., 2012). Therefore, digestive enzyme profiling aids in forecasting the ability of fish to use different nutrients in feed (Hofer and Kock, 1989). Starvation, a stunting phenomenon, causes a reduction in digestive enzyme activity that is restored when feeding resumes after a period of feed restriction (Krogdahl and BakkeMcKellep, 2005; Yengkokpam et al., 2013).

***Digestive enzyme changes in post-stunted fish***

Fish that undergo a compensatory growth phase display an elevated synthesis of digestive enzymes, which thus improve their digestive capacity (Belanger et al., 2002). Similarly, Furne et al. (2008) mentioned that fish recovering from extended starvation showed elevated digestive enzyme activity, to digest nutrients in the feed. In the re-feeding phase, the increased availability of nutrients to the intestinal lumen helps in rapid restoration or regeneration of atrophied intestine of stunted fish (Krogdhal and Bakke-McKellep, 2005; Abolfathi et al., 2012) which, on the other side, supports the faster recovery of digestive enzymes activity.

Kohla et al. (1992) reported a drastic increase in amylase (110 to 150%) and trypsin (250-600%) during re-feeding stage in *Colossoma macropomum* subjected to 7 weeks of feed starvation. Abolfathi et al. (2012) obtained a similar outcome, as juvenile roaches (*Rutilus rutilus caspicus*) displayed increased amylase activity during the re-feeding stage. Previous reports have suggested that compensatory Growth (CG) in fish occurs due to increased digestive enzyme activity (Imani, 2006; Bolasina et al., 2006; Yengkokpam et al., 2013; Fang et al., 2017; Lingam et al., 2019a). However, elevated digestive enzyme activity was restored or reached a normal level once depleted nutrients were restored by the stunted fish. Among the three major digestive enzymes, lipase was the first to be reinstated, as lipids are the first nutrients to be restored in the fish body (Jobling, 2010). Therefore, increased lipase activity was observed in the initial stages of stunted fish during the re-feeding phase. Similar patterns of lipase activity have been reported in rainbow trout, Japanese flounder larvae and Tongue sole by Imani (2006), Bolasina et al. (2006) and Fang et al. (2017), respectively.

Besides feed availability, the feeding habits of stunted fish also affect the digestive enzyme activity. In general, the protein requirement of omnivorous fish is lower than that of carnivorous fish; therefore, omnivorous and herbivorous fish display higher amylase activity to digest carbohydrates in their diets (Abolfathi et al., 2012). Indistinct reports regarding feeding habits' impact on fish's digestive enzyme activity are available. A study using stunted milkfish, an omnivorous fish, found significantly higher protease activity during the re-feeding phase (Lingam et al., 2019a). Similarly, the omnivorous *Labeo rohita* displayed increased amylase and protease activities during the refeeding phase (Yengkokpam et al., 2013). Under captive conditions, when a low-protein diet is supplemented, omnivorous fish display higher proteolytic enzyme activity to extract energy from whatever protein is available in their feed (Abolfathi et al., 2012).

**13. NUTRITIONAL QUALITY CHANGES IN STUNTED FISH DURING POST-STUNTING PHASE**

***Introduction***

Nutritionally lower quality fish, stunted fish, display compensatory growth behavior in the re-feeding phase andrapidly reinstate their depleted nutrients, which increases the nutritional quality of re-alimented fish (Jobling, 2010). In the compensatory growth phase, the re-feeding schedule plays a key role in the nutrient accretion rate and tissue deposition; however, it varies among fish species (Black and Love, 1986). The morphometric changes associated with post-stunted fish lead to various changes in the carcass composition of the fish, which, in turn, alters their nutritional quality. In one side, the evolution of modern intensive fish farming practices and the heavy usage of drugs and antibiotics in aquaculture have changed the perception of farmed fish among fish consumers, which has lowered the preference of farmed fish by consumers due to its meat quality (Verbeke et al., 2007; Beveridge et al., 2013). On the other side, fish farmers perceive CG as a vital quality changing tool that can be used in aquaculture to improve farmed fish meat quality (Jobling et al., 1994; Won and Borski, 2013). Therefore, to determine the meat quality of farmed fish, it is imperative to assess the nutritional quality of harvested farmed fish (Jobling, 1980).

***Moisture content***

The chemical composition of the carcass can be used as a critical quality check to determine compensatory growth based changes in fish. By assessing the water content, the percentage contribution of other nutrients (fat and protein) can be determined which helps to identify the nutritional quality of the fish. Usually, fish, exhibiting CG response, tend to display lower carcass moisture content due to their nutritional accretion behaviour (Collins and Anderson, 1995).

