Functional Role of Dietary Supplements on Reproductive Physiology of Fishes

17

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Abstract

Optimal nutrition and feeding influences the growth, reproduction, and health of fish. Feeding strategy, diet type, and additional supplements largely influence gonad maturation and spawning in fishes. Manipulations of feed type and source can invariably modify reproductive threshold of potential broodstock, and therefore precise knowledge on these focal areas is indispensible. Diet restriction during early phases of life cycle can delay age at first maturation, and a quantitatively restricted food supply at the time of oocyte differentiation reduces the number of egg, while reduction of food supply during later phases of oogenesis has minimal effect on egg size, composition, and hatchability. Also, at spawning time, mature female fishes can effectively utilize carbohydrate than immature fish as they valorize the energy from fats and, thus, have a low quantitative protein requirement. Addition of liposoluble vitamins and essential fatty acids in diets is necessary for normal reproduction, but fatty acids of the n-6 groups can play a more pronounced role in juveniles. Lipid and fatty acid profile of broodstock diet are regarded as major dietary factors detrimental for successful reproduction and survival of the offsprings. Also, it is observed that some species have capacity to incorporate dietary unsaturated fatty acids into eggs, even during the course of the spawning season. Alike the higher vertebrates, vitamin E deficiency affects reproductive performance, causing immature gonads and lower hatching rate and survival of offspring. Furthermore, the role of dietary supplements on quality of broods, offsprings, and even maturation time has been well documented. The

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available literature on various research outputs with regard to broodstock nutrition has been synthesized here. Thus, considering prominent role of the dietary factor in fishes, this chapter emphasizes the various nutritional strategies and role of various maturation and reproduction enhancing diets covered in finfishes.

Keywords

Broodstock · Energy · Egg quality · Protein · Fatty acids · Vitamin E

Introduction

Nutrition is one of the key aspects which decide the reproductive outcome in vertebrates, including fishes. Enhanced reproductive performance demands adequate nutrient inputs in order to supply and maintain the intensive energy demands for the developing gametes. A precise understanding about the sequential interactions between nutrition and reproductive process is imperative in formulating and developing designer feed to meet the increasing energy demands and hence redirecting the positive physiological aspects of fish reproduction. A good number of researches have been reported which examined the effects of different plant- and animal-based functional foods on early life stages and the broodstock reproductive performance in aquatic animals. In general, several studies have shown that decreased food availability/starvation causes gonad regression, with subsequent cease in spawning function as well as volume of eggs released, whereas abundant availability of food promotes growth and larger body sizes, resulting in timely maturation and increased fecundity in some species. It is well-known that the nutrient needs of fish groups differ in different life stages. Also, the complex morphological and physiological adaptations universally alter feeding and nutritional requirements of the species. In this midst, the function of few key nutrient components can improve the breeding performance of fish. For instance, inclusion of dietary lipids in broodstock feeds can improve the gamete quality, and so are the dietary protein sources and amino acids. The biological functionality of amino acids is manifold, as they take part in nutrient utilization, feed intake, and overall reproductive performance (Li et al. 2009; Wu 2009).

Life Stages in Fish Reproduction and Energy Demands

The reproductive cycle in fish includes a sequence of successive changes leading to progeny formation through fertilization of viable eggs by the spermatozoa as depicted in Fig. 17.1. Hence, the viability of the process is very much dependent on the successful advancement in each exercise involved in reproductive cycle. Here, broodstock nutrition is critical in many of these processes which decide the reproductive success. When immature juvenile fishes which can be said to be sexually quiescent reach a particular size, they will undergo puberty stage and finally

