LIPOSTATIC REGULATION EXPERIMENTALLY PROVOKED IN FARMED ATLANTIC SALMON (Salmo salar L.).

LIANG LIU

Norwegian University of Life Sciences
Department of Animal and Aquacultural Sciences
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Abstract

The present study was conducted to investigate the influence of various salmon fatty accumulations in the early summer on the growth of Atlantic salmon in the following autumn and if this may be linked to sexual maturation preparation. The effect of varying dietary supplementation treatment on the growth of Atlantic salmon was also studied.

During the build-up phase from 21st May to 8th August, the Atlantic salmon was distributed into 3 cages with an initial mean body weight of 1085 g ± 2. Three different pre-diets: T1: 100% original Cod feed, T2: 50% ration of original Cod feed and T3: 100% original Atlantic salmon feed were used in this period. The build-up phase was designed to provoke the varied muscle fat content and body weight in the early summer. Thereafter, in the second experimental period (from 9th August to 6th December), individually marked (Pit-Tag) fish were randomly selected from each build-up group and polled in 12 identical net-pens. Three different autumn diets were supported in randomized block design, which were Control feed T6, Marine feed T4 and Protein feed T5 (Control feed + 2% glutamate/arginine). The influence of different initial muscle fat content in the early summer on the growth rate (SGR and TGC), body weight and muscle fat deposition in the following autumn and if this affects the sexual maturation preparation was determined. We also investigated the effect of different ingredient supplemental diets on the growth of fish.

At the end of the build-up phase, fish fed T3 Salmon diet was shown to have a high muscle fat content. During the second experimental period, glutamate/arginine and rapeseed oil supplemental diets had no significant effect on growth rate and feed utilization. However, significant differences were observed within pre-dietary groups. Fish with low initial muscle fat content obtained a significantly higher growth (SGR and TGC) than their counterparts. Both partial compensation and over-compensation

had been achieved in the study. The obtained differences in growth and fat content accumulation could be considered as results of lipostatic regulation, meanwhile that also might be closely linked to the sexually mature preparation. We thus presumed that fish will slow down or even stop their fat accumulation once certain fat and energy reserves have been achieved according to lipostatic regulation and/or sexual maturation.

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1 Introduction

With the wild aquaculture resource decreased rapidly, domesticated and farmed aquaculture species are therefore a sustainable way to address the irrational resource deficit issues. World fisheries production, by capture and aquaculture in 1970 was 62.81 million tons and 2.56 million tons respectively. Afterward, world aquaculture production increased steeply and arrived at 55.68 million tons in 2009 (FAO 2012). Aquaculture industry was engendered and developed in a rapid rate in the worldwide in these decades and generated the modern, highly efficient and well structured fishery industry. In Norway, farmed Atlantic salmon intensely contributes to the Norwegian salmon production, which is now the fourth biggest export commodity, and with a total Atlantic salmon production of 1,006,000 tons in 2011, Norway is the largest Atlantic salmon producer and exporter in the world (Liu Y, et al. 2010; Kontali Analyse 2011).

To achieve the optimal production of Atlantic salmon, environmental factor is a prerequisite meanwhile rudimentary understanding of energy and nutrient balance should be focused. Björnsson et al. (1989) concluded that both photoperiod and temperature are important environmental parameters that affect plasma growth hormone levels in juvenile Atlantic salmon. There is no doubt that the energy and nutrient balance is a basic and original requirement in all livestock production. Furthermore, in farmed salmon industry positive energy and nutrient balance contributes to a healthily growing throughout the entire salmon life stage and eventually leads to high production prior to the sexually mature season. Exclude these primary factors surrounding circumstance, basic understanding of energy and nutrient balance, perfect management and modern technical utilizing are also essential and vital to form and support a well produced fishery. Fats and lipids are very important nutrient factors and deposit as energy inside the fish body. Fats is digested and absorbed by fish in their digestive system, and eventually used as a functional

component to provide energy and build body tissue. Plant oils like rapeseed oil and soybean oil used as a sustainable resource are also extensively supplied as supplementary ingredients to replace fish oil in the fishery industry (Bell et al. 2001; Torstensen et al. 2004a, b).

When the energy balance (the difference between energy gain and expenditure) of animals alters by providing the artificial manipulations, body fat content and body weight have been documented to have a variation (Jobling & Johansen 1999). Specifically, fish with extraordinary feeding treatment like food restriction or fed with low fat concentration diet are expected to reduce body weight and fat content; however the compensation responses will be conducted to recover the loss body weight and body fat content to a value close to the original once the food are supplied sufficiently. The original intentions of farmers promote the widely using of high fat and energy concentration diets to obtain the positive energy balance in practical production. Whereas, results obtained by Johansen et al. (2001, 2002) show that extremely high fat content in Atlantic salmon diets may result in negative growth effects, who additionally suggest that fish with varying initial fat content have a further different growth.

The main objective of the present study was therefore to investigate the influence of various salmon fatty accumulations in the early summer on the growth of Atlantic salmon in the following autumn and if this may relate to the sexual maturation preparation. Additionally effect of varying dietary supplementation treatment on the growth of Atlantic salmon was studied.

2 Theoretical background

2.1 Reproduction of Atlantic salmon

In Atlantic salmon (*Salmo salar*, *Salmonidae*), the reproductive process of these anadromous species is characterized by a huge energetic investment that results in a high probability of mortality (Fleming 1996). Sexually maturation of Atlantic salmon may reveal in freshwater called parr maturation (Thorpe 1986), first autumn in sea called jack maturation (Duncan et al. 2002), second autumn in sea called grilse maturation (Duncan et al. 2002) or after two or more sea winters (Alne et al. 2009a) as normally maturation that meets with the commercial goal of farming industry. One of the decisive stages in reproduction of Atlantic salmon is oceanic homing migration. Hansen et al. (1993b) concluded that the oceanic homing migration of sexually mature Atlantic salmon from the feeding areas in the northern Norwegian Sea to native stream in Norway is a precise and accurate ecological procedure. Meanwhile, another vital stage of Atlantic salmon reproduction is smoltification. Björnsson et al. (2007) and Hoar (1988) estimated that smoltification is a complex process where the salmon has to undergo a transformation from a freshwater living parr to a saltwater adapted smolt that coincides with numerous physiological, morphological and biochemical changes. Likewise, mating, spawning and several aggressive behaviors (Fleming 1996; Fleming et al. 1996) are energy demanding bioprocess in Atlantic salmon reproduction.

2.1.1 Spawning and energy utilization

Spawning of Atlantic salmon normally take place in late October and early November, while the accurate spawning duration varies yearly with climatic conditions in the autumn (Belding 1934a). Two alternatives sexually mature males may participate into breeding in freshwater stream with female: parr maturation in freshwater; anadromous

maturation in saltwater (Fleming 1996). Results obtained by Myers and Hutchings (1987b), also indicated that mature male parr may attend to breed with females in the absence of anadromous males. Anadromous males invest heavily in behavioral activities in spawning with females. These male behavioral activities refer to a high energy expenditure bioprocess. Consequently, the strong anadromous male in the big size and healthy body condition is a prerequisite for successful breeding (Jonsson B. et al. 1990). More detail of spawning activities reported by (Belding 1934a and Fleming 1996), illustrates that in mating males tend to press their vents towards the vents of the female, and that spawning takes 5-10 s typically and may perform a consecutive-spawning throughout the 24-hours. Simultaneously, successful female breeding comes with the invigorative female in a proper advantageous position with extraordinary fecundity.

Table 2.1 Gonadosomatic index (GSI) of anadromous and parr Atlantic salmon at maturity. Data (%) are means, with rages in parentheses (ND, no data) (Fleming 1996).

Population	Anadromous		Male Parr
	Female	Male	
Miramichi R.[a] New Brunswick, Canada)	24.1	5	ND
Exploits R.[b] (Newfoundland, Canada)	21	ND	ND
R. Imsa (Norway)	20.3[c] (17.5–24.2)	4.4[c] (3.7–5.3)	9.1[d] (3.9–13.9)
R. Drammen[e] (Norway)	20.1	3.0	ND
Farmed salmon[f] (Norway)	25.7	5.8	ND
River Almond[g] (Scotland)	ND	ND	10 (4.5–12.0)
North Tyne[h] (England)	ND	2.3	4.7

*Data from: [a]Belding (1934a), [b]Sutterlin and MacLean (1984), [c]N. Jonsson *et al.* (1991b), [d]Fleming (unpublished data), [e]N. Jonsson *et al.* (in press 1997), [f]Aksnes *et al.* (1986), [g]Rowe *et al.* (1991), [h]Gage *et al.* (1995).

Whether in terrestrial animal or aquatic animal, spawning is one of the energy consumption biological processes. Obviously, energy utilization in Atlantic salmon breeding in freshwater is well studied (Fleming et al. 1996) in the past decades. One of the primary steps for Atlantic salmon breeding is the investment in gonad. Females, in particularly, invest approximately 20-25% of their body weight into the gonads.

Nevertheless anadromous males invest approximately 3-6% and mature parr accounts for 9% (Table 2.1). Energy investment in gonad of females is approximately six times more than that of males. However, the total energy expenditure of female and male in their breeding process is in the same level about 50% of their overall body energy storage (Jonsson N. et al. 1991b). Female Atlantic salmon cost more than 20% of their body weight into the gonads and egg deposition, while anadromous male Atlantic salmon cover their behavioral activities by lost about 12% of their body weight during the breeding season (Belding 1934b).