Two months of supplementary feeding and two months of starvation in Indian major carps induced a CG response, which significantly reduced their moisture content at the end of the re-feeding phase (Mohanta et al., 2016). Similarly, different durations of stunting (4, 8 and 12 months) in milkfish provoked a CG response and produced post-stunted fish with significantly lower moisture content (Lingam et al., 2018 &2019b). However, 1-3 weeks of feed deprivation in snook (*Centropomu sparallelus*) did not trigger a CG response and produced post-stunted fish with similar moisture content (Ribeiro and Tsuzuki, 2010). The lower moisture content in re- alimented fish mostly is correlated with its nutrient (lipid) accretion behaviour. Additionally, the inverse relationship between moisture and fat, a major source of poly unsaturated fatty acids for human nutrition, could be the reason for the reduction in fat content when fish display a CG response.

***Fat and fatty acid***

Lipids are the major energy nutrients in fish and play an important role in determining their nutritional quality. In fish, lipids are stored in the liver, viscera and muscles and their distribution patterns vary among species (Love, 1970; Jobling, 1994). However, excess fat deposition in fish muscle decreases its commercial value by reducing product quality and storage stability, which also affects the consumer preference (Cowey, 1993). In addition, lipids play a crucial role in regulating compensatory growth of stunted fish during the re-alimentation phase. Usually, stunted fish follow the lipostat model, explaining the relationship between CG response and lipid restoration, where based on the lipid restoration, fish either initiate or stop the hyperphagia (Jobling and Johansen, 1999). In stickleback, the CG response stops once depleted lipids are completely restored (Zhu et al.,2003).

Lipogenesis, a process of fatty acid synthesis, observed in stunted fish during the re-alimentation phase, tends to restore fatty acids used during the stunting phase (Weatherley and Gill, 1983). The type of fat used as an energy source varies among the fish species. In elasmobranches, ketone bodies are used, whereas fatty acids are the major energy source for teleost fish. The increase in fat content during the refeeding phase changes the fatty acid composition. In contrast, 28 days of starvation did not produce any significant changes in the fatty acid composition of channel catfish (*Ictalurus punctatus*) during the re-alimentation phase (Tidwell et al., 1992). In conventional aquaculture systems, fish completely depend on a supplementary diet for nutrition, which ultimately affects their overall nutritional composition. Alcorn et al. (2003) reported that the fatty acid composition of farmed fish was influenced by the dietary lipid composition and duration of the rearing period using that diet. Under captive conditions, fish rely solely on dietary lipids for fatty acid production. However, limited studies have been conducted with little information on the restoration of fatty acids in re-alimented fish.

***Protein***

In the compensatory growth phase, fish tend to aggregate more lean body mass, weight of fish carcasses, excluding fat, rather than fat, especially protein in their tissues (Jobling, 1994). Feed deprived Giebel carp in the re-alimentation phase display increased protein deposition in their carcasses (Qian et al., 2000). Similarly, a 2-weeks feed deprived long snout catfish exhibited elevated levels of muscle protein compared to the body weight gain during the compensatory growth phase (Zhu et al., 2005).

The carcass nutrient accretion behaviour of re-alimented fish differs among species and depends mainly on the re-feeding schedule (Black and Love, 1986). For example, when fish are stunted for a shorter duration in the stunting phase, the period in which stunted fish do not exploit the reserved protein may not produce significant changes in carcass protein composition at the end of the post-stunting phase. In European sea bass, starvation for 2, 5 & 10 days and refeeding did not produce any significant differences in carcass protein content (Adakli and Tasbozan, 2015). However, when the fish are kept under optimum stunting duration, the period in which the stunted fish exploit their reserved protein to a basal protein level, may result in higher crude protein accretion in the carcass than that in their normally fed counterparts at the end of the re-feeding phase. When stunted for an optimum duration of 8 months, milkfish produced a significantly higher carcass protein than normal fish (Lingam et al., 2018; Lingam et al., 2019b). Similarly, when the fish is stunted for an extended duration in the stunting phase, the period during which the fish exhausted its reserved protein below the basal protein level may lead to a lower amount of protein restoration in the carcass tissues at the end of re-alimentation phase. A study by Wang et al. (2000) using hybrid tilapia (*O. mossambicus × O. niloticus*) found that when the fish were deprived of feed for four weeks, it was unable to restore its protein content, as in normally fed fish or two-week deprived groups in the re-feeding phase. Therefore, the duration of stunting not only influences the compensatory growth pattern but also controls the rate and quality of protein accretion in the carcass. Hence, stunting based CG response can be applied in aquaculture to enhance the quality of the protein produced.