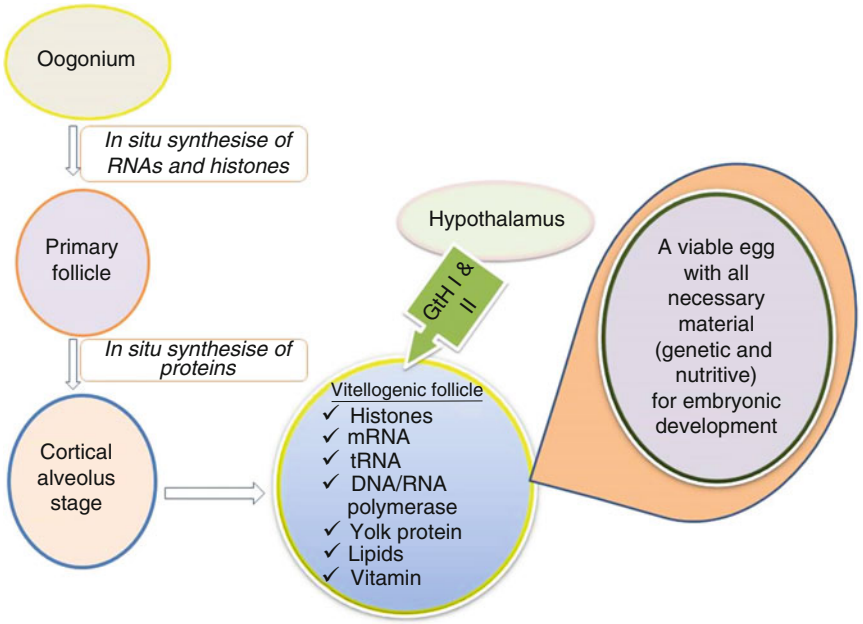

Fig. 17.1 A pictorial representation of reproductive process in fishes

on maturity start to release gametes and externally show sexual behavior. In general, the reproductive cycle comprises two distinct phases, i.e., gonadal growth and development collectively included as gametogenesis and the maturation phase, with a subsequent release of gamete and spawning commencement which follows gonadal recrudescence or the resting phase. In most cases, the mode of fertilization is external in water in majority of fish species documented.

Oviparous fishes release eggs into the environment to be fertilized externally, whereas in the case of viviparous fish species, fertilization is internal, and females produce living young ones, in which developing eggs/embryos are retained within the maternal reproductive tract. Once mature, most fish exhibit marked seasonality in their reproductive cycle, which is synchronized by annual variations in environmental factors like photoperiod, water temperature, and food availability. Spawning/mating usually occurs at specific periods of the year that coincide with optimal environmental conditions (high food availability) for growth of the offspring. Reproductive cycles are further influenced by nutritional status, besides release of gametes being controlled by the hormones. In the course of the maturing phase of the adult reproductive cycle, gonads develop until they reach a maximum size during the spawning season and produce gametes. During egg formation, females invest considerable energy to supply the egg with nutrient stores (yolk/vitellogenin). A variety of techniques is to evaluate reproductive situation in fishes, together with examination of the gonads, dimension of sex steroid level, and gonadal indices. The *gonadosomatic index*, abbreviated as GSI, is the calculation of the gonad mass as

a proportion of the total body mass. It is a tool for measuring the sexual maturity of animals in correlation to ovary development and testes development. It increases with the maturation of the fish, being maximum during the peak period of maturity and declining abruptly after spawning. The *number of eggs produced* by a *fish* differs in different species and depends on the size and age of the *fish*. It may *also* differ in different races of the same species. Thus, *fecundity* is a *measure of the reproductive capacity* of a *female fish* and is an adaptation to various conditions of the environment.

Endocrine Control of Reproduction

The endocrine system regulates the internal responses of the fish according to the cues received from changes in the external environmental factors. In fishes as well as many other vertebrates, reproductive process is coordinated and controlled by the hypothalamus-pituitary-gonadal (HPG) axis (Rather et al. 2017, 2020). First the hypothalamus produces gonadotropin-releasing hormone (GnRH), which regulates the synthesis and release of pituitary gonadotropins like luteinizing hormone (LH) and follicle-stimulating hormone (FSH) (Rather et al. 2016). These gonadotropins further will react on the gonads which stimulate gonadal development by secretion of sex steroid hormones. These steroids then relay the message back to the brain and the pituitary in a feedback mechanism.

It is seen that fishes often try to regulate their reproductive physiology as per the available energy reserves. For instance, food deprivation, leading to energy exhaustion, inhibits the HPG axis as a compensatory mechanism for energy saving to perform vital functions. A number of peptides are known to regulate both feeding and reproduction of both mammals and fish. Some significant peptides include brain factors (neuropeptide Y (NPY) and orexin), as part of few peripheral factors like leptin and ghrelin.