2.1.2 Smoltification and the performance of post-smolt Atlantic salmon

The most significant and susceptible life stage of Atlantic salmon production cycle is the incipient moment in the sea water. In the native stream, eggs hatch into alevin or sac fry, and culture in the indigenous freshwater for one to three years until developing into parr with camouflage vertical stripes. Whereafter, freshwater parr further develop into smolt that undergo a transformation from a freshwater living stage to a saltwater dwelling phase for adapting the marine environment, known as smoltification, or the parr-smolt transformation (Björnsson et al. 2007; Porter et al. 1998). This complicated bioprocess provides smolt salmon a new electrolyte balance to accommodate the seawater by osmosis. In 1988, Hoar illustrated that to obtain a normal osmoregulation in hypo-osmotic freshwater environment demands the excretion of large amounts of water as diluted urine and the acquisition of salts from surroundings and diet. While during the hyper-osmotic marine stage an appropriate internal salt concentration and fluid balance require the strict preservation of water, the drinking of seawater and the excretion of salt with urine (Figure 2.1). Meanwhile, the osmoregulation of anadromous fish species is reported abundantly by Wedemeyer (1990); Evans (1980) and McCormick & Saunders (1987).

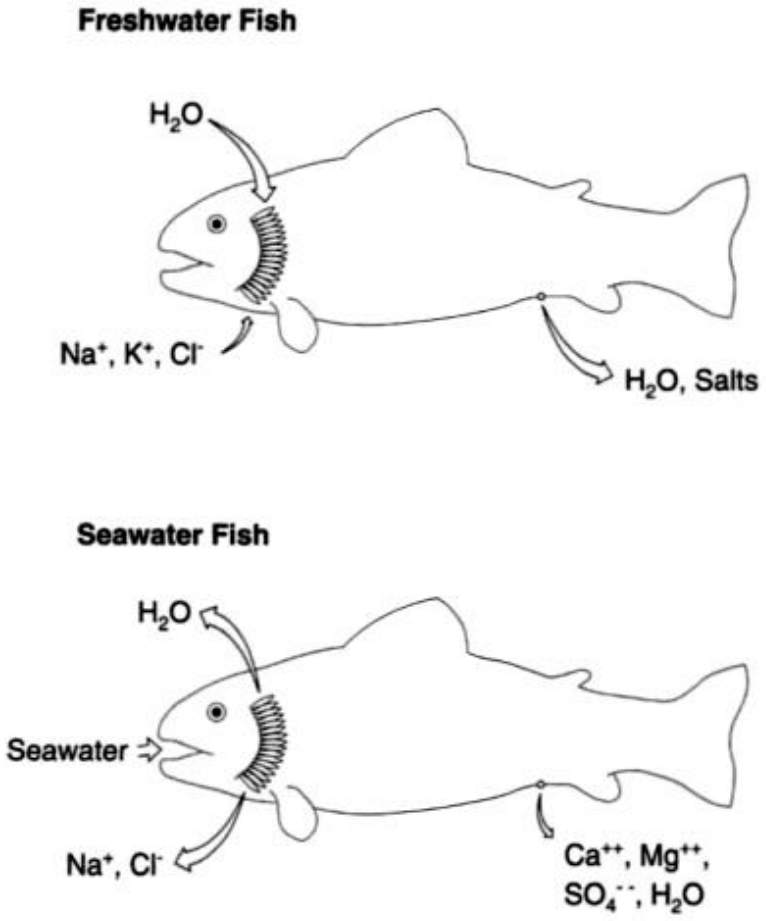

Figure 2.1 Osmoregulation of fish in freshwater and seawater environment.

In the study of the exact timing of the parr-smolt transformation in the Atlantic salmon, Porter et al. (1998) estimates that endocrine hormonal can alter the timing of seawater adaptation in Atlantic salmon parr. Additionally, seasonally changing photoperiod has been strongly admitted as the initial and primary extrinsic environmental parameter in stimulating the endogenous hormonal for the parr-smolt transformation process (Björnsson et al. 1989; McCormick et al. 1995; Saunders & Harmon 1990; Saunders et al. 1985) and temperature, lunar phase, salinity, turbidity and flow rate as environmental factors also influence the smoltification (Björnsson et al. 1989; Hoar 1988). During this critical life stage of Atlantic salmon, physiological, morphological and biochemical changes occur and functional organic changes in gill, kidney, gut, fins and urinary and urinary bladder have a positive effect in marine life of samolt salmon, where increase salinity tolerance and hypoosmoregulatory ability of

Atlantic salmon (McCormick & Saunders 1987). Within duration of parr-smolt transformation, changes in carbohydrate metabolism are reported, where reduction of liver and muscle glycogen occurs, blood glucose thereafter increase in Atlantic salmon. Concurrently, at the final stages of smolting, the hyperglycemic agent adrenaline and noradrenaline all arrives at their highest levels in Atlantic salmon. Changes thus suggest increasing the catabolism during smoltification in Atlantic salmon, which may represent that the parr-smolt transformation is the energetic demand process (McCormick & Saunders 1987).

In commercial production of Atlantic salmon, one of the most value-adding phases is the seawater phase (Oehme et al. 2010). In terms of sea water transfer, two different circumstances are copiously documented depend on the seasonal variation (Alne et al. 2011; Oehme et al. 2010). Firstly, smolt transfer in the autumn, around 8-10 months after hatching and is denoted as S0 smolt, secondly the sea transfer in the spring following their hatching is denoted as S1 smolt. In Norway, the traditional way in the production of smolt is known as S1 or called "in-season smolt", which is under the control of the natural environment. Results achieved by Björnsson et al. 1989; Saunders et al. 1985; Porter 1998 suggest that the seasonally-changing photoperiod and temperature are the primary environmental cues as a means of advancing the timing of smolt transfer. Moreover, these out-of season smolts maintain the same growth potential as smolts reared under a natural photoperiod (Duncan et al. 1998). These procedures thus provide a theoretical principle for "out-of-season smolt" production and ultimately produce smolt Atlantic salmon throughout the annual cycle to make an effort to fresh marketable product.

Alne et al. (2011) concluded that for both S0 and S1 smolt the feeding rate, rate of growth and degree of feed utilization decease during the first spring in sea, where the apparent feed intake in S0 smolt reduces by approximately 50% in the spring. Condition factor (CF), muscle fat and energy retention have been also reported declining during the first spring in the sea for S0 smolt (Alne et al 2011). Nevertheless,

S0 smolt maintain a good growth rate during the sea transfer in the autumn compared with that of S1 smolt (Alne et al. 2011), and results achieved by Lysfjord et al. (2004) suggest that S0 smolt have a higher growth rate and deposit body fat during the first month in the sea. Undergoing a subdued performance spring in the sea, feeding rate and growth have been studied and concluded to increase during the following autumn by glutamate and arginine supplementation dietary treatment (Oehme et al. 2010). In the second period of the experiment from July to September in the study by Oehme et al. (2010) show that specific feeding rate (SFR), thermal growth coefficient (TGC) and specific growth rate (SGR) ($P < 0.05$) increase in supplemented diet group (Table 2.2).

Table 2.2 Feed intake, growth and feed conversion (mean ± SEM, n=3) (Oehme et al. 2010).

		Diet C	Diet E	Feed effect
Period 1	IBW (g ind^{-1})	106 ± 2.7	106 ± 1.3	0.78
	FBW (g ind^{-1})	175 ± 8.3	179 ± 3.6	0.71
	FCR	0.79 ± 0.01	0.80 ± 0.01	0.18
	SFR	0.71 ± 0.02	0.74 ± 0.02	0.07[a]
	SGR	0.91 ± 0.04	0.93 ± 0.04	0.06[a]
	TGC	1.28 ± 0.07	1.32 ± 0.06	0.20
	FI (g ind^{-1})	55.1 ± 3.7	57.9 ± 2.4	0.57
Period 2	IBW (g ind^{-1})	180 ± 7.7	183 ± 4.2	0.78
	FBW (g ind^{-1})	468 ± 24.5	529 ± 10.1	0.08
	FCR	0.84 ± 0.01	0.84 ± 0.02	0.80
	SFR	1.09 ± 0.03	1.21 ± 0.03	0.03
	SGR	1.39 ± 0.05	1.56 ± 0.02	0.04
	TGC	2.32 ± 0.10	2.65 ± 0.04	0.04
	FI (g ind^{-1})	241 ± 16	293 ± 11	0.06

IBW, initial body weight.
FBW, final body weight.
FI, feed intake.
FCR = feed intake (g) / weight gain (g).
SFR = (feed intake during time interval (kg)/average weight during time interval (kg)) × 100.
SGR = ((ln(bulk weight at start of period) − ln(bulk weight at end of period)/days fed) × 100.
TGC = ((FBW$^{1/3}$ − IBW$^{1/3}$)/sum of daily temperatures) × 1000.
[a] Significant block effect ($p<0.05$).

The low-performance of S0 and S1 smolt in their first spring in the sea often coincides with outbreaks of infectious pancreatic necrosis (Rørvik et al. 2007; Alne et

al. 2011), which may act as a negative factor in the growth of smolt. Several other parameters such as season and photoperiod have been stated that may influence the performance of the smolt also (Alne et al. 2011).

2.2 Sexual maturation and reduction of early sexual maturation

2.2.1 Sexually maturity of Atlantic salmon

In commercial Atlantic salmon production, photoperiod as a critical environment cue has been studied abundantly and intensively both in "out-of-season smolt" production aspect and in reducing or postponing sexual maturation side (Björnsson et al. 1989; Saunders et al. 1985; Porter 1998; Duncan et al. 1998; Alne et al. 2009a). Success of the photoperiod technology, artificial photoperiod application or combination of natural and artificial photoperiod procedure, can partially make a contribution to marketable fish of consistent size and quality throughout the year round (Duncan et al. 1998; Duncan et al. 2002). Widely accepted hypothesizes related to Atlantic salmon sexual maturation are that fish must have attained a certain level of fat reserves in the body (Kadri et al. 1996; Thorpe et al. 1990; Alne et al. 2009a), and are that individual fish use a genetically-determined threshold fat level as an indicator for cessation of feeding (Thorpe 1986; Duncan et al. 1998).