***Carbohydrate***

In fish, carbohydrates, organic compounds with carbon, hydrogen and oxygen atoms, play a minor role as storage materials. Additionally, the liver and other tissues have a limited ability to store carbohydrates in fish, which makes the total carbohydrate, glycogen, contributions very low (<1%) in the total proximate composition on wet weight basis (Cowey and Sargent, 1972). On the other hand, fish do not require much carbohydrate in their diet; however, limited carbohydrate in the fish diet leads to the utilization of protein and lipid, for energy production (Wilson, 1994), which ultimately affect the deposition of nutrients in fish carcass. In addition, the lower incorporation of carbohydrates in fish feed increases the feed cost (Kamalam et al.,2016) which makes the production of quality fish mush costlier.

Glycogen, a major carbohydrate energy reserve in fish, is primarily stored in liver and muscle tissues. The rapid renewal of hepatic reserves leads to the restoration of glycogen during the re-feeding phase. Nagai and Ikeda (1971) found an overshoot of glycogen in 2-months starved carp muscle during the re-alimentation phase. Similarly, in the compensatory growth phase, muscle glycogen in perch had an increase (Collins and Anderson, 1995). The relative importance of rebuilding liver and muscle tissues subsequently increases glycogen content in fish during re-alimentation, as the liver and muscle are the major storage sites for glycogen in fish.

***Ash content***

During compensation, the restoration of nutrients in muscle, the edible portion, reduces the overall ash content, non-edible portion, of the fish. There has been specific investigation on the ash content of fish; however, to date, proximate nutrient analysis of re-alimented fish has been used to draw conclusions about ash content in the compensatory growth phase. An irregular pattern of ash content was observed in the muscles of long snout catfish during compensation (Zhu et al., 2005). Gabriel et al. (2018) found lower ash content during compensatory phase of tilapia (*O. mossambicus*). The allometric growth pattern, which gives more improtance to the development of the liver, gut, skin and visceral organs, has been reported in normally fed fish (Fauconneau and Laroche, 1996; Sahu et al., 2000; Weatherley and Gill, 1983). On the other side, stunted fish place greater emphasis on the restoration of LBM and energy reserves in the re-feeding phase (Jobling, 2010). The difference in growth pattern could be the main reason for the ash content variations between the normal and realimented fish,

**14. CONCLUSION**

The current trend indicates that in the near future there will be a need for more efficient animal protein production systems due to competition and unavailability of feed ingredients. At present, the animal protein required for humans are supplied by all animal production sectors, including fisheries. However, in the recent past fish supply faced severe problems due to reduced catches from both inland and marine capture fishing. The decline in catch from capture fisheries has paved the way for rapid fish production through aquaculture. Moreover, fish production through farming is the most efficient animal protein production system compared to other animal protein production sectors and is also the cheapest source of animal protein. Therefore, there will be a huge demand for farmed fish in the future due to declining catches from the wild, especially from the marine sector. To meet the future requirements of this emerging population, the sector needs to intensify with different species (diversification) by adopting eco-friendly farming practices. Additionally, aquaculture plays an important role in socio-economic upliftment, employment generation and nutritional security of the country.

The increasing demand for nutritious food produced in a sustainable manner creates an immense pressure on the food sector, especially the fish production sectors. As the scope for expansion of production from natural systems is limited, the pressure to enhance fish production through aquaculture sector is burgeoning. Sustainable yet profitable culture options must to be executed to meet the growing demand. Stocking of stunted seeds in grow-out ponds is already practiced by farmers to increase production in a shorter duration with reduced feed utilization. To date, stunted seeds are produced either by inflicting crowding stress (stocking a greater number of seeds in a limited area), restricted feeding (feeding sub-optimal ration to fish) environmental stress (rearing of fish in unfavourable environmental conditions) or a combination of these conditions. The produced seed undergoes a catabolic phase to utilize the endogenous energy reserve under unfavourable conditions and shows a compensatory growth response, anabolic phase, in favourable conditions. Although, the hyperphagic response of stunted seeds in the re-alimentation or post stunting phase significantly reduces the feed conversion ratio in many fish, the stunting process also alters fish growth, physiology and carcass quality. The CG response depends on the fish species, age, duration and severity of imposed stunting practices. Depending on the degree of recovery, three types of compensatory growth have been reported; over compensation, complete growth compensation and lower growth compensation. Hence, it is essential to optimize the stunting protocol to obtain good quality stunted seeds which can ensure a higher yet nutritious fish production in a sustaianble manner.

**DISCLAIMER (ARTIFICIAL INTELLIGENCE)**

**COMPETING INTEREST**

Authors have declared that no competing interests exist.

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