Effect of Nutrition on Fish Reproduction

In wild, fishes are often challenged with limited supply or deprivation in food during their life cycle, particularly during the seasonal cycles and spawning migrations. The sensory and endocrine systems sense these extrinsic and intrinsic circumstances like size, age, and storage of macromolecules (sugars, amino acids, and lipids) and react on prevailing conditions for reproduction to proceed further. Reproduction process can be completed only if conditions are optimal; however, it may also be delayed/terminated when nonexistence of the optimal conditions is figured out. In situations like malnutrition, female fishes tend to exhibit serious reproductive failure like inhibition of vitellogenesis, oocyte maturation, and spawning as compared to male counterpart which is particularly reflected in decreased sperm volume and diminished milt fluidity, which negatively affect the success of egg fertilization. However, the mechanisms involved in such complex process still remain unexplained.

Effects of Food Restriction

Most of the research outcomes show high variability with regard to effects of fasting on reproductive consequences in fishes. These accounts mostly due to the dissimilarities in age as well as size at puberty in fishes reported and, further, between different sexes of the same species. It is reported that growth in male groups typically slows when they are small in size and age, as the compared to females. In fishes, puberty is attained only after attaining an optimal age/size. Therefore, this is assured only in conditions where the individuals have stored sufficient energy reserves to overcome the nutritional and reproductive energy required for maturation. It is assumed that the start of puberty in fish is partially connected to the absolute levels/rates of lipid reserves stored. Besides, increased plasma levels of sex steroid too contribute to puberty initiation. The onset of puberty has positive effects on appetite and somatic growth, with relatively larger ones advancing much earlier than smaller ones in a population. However, in its advancement, further energy reallocation from body buildup process to other reproductive expenses like migration and/or sexual behavior continues. Also, it is documented that appetite is often low, just prior to onset and during extended part of the spawning process. Studies have shown that, in few species, feeding restriction lowers energy reserves and adiposity and can lower the population that accomplishes full maturation. In many species, reduction in rate of feeding during maturation decreases growth, GSI, gonadal maturation, spawning frequency, and duration during the reproductive peak periods. There are also cases of sex-specific reaction to the food restriction, with females found to be comparatively responsive. Food-restricted female fishes exhibit decreases in final oocyte maturation and egg quality and produce smaller eggs/hatched larvae, as related to those fed standard food quantity. Additionally, in some fishes, fasting decreases brain GnRH and plasma estradiol levels in female fishes. Therefore, it can be established that fasting negatively inhibits the HPG axis and there occurs a close relationship between food intake and reproduction in fishes.

Effect of Food Quality on Fish Reproduction

Obviously, nutritional requirement are dependent on the species and on their feeding habits, for example, carnivorous fish requiring higher protein level as compared to herbivorous/omnivorous species, and also the requirement variability among marine and freshwater fish species. Regardless of these, nutrition is quite linked to body growth and also interferes directly/indirectly in fish reproductive processes like gonadal development, reproductive performance, spawning rate, fecundity, and egg and sperm quantity and quality, vis-à-vis the quality of offspring. Among the most important nutritional factors, lipids (EFAs), proteins, and vitamins (A, E, and C) are inseparable when reproduction is concerned. Nutrient components like proteins, carbohydrates, and lipids are key nutrient required by the body to metabolize and generate energy needed for various physiological functions. There are considerable variations in the competence of the fish species to utilize these

energy-yielding constituents. This variation is much linked with the feeding habits in the natural environment. Thus, there is a direct connection between feeding habits in wild and the protein needed from diet. It is known that herbivorous and omnivorous fish need low dietary protein than some carnivorous fishes. On the other side, carnivorous species can efficiently utilize dietary protein and lipid for energy but less efficient towards carbohydrate uptake.

Lipids

Lipids and its related fatty acids components play an important part towards accomplishing various metabolic and reproductive functions of fish. Fish growth performance and metabolic efficiency will vary depending on the supplied carbohydrate and lipid levels in diets. Dietary lipids, which include triglycerides, provide energy, and EFA which are essential in maintaining structural and cellular function. However, fish cannot synthesize some of these EFAs, and therefore it is required to be delivered through diet. In fishes, lipids are mostly stored in the muscle tissue and liver, which are further used during period of gametogenesis, relayed to the ovaries and absorbed as nutritive material in the egg/yolk (utilized as the sole food for developing embryo in later stages). It is seen that low levels of lipids and fatty acids in diets have negative effects on reproduction and larval survival in several fish species such as carp, European sea bass, and flounder. Additionally, excess dietary lipid has been reported to cause inadequate protein intake and suppress growth.