Comparison to immature fish, maturing Atlantic salmon accumulates sufficient reserves to surpass a critical threshold and then ceases to feed. During nutrient-accumulation period maturation fish have a larger size and a better body condition. These results are testified by Kadri et al. (1996). In post smolt Atlantic salmon, fish in maturation-preparation stage have a greater growth than their immature counterparts and obtain a preferable development of gonad approximately one year before spawning (Fleming 1996; Arge et al. 2012). Additionally, the body weight of maturing is higher than that of immature fish and the largest body weight

discrepancy appears around June (Aksnes et al. 1986; Kadri et al. 1996). Furthermore, differences in body weight become progressively larger from September to June, whereas body weight start to converge in July as growth reducing in the maturing fish and the body weight of immature fish increasing consistently (Figure 2.2-a). Results obtained by Aksnes et al. 1986, also illustrate that the body weight of immature fish increase gradually, but maturing females gain weight until July and lose weight afterwards. As can be seen clearly from Figure 2.2-b, body lipid of mature fish and immature fish rise sharply in the early winter and increase steadily during the spring. From May to July, percent body lipid increase significantly to peak in June and then drop precipitously in July. Studies suggest that to obtain the desired maturation of post smolt Atlantic salmon, fish may need to accumulate adequate energy to achieve a proper body condition.

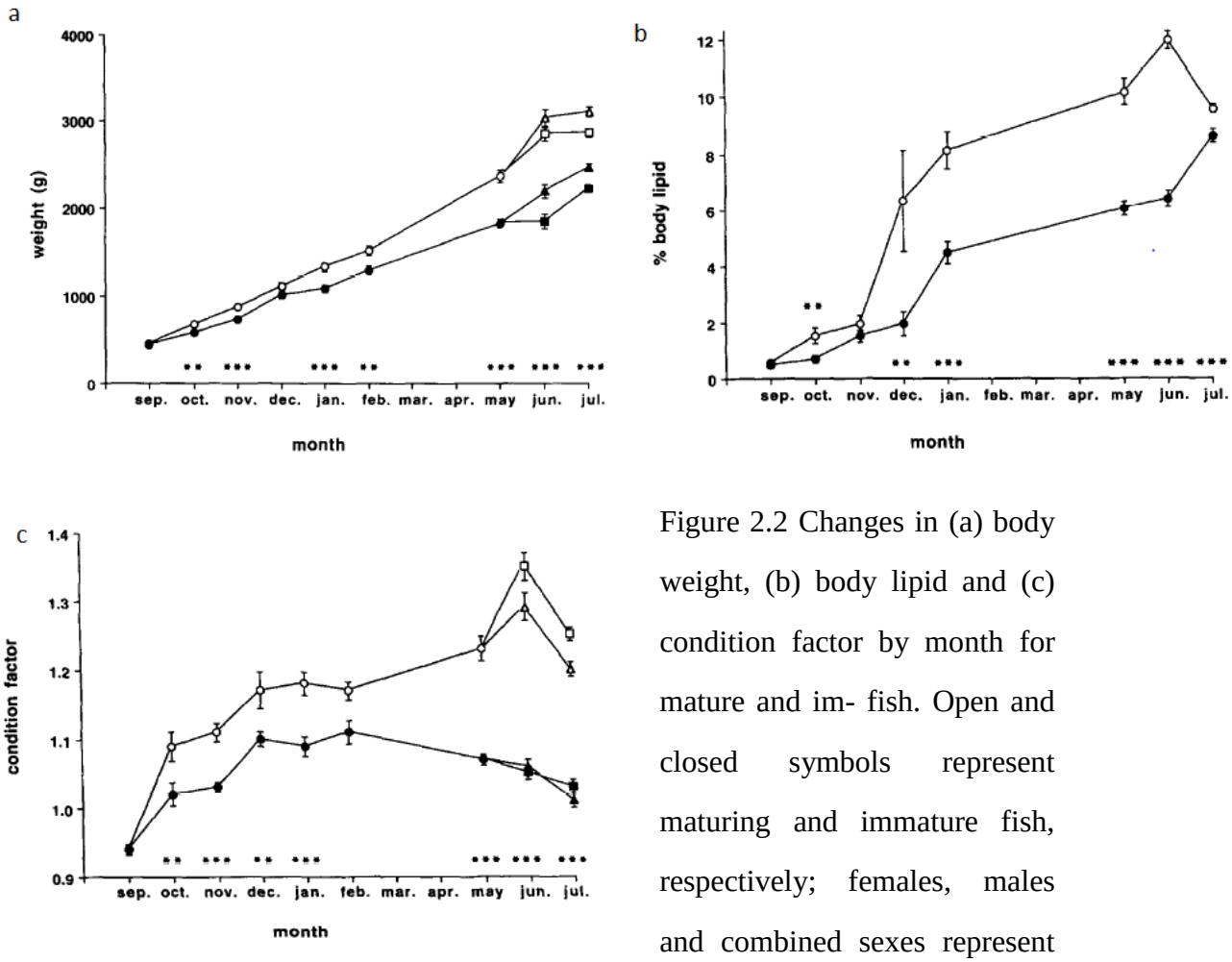

Figure 2.2 Changes in (a) body weight, (b) body lipid and (c) condition factor by month for mature and im- fish. Open and closed symbols represent maturing and immature fish, respectively; females, males and combined sexes represent

by squares, triangles and circles, respectively (Detail see Kadri et al. 1996).

2.2.2 Reduction of early sexual maturation of Atlantic salmon

"Early sexual maturation" as a discouraging factor related to product quality in commercial salmon farming refers to fish acquiring sexually mature either during the first or second autumn in the sea (Alne et al. 2009a). Moreover, sexual maturation results in a reduced growth rate, poor muscle quality and color downgrading, which thus lead to economic losses in Atlantic salmon farming (Aksnes et al. 1986). The basic parameters that affect sexual maturation of Atlantic salmon can divide into internal factors like the growth rate, age at smolting and state of energy reserves and external factors like photoperiod and food supply (Thorpe et al. 1990; Alne et al. 2009a).

Precocious sexually mature has been, and still is, a challenge in Atlantic salmon farming (Thorpe et al. 1990). Consequently, a strong and desired objective on how can we reduce the maturity rate of farmed Atlantic salmon without influencing the growth rate has been studied. Numerous studies demonstrate that restricted feeding or food deprivation in first winter and spring can reduce the maturity rate of fish (Thorpe et al. 1990; Duston & Saunders 1999). Results obtained by Rowe & Thorpe (1990) also support the standpoint that restricted feeding procedure leads to a significant reduction in proportions of male parr maturing April, May and June. Simultaneously, food deprivation in winter reduces the maturity rate significantly (Duston & Saunders 1999), where food deprivation in early winter, late winter and both early and later winter (double deprived) drop the female grilse rate to 4%, 7% and 2% versus 18% in the control. In addition, photoperiod manipulation is an effective tool for reducing or postponing sexually mature (Taranger et al. 1998; Endal et al. 2000; Alne et al. 2009a). Taranger et al. (1998) indicated that the proportion of sexual maturation females reduce from 91% in the natural light group to 67% in the continuous additional light group (treatment range from March to July) and 9% in the continuous additional light

group (treatment range from January to July) , while the similar observation has been found among the males. Photoperiod operation during first winter and spring may also result in a negative performance as maturity rate increasing in an eccentric and undesirable way (Endal et al. 2000).

Tetradecylthioacetic acid (TTA) as a functional saturated fatty acid can reduce early sexually maturation in male Atlantic salmon (Alne et al. 2009a; Arge et al. 2012). TTA has been shown to increase mitochondrial beta-oxidation in white muscle and drop body fat reserves (Rørvik et al. 2007). In the same study, Rørvik et al. (2007) illustrated that the mobilization of stored energy in fish may bring a positive effect during energy demanding periods for the Atlantic salmon. Results achieved by Alne et al. (2011) also indicated that mobilization of deposited lipids increase the amount of available energy for the fish to cover energy deficit during the low performance of Atlantic salmon in the first spring in the sea. Studies have been shown that Atlantic salmon need to accumulate adequate nutrient reserves to surpass a certain energy threshold, and then getting anorexia stage. However, TTA can increase the utilization of deposited lipids and thereafter postpone the timing of exceeding the certain energy threshold; ultimately, reduce the proportion of sexually maturation in male Atlantic salmon.

2.3 Effect of different supplemental diets on the growth of Atlantic salmon

2.3.1 Effect of rapeseed oil replaced diets on the growth of Atlantic salmon

In carnivorous species production like Atlantic salmon, marine fish meal and fish oil have been considered as the main protein and oil sources. Obviously, the commercial Atlantic salmon farming has a intense dependence on fish meal and fish oil, which may affect the production process negatively and decrease the ending production,

since the restricted fish meal and fish oil have been produced yearly, whereas the demand for these commodities by Atlantic salmon production industry will increase in the next decade significantly (Tacon 2004). Hence, the desired sustainable alternatives, for instance, plant products, emerge to liberate the dependence of fish meal and fish oil in commercial production.

There is a congenital defect for plant oils that these vegetable oils do not contain fatty acids longer than 18 carbon atoms and three double bonds and thus lacking the n-3 polyunsaturated fatty acids (PUFAs), which are abundant in fish oil; the n-3 PUFAs, especially eicosapentaenoic (20:5n-3; EPA) and docosahexaenoic acids (22:6n-3; DHA), but plant oils generally contain higher levels of saturated and n-6 fatty acids (Jordal et al. 2007; Torstensen et al. 2004a). Furthermore, the fatty acid composition of the fish tissues mirrors the fatty acid composition of the diets; accordingly replacement of fish oil with plant oil results in reductions of EPA, DHA and the n-3/n-6 fatty acid ratio, and directly affects the nutritional quality of fish (Torstensen et al. 2004a).

Rapeseed oil as a remarkable sustainable substitution for marine fish oil has been successfully used in amounts of previous researches with Atlantic salmon (Bell et al. 2001; Torstensen et al. 2004a, b). Studies show that there are no significant differences found between regular or control diets group and rapeseed oil supplementation group even up to 100% replaced: the salmon weight increased from 0.16 g at start feeing in April 2002 to 103 g at smoltification and sea transfer in February 2003, and further to 890 g in August 2003, and no differences were found in mean body weight, specific growth rate or feed conversion ratio between the two dietary groups during the experimental period (Jordal et al. 2007). Results obtained by Torstensen et al. (2004a, b) also support the previous standpoint that no significant differences are observed in growth between the dietary groups.

2.3.2 Effect of protein supplemental diets on the growth of Atlantic salmon

Protein is the building block of all life and is essential for growth of cells and tissue maintenance. In Atlantic salmon farming, protein is extremely required for growth, normal development, reproduction, health and survival of fish. The primary structure of a protein consists of amino acids, which can divide into two groups, essential or indispensable and nonessential or dispensable amino acids. The essential amino acids are those that the fish cannot synthesize and must be provided through the feeds. While the amino acids can be synthesized inside the fish body to obtain the natural growth is considered as nonessential amino acids. The essential amino acids are: methionine, arginine, threonine, tryptophan, histidine, isoleucine, lysine, leucine, valine and phenylalanine.

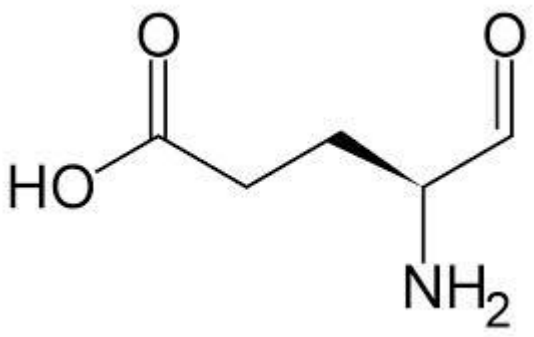

Figure 2.3 The chemical structure of glutamate.

Glutamate a nonessential amino acid (Figure 2.3) is described as the significant mediator of excitatory signals in the mammiferous central nervous systems and may also implicate in the normal brain function, like cognition, memory and learning (Collingridge & Lester 1989). The amino acid glutamate plays a central role in nitrogen metabolism and participates in multiple biochemical pathways (Kelly & Stanley 2001). Specifically, glutamate acts as a principal intermediary in protein synthesis and degradation through fully reversible reactions (see Equation 1).

Aminotransferases, in freely reversible reactions, transfer amino nitrogen to and from glutamate in the degradation and synthesis of amino acids (Kelly & Stanley 2001).

$$[\text{Glutamate} + H_2O + NAD(P)^+ \leftarrow\rightarrow \alpha\text{-KG} + NH4^+ + NAD(P)H \qquad [\ 1\ ]$$

Arginine (Figure 2.4) is defined as an indispensable amino acid for young, growing mammals and for carnivores, but as a nonessential amino acid for healthy humans has been investigated extensively in the past, and results show that arginine serves as a precursor for protein synthesis and production of nitric oxide, urea, polyamines, proline, glutamate, creatine and agmatine (Wu & Morris 1998). Mommsen et al. (2001) illustrated that arginine have a positive effect on hormones release, such as, insulin, growth hormone and glucagon. Cirtrulline and nitric oxide as medium products could be achieved in oxidation of arginine through nitric oxide synthase, where nitric oxide makes a contribution to various physiological functions like neurotransmitter and mediator of the immune response. Additionally, nitric oxide will be oxidized to the stable ending products nitrite and nitrate (Obled et al. 2002).

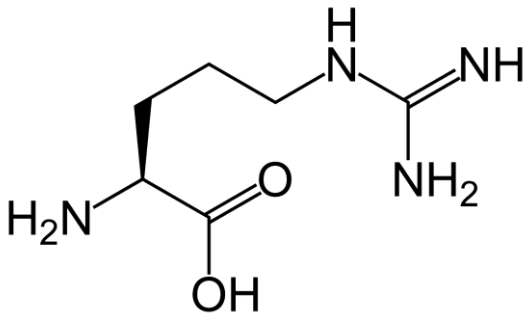

Figure 2.4 The chemical structure of arginine.

Strategic dietary supplements with glutamate and/or arginine may affect the fish performance in an affirmative way (Rørvik et al. 2007). Results obtained by Oehme et al. (2010) show that fish fed the supplemented diet has a higher specific feeding,

thermal growth coefficient and specific growth rate during the second experimental period from July to September. Although no significant differences are found during the first experimental period from May to July, the results achieved during the second period still detected that fish fed functional protein diet has better performance, and a trend for increased final body weight has also been suggested.

2.4 Lipostatic regulation in Atlantic salmon

In terms of lipostatic theory, several definitions should be well introduced that compensatory, or catch-up, growth refers to the growth of fish explode to compensate the lost body weight to a certain value close to the original when the feed restriction or deprivation fish are transferred to the condition of unlimited feed availability (Jobling & Johansen 1999; Johansen et al. 2001). The lipostatic hypothesis was established that adipose tissue has a regulatory role in governing feed intake and body weight by negative feedback circulation; in other words, if a variation in energy balance is sufficient to alter adiposity, a change in feed intake for compensation may occur as a result of the change in the amount of negative feedback (Kennedy 1953). Consequently, with a restricted feeding treatment fat deposition is mobilized and thus resulting in a loss in fat reserves, and eventually leading to an ablation in negative feedback. In contrast, negative feedback appears to increase and arrive at a normal level and the restoration of fat reserves is manipulated once the feeding condition has been acquired in an appropriately available manner (Jobling & Johansen 1999). And the mechanism of these processes could probably be illustrated as that the feeding intake and energy balance regulation commands received from the brain is attributed to humoral signals which are generated according to the size of lipid reserves (Jobling & Johansen 1999). However, specific procedures on lipostatic regulation are still not completely understood (Friedman 1998).

During the critical compensatory growth period, fat reserves are re-deposited gradually relative to body size, and growth compensation comes to a termination once fat reserves restoration has been achieved. Accordingly, results have been obtained that there are two different situations in growth compensation: Partial and Complete compensatory responses (Figure2.5) (Jobling & Johansen 1999; Johansen et al. 2001). Since fat reserves are mobilized and depleted to meet the daily requirement during feed restriction treatment, less energy is available for storage and thus inevitably resulting in lean body mass (LBM). Particularly, in the feed deprivation experiment, endogenous reserves may mobilize and thus dramatically lead to an increasing in the LBM proportion (Johansen et al. 2001). In addition, an inequality feeding regime may occur due to the competition for the limited available resource during feed restriction experiment and generate the variability in growth.

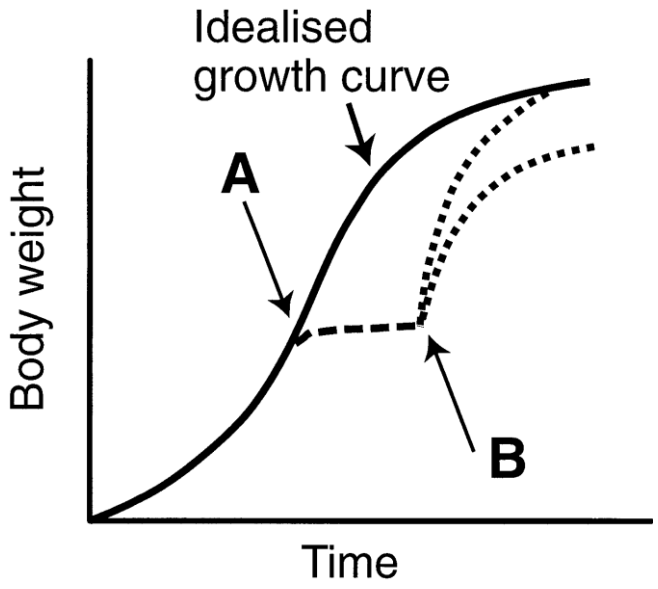

Figure 2.5 The normal growth (idealized growth curve) and deviations from the idealized growth curve during periods of restricted feeding and compensatory growth. The restricted feeding is imposed at time point A, while the full feeding is carried out at time point B. With full feeding treatment, growth rate is incipiently rapid, but then slows down (Jobling & Johansen 1999).

Results obtained by Miglavs & Jobling (1989a, b) conclude that in the experiment with juvenile Arctic char the compensatory responses result in a partial recovery of body weight compared with the control group held by fully feeding. Body weight increases from 8.5 g at the start of the experiment to 54 g after the 16-week trial in fully feeding group. In feeding restricted group, body mass of the fish increase slightly from 8.5 g to 9.5 g in the first 8 weeks, while the body weight increases rapidly from 9.5 g to 35 g in the second 8 weeks since the rich feeding treatment had been introduced. In the experiment with post-smolt Atlantic salmon, a complete compensation after a period of feeding restriction has been achieved, where initial body weight is 73 g and the ending body weight after 16-weeks trial is 276 g and 281 g for control group and feeding restricted group, respectively (Johansen et al. 2001). Although, the hundred-percent compensation can be obtained, fish undergoing the feed-restricted treatment have a leaner body composition once fully compensation completed and still has potential for further growth. Results documented by Johansen et al (2001) give evidence for the previous standpoint.