Proteins

Dietary protein is relatively expensive, and nutritionists aim to formulate diet in such manner that the energy required by an animal is provided by nonprotein sources. Although lipids are the primary source of energy in fish, dietary proteins supply essential amino acids (EAAs), considered prime for growth and development of fish. A very well-balanced pretentious diet usually increases mean total weight of eggs/female and the number of eggs produced/released by females. Conversely, low-protein diets have been shown to increase maturation time and reduce reproductive performance, oocyte maturation and ovulation, number of eggs produced, and egg viability in some carnivorous fishes like seabream, sea bass, and catfish, often by altering the GnRH and gonadotropin release. Moreover, in some species (e.g., pacu, rohu), an excessive protein diets can additionally set off induced low reproductive performance, fertilization, and hatching rates. However, supplying excessive levels of dietary protein can also increase the excretion of nitrogenous waste with due production of excessive ammonia level, which might affect feed intake and growth and indirectly reproduction of fish. Therefore, there is an obvious need to optimize dietary protein level for better reproduction in fishes. For example, Watanabe et al. (1984a) found an interesting relationship between dietary protein quality and reproductive success. Efforts are also currently being made to replace

fish meal with cheaper, more readily available grain meals. Cumaranatunga and Thabrew (1989) substituted legume meal for fish meal and reported better ovarian growth and significantly larger oocytes, indicating that legume meal is an inadequate source of nutrients for egg production. They attributed this difference to higher level of vitellogenic proteins and or/lipids in fish meal.

Carbohydrates

Carbohydrates, also known as sugars or saccharides, are one of the most essential components of all living organisms, having roles as readily metabolized energy source, as molecules which facilitate transfer of energy throughout the organism and as structural component. The saccharides are divided into four chemical groups: monosaccharides, disaccharides, oligosaccharides, and polysaccharides. Some of the carbohydrate is deposited in the form of glycogen in the liver and muscle, where it is available as a ready source of energy in times of need. Additionally, some carbohydrate is converted to lipid which is deposited in the body as energy reserves. For example, omnivorous/herbivorous freshwater fish can metabolize excessive portions of carbohydrate in diets, whereas carnivorous species make use of it much less efficiently. Very low carbohydrate levels do not compromise reproductive performance. Tolerable levels for carbohydrate varies with the species as a function of feeding habits, with herbivores tolerating the highest levels, accompanied through omnivores and carnivores fishes.

Vitamins

Vitamins are organic substances necessary for health, growth, maintenance, and also spermatogenesis and oogenesis in aquatic animals. It is often not synthesized by fish but is necessary, though in small amounts, for their normal growth, metabolism, health, and also reproduction. Important vitamins include water-soluble vitamins like vitamins B and C (ascorbic acid) and fat-soluble vitamins (vitamins A, D, and E). Vitamin deficiency may result in less growth and impairments in coloration and reproduction. Among these, vitamins like A, E, and C are widely researched in fishes. Requirements of vitamin in different fish species depend on the diet and the structure of the gastrointestinal tract, and within a species, requirements can also vary according to age and the physiological state of the fish. Vitamin E is very crucial for fertility and reproduction in fish, and fishes do not have ability to synthesize vitamin E in their body, so the need for exogenous supply prior to oogenesis is an important determinant of reproductive fitness (Halver 2002; Mandal et al. 2013). Studies have shown that vitamin E influences the quality of gonads, fecundity, egg quality, embryonic development, percentage of fertilization, hatching, and survival of larvae in both herbivorous/omnivorous (e.g., carp, ayu) and carnivorous (e.g., seabream, salmon). Deficiency will result in immature gonads, low fecundity and fertility, and low hatching rates and fry survival. Conversely,

increased levels of dietary vitamin E in diets increase development of gonads and the GSI and gonadal maturation and improve egg quality and viability, hatching rates, and percentage of normal larvae. Vitamin E is a lipid-soluble antioxidant and also reported as important in fish reproduction. Subsequently, vitamin C has an effect on ovarian development, steroidogenesis, vitellogenesis, and embryogenesis. Low level of dietary vitamin C induces a decrease in the reproductive performance of females by reducing fecundity, restricting hatchability, and increasing both the number of deformed larvae and their mortality. It is reported that male fishes are less sensitive to low vitamin C supply as this does not affect sperm motility. Embryos and juvenile fish seem more affected by vitamin C deficiency than adults, due to the fact that these vitamins are necessary for the synthesis of collagen during embryonic development and growth.

Minerals

This nutrient group consists of inorganic elements the body requires for various purposes. Fish require the same minerals as terrestrial animals for tissue formation, osmoregulation, and other metabolic functions. However, dissolved minerals in the water might also satisfy some of the metabolic necessities of fish. Minerals are typically classified as either macro- or micro-minerals, based on the quantities required in the diet and stored in the body. Macro minerals are calcium, phosphorus, magnesium, chloride, sodium, potassium, and sulfur. Minerals like phosphates and calcium are required in the formation of embryos and are acquired through vitellogenin (Vtg) in yolk. In fish reproduction, phosphorus deficiency can induce low female fecundity, low hatchability rates, and high rates of deformities. Calcium is important for activation of eggs, which occurs when eggs come into contact with water for hardening. Micro-mineral deficiencies in diets apparently have no effect growth or reproductive processes however might also have negative impact if fish are exposed for prolonged intervals of time.

Broodstock Nutrition and Reproductive Interaction

In most cases on broodstock nutrition, it is well defined for high-value fishes raised in intensive systems; however, little effort is paid to significantly enhance reproductive success of fishes in low input level farming systems. These days, increased attention is laid towards functional role of different dietary components on broodstock performance. It is reported that EFAs, vitamins like A, E, and C, trace minerals, and carotenoids like β-carotene can affect fecundity, egg quality, hatchability, and larval quality (De Silva and Anderson 1995). It is observed that the dietary amino acid requirements of brood fishes are much like the body requirements of the fishes (De Silva and Anderson 1995). Further, greater variation of the nutritional requirement for fishes of species groups which have consequences on reproductive performances. Common carp, *Cyprinus carpio*, as a model species

has been studied in depth among carps in this regard; however, most other studies have been done for carnivorous fish species (De Silva and Anderson 1995; Izquierdo and Fernandez-Palacios 1997) of marine origin; therefore, reasonably little is known about its condition in freshwater counterparts. In this connection, there seems to be an urgent need to study about the nutritional role on broodstock performance and reproductive function for other commercial freshwater fish groups.

While, the nutritional needs of female broodstock is adequately researched, but the studies on male fishes have received minimal attention. The possibility of improving of sperm quality through dietary induction/supplementation calls for immediate action. Though, initial research has been done quite a long time ago, where Watanabe et al. (1984a) reported that EFA (n-3 PUFA)-deficient diets in red seabream produced eggs with significantly lower survival and high levels of larval deformity. Some other interesting short-term effects of dietary nutrients on males have also been described in this species. For example, it is found that specialized diets given immediately prior to, or during, spawning of red seabream affected the egg composition. Available pigments like carotene, canthaxanthin, or astaxanthin also have a role on improving buoyancy of eggs. Looking at these, the dietary role of functional nutrients needs to be evaluated for different steps of broodstock nutrition. Likewise, the nutritional requirements of brood fishes can also vary, which may depend on the reproductive phases. Shortly, these periods can be demarcated as:

- Time between commercial size to broodstock size
- Immediately prior to, or during, spawning
- Post-spawning period

Therefore, designing complete formulated diets should, therefore, be taken into consideration for life stage-specific, as well as species-specific nutritional requirements of the brood fishes. Thus, our research approach and commercial formulation strategies for broodstock diet formulation should be directed towards three specific groups of diets like:

- Conditioning diet
- Reproduction diet
- Recovery/maintenance diet

Firstly, the broodstock conditioning diet can be formulated as an optimized grow-out diet to meet the complete nutritional requirements of the fishes from commercial to broodstock size in maximal synergy with the environment. Further, the reproduction diet used before or during spawning should consider the maximal reproductive performance (spawning success and fecundity) needs, gamete quality, and vertical transfer of nutrients and other biologically active substances to offspring. Lastly, the recovery/maintenance diet should potentially help recover the fishes from reproductive stress and look forward for reconditioning for the next reproductive cycle.