High fat concentration feeds provides fish adequate energy for maintaining bodily functions and activity effectively and expeditiously and then the remaining dietary resource can be utilized for growth and fat storage (Johansen et al. 2003). Simultaneity, this is the reason for that high dietary fat inclusion feeds have been admitted widely, because these diets are thought to increase body fat deposition directly (Yamamoto et al. 2001a). But passive impact in feed intake and growth may appear due to high fat content in feeds resulting in adiposity, according to lipostatic model (Kennedy 1953; Jobling & Johansen 1999; Johansen et al 2001; Johansen et al. 2002). The results obtained by Johansen et al. (2003) illustrate that when high-fat fish reduce their feed intake, fat reserves in the carcass, low-fat fish deposit fat in all body compartments. Therefore, fish fed high fat concentration feeds may emerge a gradual reduction in growth as the fish become fatter. Trials carried out by Johansen et al (2002) conduct that fish prefer low-fat feed to high-fat feed and leaner fish have a high feed intake comparison with high-fat fish (Figure 2.6), and significant

differences are observed after 8 weeks. In other words, compared to high fat diet, more consumption in a low fat diet appears and is thought to meet the nutrient and energy requirements of fish (Yamamoto et al. 2001a). A hypothesis had been pointed out by Johansen et al (2002) that increasing fat concentration in fish feeds leads to a reduction in ration sizes, which might be considered as a parameter that affects feed: gain ratio in a positive way. Furthermore, long-term supported with high fat feeds may result in the accumulation of body fat in an abnormally high level and thus affect feed intake and ration sizes in a gloomy way. Additionally, fillet fat contents of over 20% may also induce product quality problems (Sinnott 2001; Johansen et al 2003).

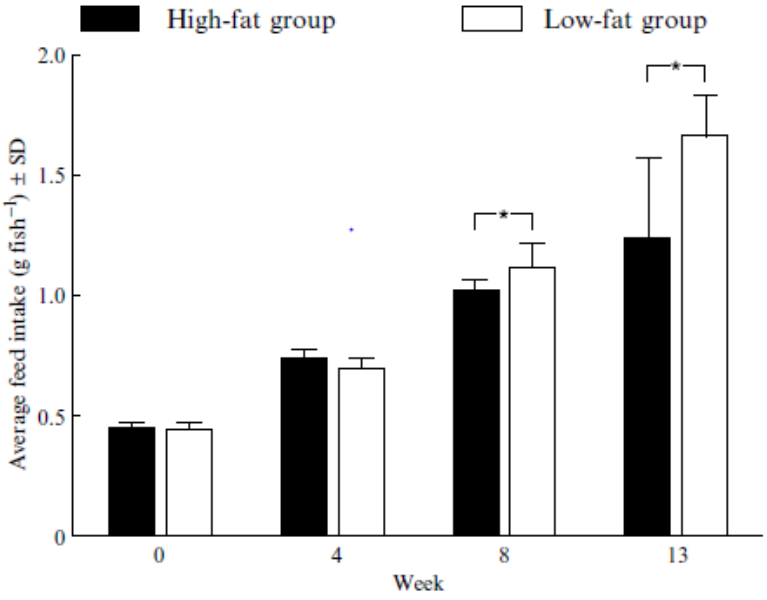

Figure 2.6 Feed intake of Atlantic salmon fed high-fat or low-fat feed during the build up phase (Johansen et al. 2002).

2.5 Objectives

The present study was performed to evaluate the general effect of different initial muscle fat content for Atlantic salmon production during the sea water phase and the effect of different ingredient supplemental diets for Atlantic salmon.

Specific aims:

- Evaluate the impact of various salmon fatty accumulations in the early summer on the growth of Atlantic salmon in the following autumn.

- Whether fish need to deposit a certain fat and energy reserves in the summer and/or autumn for the sexual mature in the following autumn.

- Determine the influence of glutamate/arginine and rapeseed oil supplementation dietary treatment on the growth of Atlantic salmon.

3 Materials and methods

3.1 Fish and experimental design

The feeding trial was carried out at Nofima Marin sea water research station at Averøy, on the west coast of Norway, over a period of six months from 21st May to 6th December. In built-up phase, the Atlantic salmon with an initial mean body weight of 1085 g ± 2 at start of experiment was fed with three different diets, Cod 100 diet (T1), Cod 50 diet (T2) and Salmon diet (T3), in three cages from 21st May to 8th August. Whereafter, in the second experimental period, randomly selected 300 salmons from each cage were tagged and transferred to six net-pens (5 × 5 × 5m) evenly in block one and randomly caught 240 fish from each cage were tagged and transferred to six net-pens (5 × 5 × 5m) evenly in block two. Four net pens were used for each of the three diets marine (T4), protein (T5) and control (T6) treatments in a randomized block design during the second period range from 9th August to 6th December. The net-pens set up in the same pier and evenly divided into two blocks (Figure 3.1). During the whole experimental period of six months at Nofima Marin sea water research station at Averøy, four samplings in 22ed May, 9th - 11th August, 18th - 19th October and 6th – 9th December were done.

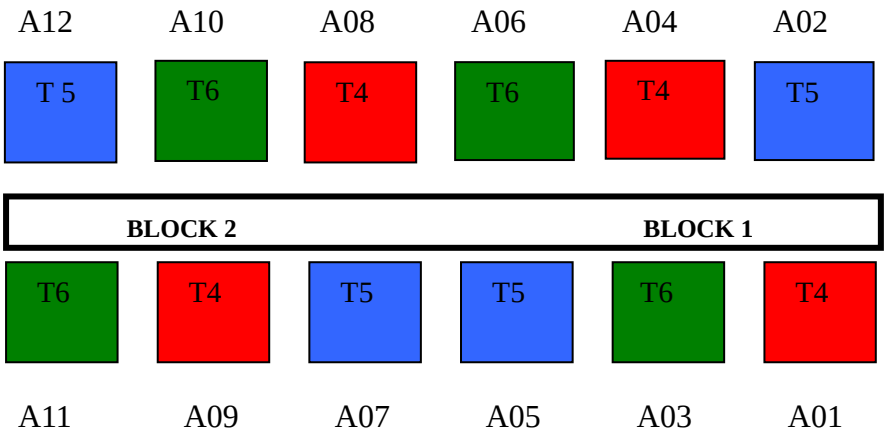

Figure 3.1 the experimental design: The boxes represent the net pens and different

colors and numbers represent the different dietary treatments.

3.2 Feed treatment

The feed used in the build-up phase was original Cod feed and Atlantic salmon feed: T1: 100% original Cod feed, T2: 50% ration of original Cod feed and T3: 100% original Atlantic salmon feed manufactured by Skretting AS, Averøy, Norway. Astaxanthin (0.05 ‰) was coated onto basis Cod diets. During the second experimental period T4 marine diet: 70% marine oil and 30% rapeseed oil and T6 control diet: 30% marine oil and 70% rapeseed oil were pre-produced by Skretting AS, Averøy, Norway. T5 protein diet was achieved as follows: L-glutamate and L-arginine was dissolved in distilled water to an inclusion level of 2% and coated onto the T6 control diet.

Control T6: 30% marine oil and 70% rapeseed oil + standard protein
Marine T4: 70% marine oil and 30% rapeseed oil + standard protein
Protein T5: 30% marine oil and 70% rapeseed oil + High Protein

Fish farmed in net pens was fed abundantly four times per day with automatic feeders, and uneaten pellets were collected rapidly by the feed-waste collecting system after each feeding as described by Einen et al (1999). Each diet was tested for recovery of dry matter under the environmental conditions present during the experiment as described by Helland et al. (1996), and the weight of uneaten feed registered was corrected for dry matter losses during feeding and collection.

3.3 Sampling and recording

3.3.1 Sea temperature

The sea water temperature was recorded everyday from 22nd May to 6th December (Figure 3.2). The sea temperature at 3 meter depths averaged 11.50℃ during the experiment, with a minimum of 7.4℃ at the 6th December and a maximum of 14.9℃ at the 10th -12th September.

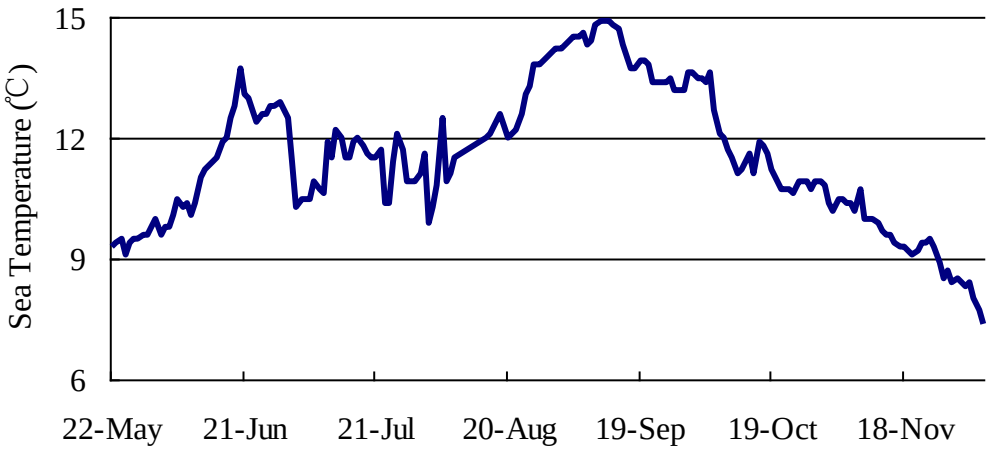

Figure 3.2 sea water temperatures during the experiment from 22nd May 2011 to 6th December 2011.

3.3.2 Sampling and recording

All fish within a net pen were anesthetized in batches in a 1000 liter tank with seawater inside (MS 222 metacaine, Alpharma, Animal Health Ltd., Hampshire, UK, 0.1 g/L) and individual weight of fish was measured at each sampling time-point for the determination of the growth rates. Each of 10 fish from T1 diet group, T2 diet group and T3 diet group, representing the average weight was sampled, killed (gill-cut) and bled in seawater for approximately 10-15 minutes. Fish were selected based on the electronic PIT-tag marked in the abdomen. The fish was therefore transferred to the land based facilities for washing, gutting and filleting to further calculations and measurements. The weight and the length were measured for each fish. All the calculations and measurements were carried out by sophisticated persons. Norwegian

Quality Cut (i.e. the cutlet between the posterior end of the dorsal fin and the gut, NQC; Figure 3.3) was collected and analyzed for fat and pigment content by photographing the fish.