Energy Partitioning for Reproduction

Initially, animal use energy for maintenance requirement of animal then extra energy is splited between growth and reproduction. The relative partitioning of energy between somatic growth and gonadal growth depends on different species or different strains of same species, and more generalizations are challenging to draw. The overall amount of energy on hand for utilization in the various physiological processes has been found to affect the size, quality, and number of eggs produced. In one of the earliest studies of its type, Scott (1962) described a relationship in which various starvation regimes caused regression of the gonads in rainbow trout, *Oncorhynchus mykiss*.

The second is that broodstock on reduced rations grow less throughout the experimental period (6 months) and the proportion of the body present as gonad is greater in the smaller fish. That study is confounded by the fact that the animals fed at 0.35% per day were smaller at spawning than those fed twice as much. However, there is evidence that total egg volume is significantly greater in fish fed a lower ration when the influence of fish size is removed (Bromage and Cumaranatunga 1988). The other effects of reducing rations for rainbow trout are modest reductions in the numbers of fish reaching maturity and a delay of 2–3 weeks in the time of onset of spawning (Bromage and Cumaranatunga 1988). Therefore it is apparent that reducing rations to rainbow trout, and possibly generally, results in reduced egg size but greater relative fecundity.

Effects of Nutrition on Fecundity of Brood Fish

Fecundity can be defined as the total number of ova produced by each fish during the spawning season. It is expressed in terms of either eggs/spawn in case of absolute or individual fecundity or eggs/body weight in case of relative fecundity. The dietary lipid levels from 12% to 18% in broodstock diets for rabbit fish (*Siganus guttatus*) resulted in an increase in fecundity and hatching (Duray et al. 1994). Lipid is one of the major nutritional factors that has been found to significantly affect have a bearing upon reproductive efficacy in fish is the dietary essential fatty acid content (Watanabe et al. 1984a, b). Fecundity in gilthead seabream (*Sparus aurata*) was chanced on to noticeably expand with a rise in dietary n-3 HUFA polyunsaturated fatty acids with 20 or more carbon atoms, essential for marine fish. In research on the reproductive efficacy of Nile tilapia (*Oreochromis niloticus*) as indicated by the number of females that spawn, spawning frequency, collection of fry per spawning and total number of fry production over a 24-week period, the efficacy was much greater in fish fed a basal diet supplemented with soybean oil rich in n-6 fatty acids, predominant for this fish species (Watanabe 1982) and comparatively low in fish fed a 5% cod liver oil-supplemented diet elevated in n-3 fatty acids (Santiago and Reyes 1993). In sparids, the fatty acid composition of the female gonad is greatly plagued by the dietary fatty acid content, which considerably influences egg quality within a short period of time (Harel et al. 1992). In gilthead seabream, the fatty acid

composition of eggs is directly influence by the n-3 HUFA content of the broodstock diet. In some fish species similar to cod *Gadus morhua*, a transparent impact of predominant fatty acid on fecundity was not noticed in fish fed commercial diets coated with different types of oils (Lie et al. 1993). However, dietary EFA deficiencies causing detrimental consequences in fish and their extra have been also reported to have a negative impact on reproductive efficacy of fish species. For example, higher levels of dietary n-3 HUFA decreased the total amount of eggs produced by gilthead seabream broodstock spited an increase in egg n-3 HUFA concentration (Fernandez-Palacios et al. 1995). Other nutrients which were proven to affect fecundity include vitamin E (Izquierdo and Fernandez-Palacios 1997; Fernandez-Palacios et al. 1998) and ascorbic mg/kg resulted in an enhancement in fecundity of gilthead seabream as expressed by the total number of eggs produced by female and egg viability. Vitamin C content of rainbow trout eggs manifested the content of this nutrient in the diet and was related to improved egg quality (Sandnes et al. 1984). Dietary tryptophan, a precursor of the neurotransmitter serotonin, may positively impact gonadal maturation of both males and females. Supplementation of 0.1% tryptophan in the diets of ayu (*Plecoglossus altivelis*) resulted in a significant increase in the serum testosterone levels thus advancing time of spermiation in males and induced maturation of females (Akiyama et al. 1996).

Impact of Diet Quality on Reproductive Output

There are very few studies pertaining to a particular nutrient requirement of aquatic animals for proper gonadal development, but few reported indicate a great variability on species experimented. Watanabe et al. (1984c, d) observed that low-protein, low-phosphorous, and EFA-deficient diets produced eggs significantly low in hatchability, with higher lot of the hatched larvae showing signs of deformity. They underline that the most significant nutrients comprise of n-3 PUFA, which are found to be high in eggs of broodstock-fed diets with high levels of n-3 PUFAs. However, they fail to define clearly the relationship between quality of eggs and their fatty acid distribution. Subsequently, Takeuchi et al. (1981) reported that fish fed on diets without supplemental trace elements produced significantly lower percentages of both eyed and viable eggs than fish fed a sufficient diet. The contents of manganese, zinc, and iron in the eggs of fish fed diet without supplemental trace elements were also found to be significantly lower. In other studies, feeding broodstock rainbow trout a diet deficient in EFA resulted in low growth rate, low rates of eyed eggs, and low hatchability (Watanabe et al. 1984a).

Feeding Specialized Diets prior to Spawning

Specialized diets provided just prior to or during spawning of can affect the composition of the eggs (Watanabe et al. 1984a). Pigments like β-carotene, cantha-xanthin, or astaxanthin can contribute towards improvement in the percentage of

buoyant eggs. On the other hand, feeding with corn oil can result in reduced viability of eggs. Similarly, fatty acids and vitamin E, but not cholesterol, fed immediately prior to or during spawning resulted in increased levels of these compounds in eggs. Apart from fatty acids and α-tocopherol, numerous other nutrients have also proven to impact reproductive efficacy of marine fishes. However, the consequences in regard to the impact of carotenoid egg content on egg quality in salmonids are contradictory. Limited number of studies has been conducted towards controlling the level of dietary carotenoid equipped in broodstock diets (Harris 1984; Watanabe and Kiron 1995). The addition of purified astaxanthin to broodstock diets for red seabream is known to improve the percentage of buoyant and hatched eggs, moreover because of proportion of normal larvae (Watanabe and Kiron 1995). By contrast, the inclusion of β-carotene has no impact on these parameters. This variability in results is possibly due to the lower intestinal absorption to those compounds. Alternative dietary nutrients which are found to have an impact on the reproductive efficacy of marine fish have included dietary protein and vitamin C. Ascorbic acid has been shown to play vital roles in salmonids reproduction (Eskelinen 1989; Blom and Dabrowski 1995). Rainbow trout (*Oncorhynchus mykiss*) broodstock needs for this vitamin seemed to be about eight times greater than those of juveniles (Blom and Dabrowski 1995). However, less demands for ascorbic acid are according in broodstock diets for cod (Mangor-Jensen et al. 1993). Supplemented dietary vitamin E up to 250 mg kg^{-1} can be helpful for improving the sperm and egg quality of Black Sea trout.

Supplementing Plant Extracts for Early Maturation

The functional role of several herbal products towards maturation of fishes is well studied, and several herbals are found to have aphrodisiac properties and have control on the reproductive success and larval quality. The herbal maturation diet triggers maturation by reducing stress and regulate the hormonal cycle. Commercially available herbal maturation diet such as *Nutra-Brood* (manufactured by Australian-based feed company) contains adaptogenic, hepato-protective, antioxidant and immune-modulating herbal extracts. These also enhance the hepato-pancreatic activity and thus contribute towards digestive function and nutrient assimilation. There are also reported products with high capacity to stimulate spermatogenesis in male fish and gonadal maturation and effective egg viability in females (Babu 1999). The key advantage of these extract diets links to achieving viable spawners from wild, especially outside the breeding period and a further improvement in egg quality and fecundity. Among many reports, combination of *Withania somnifera* and *Mucuna pruriens* with other herbals could improve maturation and offspring quality of the spent spawners of marine shrimp, *Penaeus monodon* (Citarasu et al. 2013; Babu 1999). Dhas et al. (2015) have reported an elevated level of GSI in the herbal diet (a combination of *Moringa pruriens* (prepared in methanol) *W. somnifera* (prepared in ethanol) and *M. oleifera* (resin)). They also reported an increase in fecundity, fertilization rate, and hatching rate and increased level in

striping response when compared with control (non-supplemented diet). Further, a decrease in the proportion of the deformed larvae and an increase in the populace of normal larvae in diets administered with this formula were reported. Thus, herbal diets can be used to overcome the problems created by the chemical.