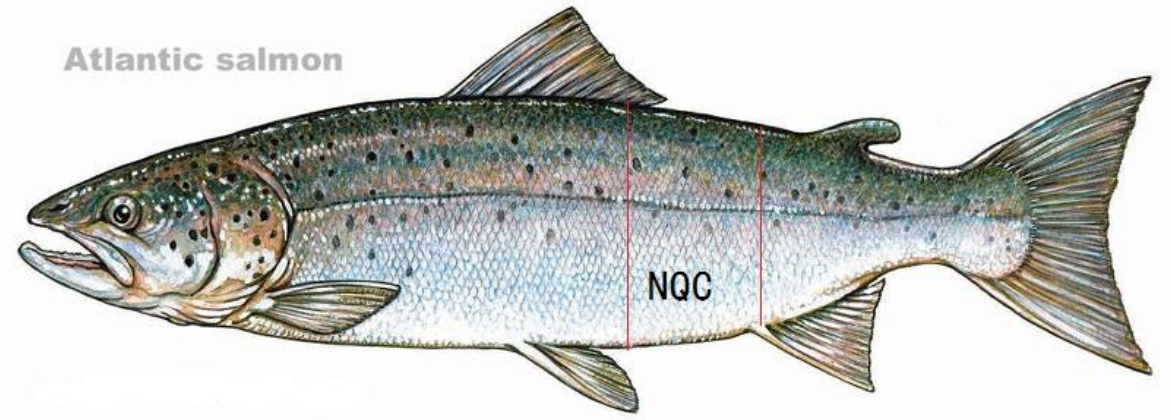

Figure 3.3 NQC-sampling parts for analysis of fat and pigment content.

3.4 Chemical analysis of feed

The diets were analyzed for dry matter, ash, crude protein, crude lipid, starch and energy content. Dry matter was analyzed gravimetrically by drying at 105 ℃ to constant weight, and ash was determined by flame combustion and heating to 550℃ to constant weight. The crude protein was analyzed as Nitrogen x 6.25 using the automated Kjeldahl method (Kjeltec Auto System, Tecator, Sweden). Crude lipid was analyzed by Auto fat extraction system, Soxtec^{TM} 2050 which consist of an Extraction Unit, a Control Unit and a Drive Unit (Sweden). Starch was analyzed as glucose after enzymatic hydrolysis using a Megazyme K-TSTA 05/06 total starch assay kit (Megazyme International Ltd, Wicklow, Ireland). The chemical composition of the experimental diets is shown in Table 3.1 and Table 3.2.

3.5 Fat content of muscle

The left side of fish between the posterior end of the dorsal fin and the gut (NQC) was photographed where used the image analysis system. A digital camera, a calibration

card, standardized illumination and color conditions were the basic configurations and applications of the image analysis system (Folkestad et al. 2008).

Table 3.1 the composition of the experimental diets during the build-up phase from May 2011 to August 2011.

Diets	Salmon diet (T3)	Cod diet (T1/ T2)
Crude protein (%)	33.5	49.9
Dry matter (%)	93.4	91.7
Ash (%)	4.6	7.2
Crude lipid (%)	34.1	17.5
Starch (%)	9.3	6.2

Table 3.2 the composition of the experimental diets during the second period from August 2011 to December 2011.

Diets	Control-7mm (T6)
Crude protein (%)	41.4 (+2% in Protein diet)
Dry matter (%)	94
Ash (%)	4.8
Crude lipid (%)	35.6
Starch (%)	6.1
EPA + DHA	2.9 (+5.5 in Marine diet)

3.6 Calculations

Relative growth rate was calculated as follow:

Relative growth rate = $(BW_1-BW_0) / BW_0 \times 100$, where BW_0 is the initial weight, BW_1 is the final weight.

Specific feeding rate was calculated as follow:

SFR＝(weight of feed supplied x $((B_0+B_1)/2)^{-1}$) x 100, where B_0 is the initial biomass and B_1 is the final biomass.

Feed conversion ratio (Biological FCR) was calculated as:

FCR＝W/(B_0- B_1+B_2), where W is the feed intake during the period, B_0- B_1+B_2 is the weight gain during the period, B_0 is the initial biomass during the period, B_1 is the final biomass during the period and B_2 is the dead fish biomass during the period.

Thermal growth coefficient was calculated as:

TGC＝($BW_1^{1/3}$-$BW_0^{1/3}$) x (∑T) x 1000, where BW_0 is the initial weight , BW_1 is the final weight and ∑T is the sum of day degrees in Celsius.

Specific growth rate was calculated as:

SGR＝((ln BW_1-ln BW_0)/ number of feeding days) x 100, where BW_0 is the initial weight and BW_1 is the final weight.

3.7 Statistical analysis

The experiment was done as a randomized block design and data were statistically analyzed by analysis of variance by using the general linear model or one-way ANOVA, using IBM SPSS Statistics 20 for Windows. A total of six dietary treatments during the experimental period were tested. During the statistical model run net pen was used as the experimental unit, where body weight, SGR, TGC, FCR, SFR and muscle fat content were used as dependent variables. Sampling date, diet and block were used as class variables. The level of significance was indicated at $P \leq 0.05$ and the results are presented as mean ± standard error of the mean (SEM), if not otherwise stated.

4 Results

4.1 Muscle fat content and growth during the build-up phase

Atlantic salmon fed the different diets during spring period had an initial muscle fat content of 12.2% ± 0.2 in May 2011. With Cod 100 diet, Cod 50 diet and Salmon diet treatments, the muscle fat content were measured at sampling in August and indicated to increase at 13.2% ± 0.9, 11.3% ± 1.3, and 16.4% ±1.3, respectively (Figure 4.1). The Salmon diet group had a numerically higher fat content compared with both Cod 50 diet group and Cod 100 diet group, meanwhile Cod 50 diet group had a numerically lowest fat content compared with Salmon diet group and Cod 100 diet group.

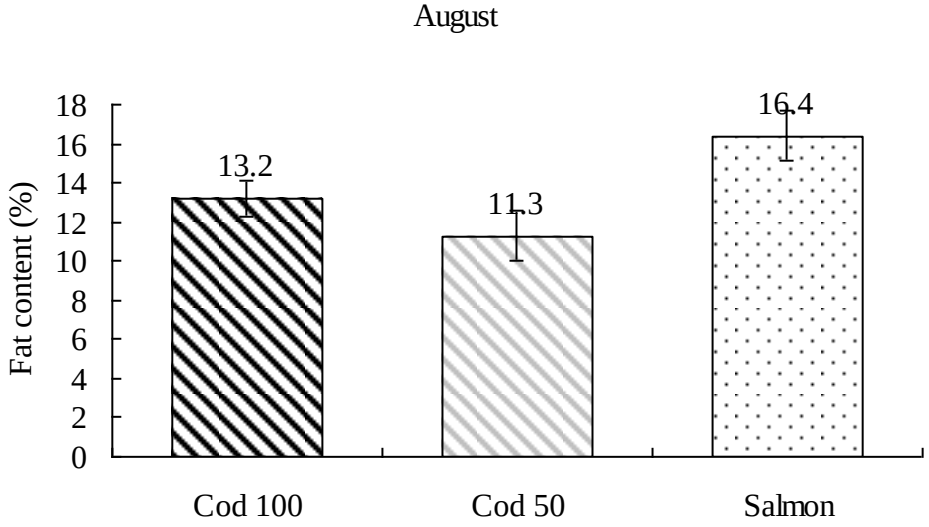

Figure 4.1 the muscle fat (%) content of Cod 100 diet group, Cod 50 diet group and Salmon diet group were measured at sampling in August. Results are given as means ± standard error (SE).

The development of body weight during pre-dietary period in the spring had a numerically variation between Cod 100 diet group, Cod 50 diet group and Salmon

diet group. With an initial mean body weight of 1085 g ± 2 in May, at sampling in August the mean body weight of Cod 100 diet group, Cod 50 diet group and Salmon diet group were increased at 2511 g ± 14, 1879 g ± 12 and 2659 g± 11, respectively (Figure 4.2). Cod 50 diet group had a lower growth rate compared with Cod 100 diet group and Salmon diet group. The mean body weight of Atlantic salmon at August sampling was 2350 g ± 58.

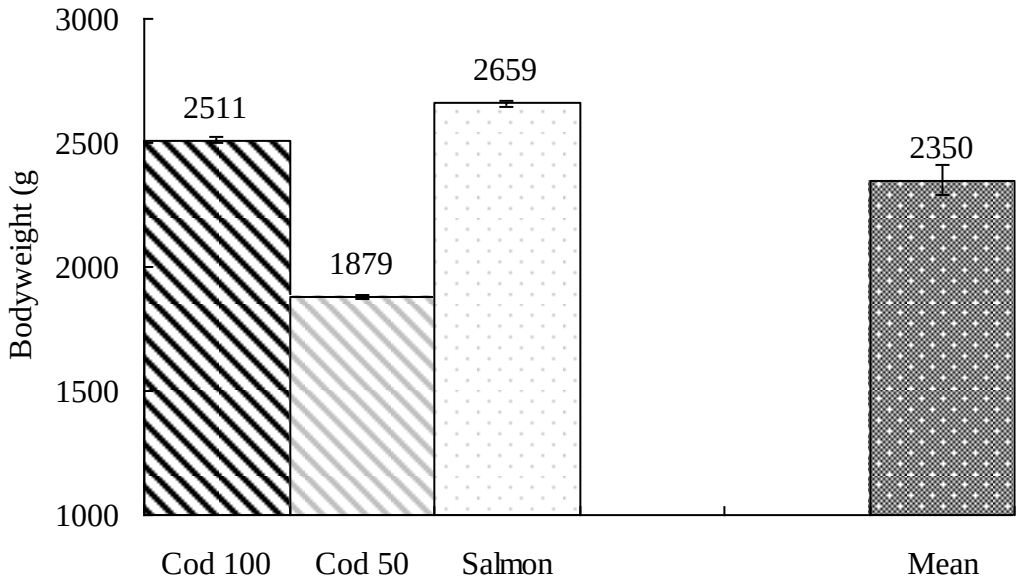

Figure 4.2 Body weight for Atlantic salmon fed Cod 100 diet, Cod 50 diet and Salmon diet in August sampling period. Results are given as means ± standard error (SE).