Dietary Oils: Plant vs Marine Fish Oils

Dietary oils are considered as predominant nutritional components which modulate many reproductive assignments in fish. Studies with *Dicentrarchus labrax* revealed that PUFAs, particularly *n-3* HUFAs, are among the most important dietary oil components that facilitate a change in sex steroid hormones, which decides fate of fecundity success (Zhang et al. 2017). Effect of supplementation of different dietary oils are found to have effect on the *kisspeptin* system which responds to intrinsic factors like sex steroids and metabolic factors and extrinsic factors like environmental signals (Bogevik et al. 2014). Among different forms, *Kiss2* is known to have better potency than *Kiss1* in stimulating the levels of FSH and LH mRNA in the pituitary (Kitahashi et al. 2009). The expression of *Kiss2* mRNA was higher in the brain and gonad of the male *D. labrax* fed diets with fish oil, while, *Kiss1* expression was similar to those fed plant-/salmon oil-supplemented diets. Further, a delayed maturation in males fed plant/salmon oil, corresponding to higher expression of Cyp19b (a gene initiating gonadal maturation via GnRH stimulation of FSH synthesis) in the brain was observed by these authors. However, possible insight mechanisms revolving around the inhibition of early sexual maturation-associated hormonal gene expression from plant-based fatty acid are yet to be confirmed.

Effect of Food Restriction

Research towards role of feeding rate on reproductive performances of fishes is given little importance. Dietary restriction can be used as a strategy to minimize feed input and reduce production costs. Food restriction is indeed an important aspect from the economical viewpoint as in high-value fishes like rainbow trout. As the high feed cost in feeding carnivorous species like trout and salmon which contributes around 60%–80% of the cost of production. Therefore, the present focus in farming activity is towards feed restriction. Studies in salmonid fishes concealed that restriction of food to half of total ration can deplete the spawning success (Imsland and Gunnarsson 2011) and, in extreme cases, can lead to arrest of reproductive process (Cladwell et al. 2013). Additionally, food restriction can negatively affect egg size and quality of *O. mykiss* (Cleveland et al. 2017). Also, food restriction resulted to higher GSI, thus relating a positive side of the food restriction on reproductive process (Imsland and Gunnarsson 2011; Cladwell et al. 2013). Nevertheless, restriction did not affect hepato-somatic index, which is considered a reliable index of the body reserves which relates to the nutritional status of the species. A beneficial aspect of food restriction is the production of big size eggs with low intra-female size

variability as observed in *O. mykiss* (Cardona et al. 2019). These authors also reported that with no much difference observed in egg lipid content, feed restriction alters the egg's fatty acid composition, where it's composition in restricted female shifted towards higher content of n-6 PUFA and subsequent decrease in MUFA. An elevated level of PUFAs is very much linked to superior quality of the eggs. Among PUFAs, AA, ALA, and EPA in higher proportion in egg play a pivotal role in reproduction (Rønnestad et al. 1998; Torcher 2010). The n-3 PUFAs stored as reserves can potentially be used during developmental process or catabolized for energy release, post-hatching (Torcher 2010). On the other hand, ALA helps in optimum growth, egg development, and offspring survival. Thus, it is obvious that fish fed ad libitum utilize their energy mostly for growth and storage, while restricted fish show tendency for their gonadal development to ensure reproductive success.

Conclusion and Future Direction

Information regarding nutritional requirements of fishes is scarce and confined only to a few species. Key nutrients such as EFAs and vitamins are known to play an important role in successful reproductive program. Besides, minerals, such as phosphorous, and other nutritional aspects, such as protein quality, are known to be essential for fish reproduction. Recent reports on strategies of feeding at and before maturation are deciding factors of reproductive success. The importance of many other nutrients such as vitamin A, vitamin B6, and folic acid is yet to be established within broodstock feeds and deserves future research focus.

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