4.2 Fat content within pre-dietary groups throughout second period

With different muscle fat content in August, Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group were reared throughout the Autumn and early Winter. Significant differences of muscle fat content were found between three different groups at October sampling and December sampling (Figure 4.3).

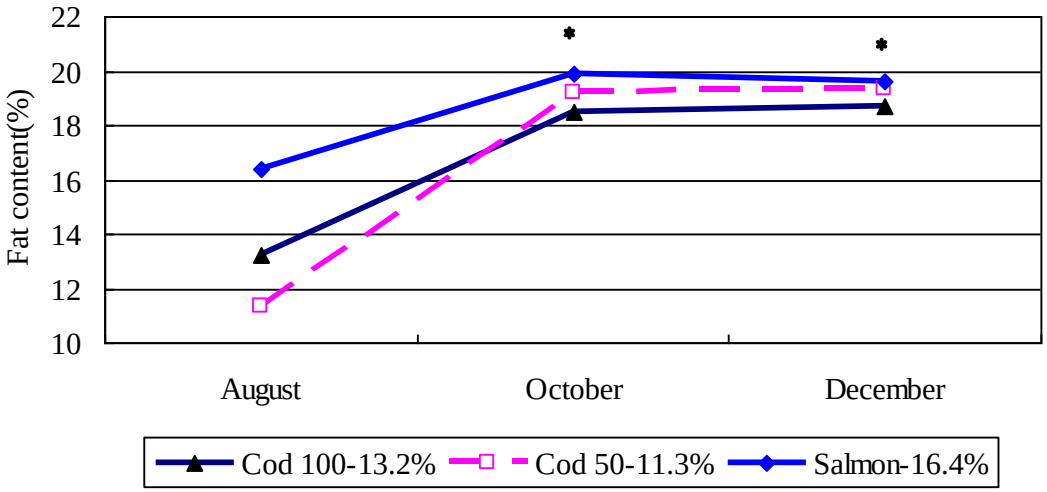

Figure 4.3 Development in muscle fat of Atlantic salmon within Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group during the experimental period, where significant differences were observed between three groups are indicated by *. Results are given as means ± standard error (SE).

The Salmon- 16.4% group (19.9 ± 0.3) had a significantly higher muscle fat content compared with Cod 100 diet group (18.5 ± 0.4) at sampling in October ($P = 0.024$). No significant differences were observed between Cod 50- 11.3% group and Cod 100- 13.2% group and between Cod 50- 11.3% group and Salmon- 16.4% group (Figure 4.4). At sampling in December, Salmon- 16.4% group (19.6 ± 0.2) and Cod 50- 13.2% group (19.3 ± 0.2) had a significant higher ($P = 0.015$ and $P < 0.05$, respectively) muscle fat content compared with Cod 100- 13.2% group (18.7 ± 0.19). Significant difference was not found between Salmon- 16.4% group and Cod 50- 13.2% group (Figure 4.5). Block ($P < 0.0005$) was found to significantly influence muscle fat content at sampling in December, where block one (19.71 ± 0.14) had a significantly higher muscle fat content compared with block two (18.67 ± 0.14).

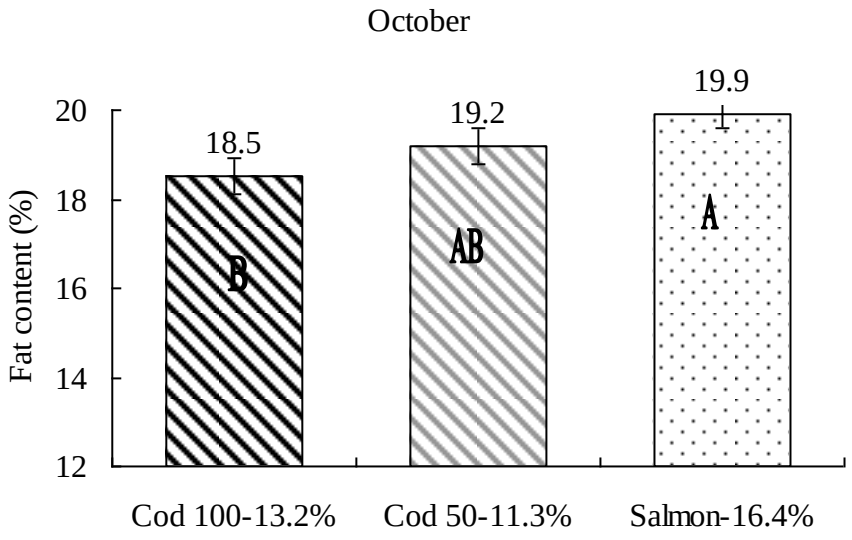

Figure 4.4 The muscle fat content of Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group in October. Results are given as means ± standard error (SE).

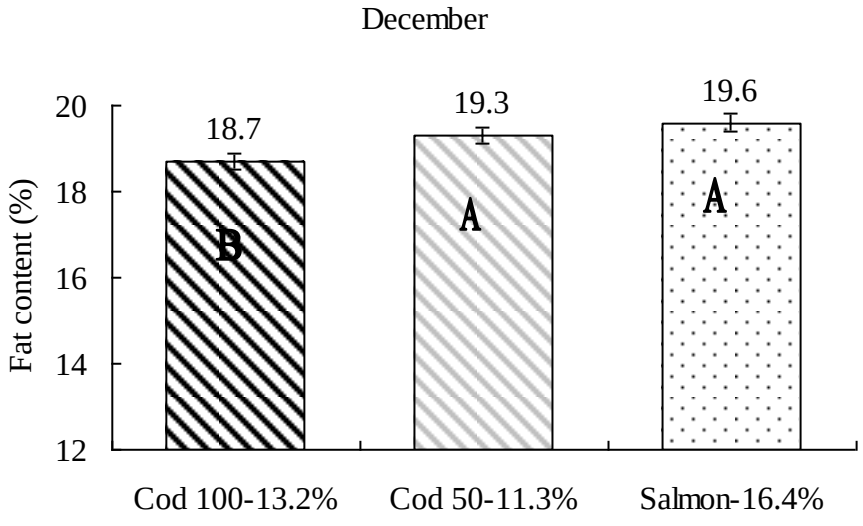

Figure 4.5 The muscle fat content of Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group in December. Results are given as means ± standard error (SE).

4.3 Production date within pre-dietary groups throughout the second period

4.3.1 Specific growth rate (SGR)

Significant differences in mean specific growth rate were observed between Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group (Figure 4.6). The mean specific growth rate (SGR) was significantly higher ($P < 0.0005$) in Cod 50- 11.3% group (0.96 ± 0.01) compared with Cod 100- 13.2% group and Salmon- 16.4% group. Meanwhile, the Salmon- 16.4% group (0.63 ± 0.01) had a significantly lower mean SGR ($P < 0.0005$) than Cod 100- 13.2% group (0.72 ± 0.01). The overall mean SGR of all net-pens was 0.77 ± 0.02.

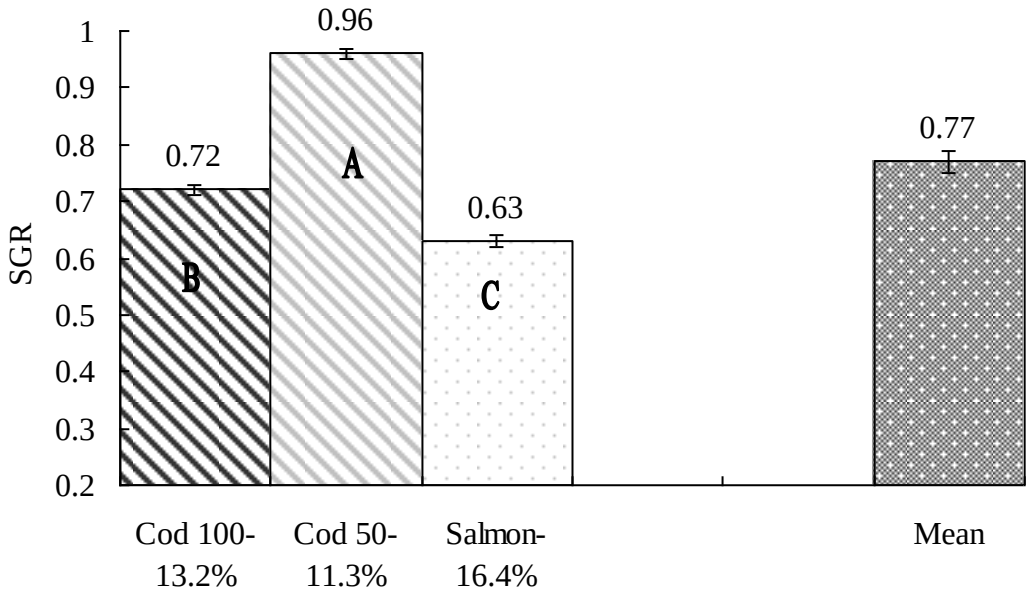

Figure 4.6 Mean specific growth rate (SGR) in Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group. Results are given as means ± standard error (SE). Significant differences were observed between three groups ($P < 0.0005$).

Specifically, during August – October period (Table 4.1), Cod 50- 11.3% group was significant higher than other group ($P < 0.0005$), and salmon- 16.4% group had a significantly low SGR than Cod 100- 13.2% group ($P = 0.001$) and Cod 50- 11.3% group ($P < 0.0005$). Then, during October – December period, Cod 50- 11.3% group ($P = 0.011$) was significantly higher than the other group, and no significant differences were observed between salmon- 16.4% group and Cod 100- 13.2% group.

Table 4.1 Specific growth rate (SGR) in Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group during different experimental period. Results are given as means ± standard error (SE). Significant differences were observed between three groups.

SGR	Aug-Oct	Oct-Dec	Aug-Dec (Mean)
Cod 100- 13.2%	0.92 ± 0.02^{b}	0.42 ± 0.03^{b}	0.72 ± 0.01^{b}
Cod 50- 11.3%	1.26 ± 0.01^{a}	0.52 ± 0.03^{a}	0.96 ± 0.01^{a}
Salmon- 16.4%	0.79 ± 0.01^{c}	0.39 ± 0.02^{b}	0.63 ± 0.01^{c}

4.3.2 Thermal growth coefficient (TGC)

Significant differences in mean thermal growth coefficient were observed between Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group (Figure 4.7 and Table 4.2). The mean thermal growth coefficient (TGC) was significantly higher ($P < 0.0005$) in Cod 50- 11.3% group (3.83 ± 0.03) compared with Cod 100- 13.2% group and Salmon - 16.4% group. Meanwhile, the Cod 100- 13.2% group (3.05 ± 0.03) group was detected to have a significantly higher mean TGC ($P < 0.0005$) than Salmon - 16.4% group (2.70 ± 0.03). The overall mean TGC of all net-pens was 3.19 ± 0.08.

Detailedly, during August – October period (Table 4.2), Cod 50- 11.3% group was

significant higher than other group (P < 0.0005), and salmon- 16.4% group had a significantly low TGC than Cod 100- 13.2% group (P = 0.003) and Cod 50- 11.3% group (P < 0.0005). Then, during October – December period, Cod 50- 11.3% group (P = 0.025) was significantly higher than the other group, and no significant differences were observed between salmon- 16.4% group and Cod 100- 13.2% group.

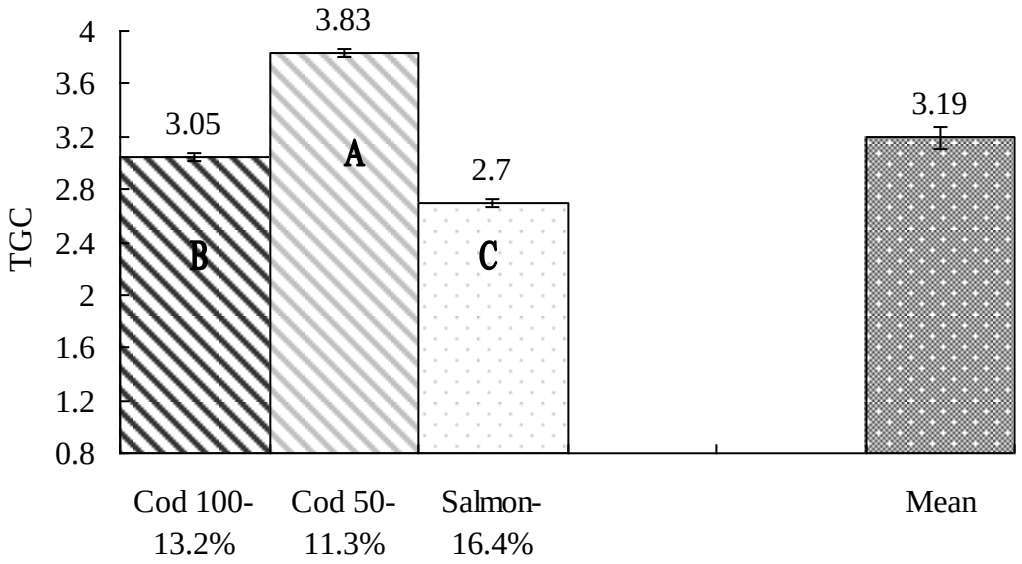

Figure 4.7 Mean thermal growth coefficient (TGC) in Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group. Results are given as means ± standard error (SE). Significant differences were observed between three groups (P < 0.0005).

Table 4.2 Thermal growth coefficient (TGC) in Atlantic salmon of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group during different experimental period. Results are given as means ± standard error (SE). Significant differences were observed between three groups.

TGC	Aug-Oct	Oct-Dec	Aug-Dec (Mean)
Cod 100- 13.2%	3.41 ± 0.07^{b}	2.29 ± 0.16^{b}	3.05 ± 0.03^{b}
Cod 50- 11.3%	4.38 ± 0.05^{a}	2.79 ± 0.18^{a}	3.83 ± 0.03^{a}
Salmon- 16.4%	2.97 ± 0.03^{c}	2.15 ± 0.11^{b}	2.7 ± 0.03^{c}

4.3.3 Body weight and growth

The growth in body weight during experimental period (Figure 4.8) showed that significant differences were observed between Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group in October and December. The mean body weight of Atlantic salmon in the trial was increased steady from 2350 g ± 58 in August to 3847 g ± 54 in October and end at 4750 g ± 35 in December.

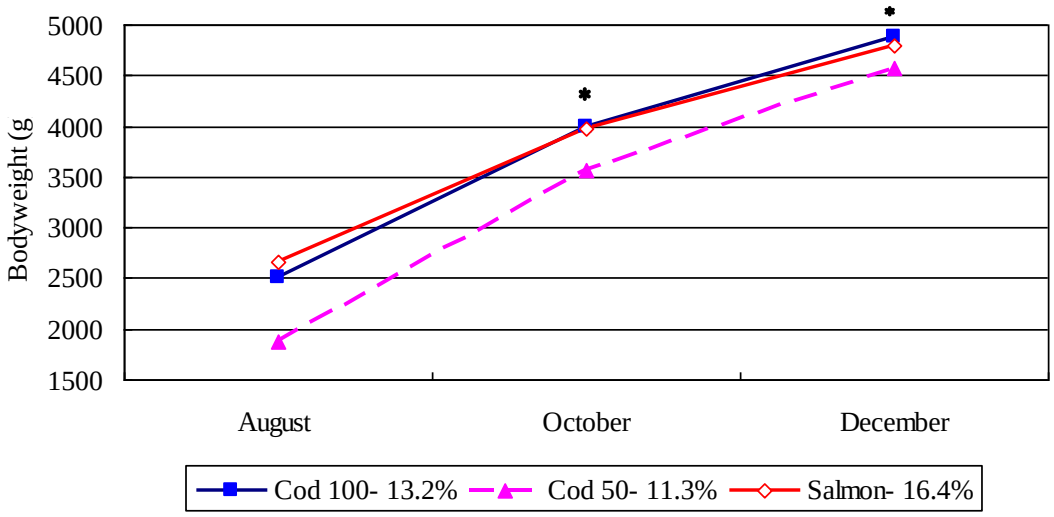

Figure 4.8 Development of body weight of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group during experimental period (from 27th August 2011 to 9th December 2011), where significant differences were observed between the three groups are indicated by *. Results are given as means ± standard error (SE).

At sampling in October (Figure 4.9) significant differences were detected that Cod 100- 13.2% group (3995 g ± 55) and Salmon- 16.4% group (3983 g ± 12) had a significant higher body weight ($P < 0.0005$) than Cod 50- 11.3% group (3563 g ± 44). Significant difference between Cod 100- 13.2% group and Salmon- 16.4% group was not observed during this sampling period. At the final sampling in December (Figure

4.10) Cod 100- 13.2% group (4887 g ± 50) and Salmon- 16.4% group (4796 g ± 38) were indicated to have a significant higher body weight than Cod 50- 11.3% group (4567 g ± 51) ($P < 0.0005$ and $P = 0.004$, respectively). No significant difference between Cod 100- 13.2% group and Salmon- 16.4% group was observed during this sampling period.

The relative growth rate (Table 4.3) was numerically high during the August-October period (First 6 weeks) compared to that in the October-December period (Second 6 weeks) (63.7% and 23.4%, respectively). Especially, in Cod 50- 11.3% group relative growth rate during first 6 weeks (89.5%) was over three times more than that of second 6 weeks (28.18%).

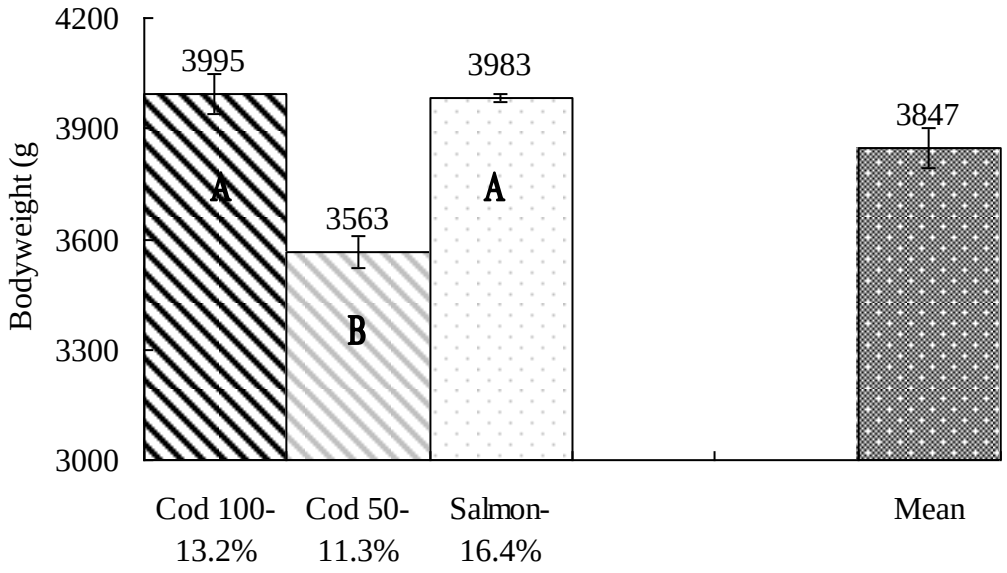

Figure 4.9 Body weight of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group were measured in October sampling period. Results are given as means ± standard error (SE). Significant variations were indicated between Cod 100- 13.2% group and Cod 50- 11.3% group ($P < 0.0005$) and between Salmon- 16.4% group and Cod 50- 11.3% group ($P = 0.004$).

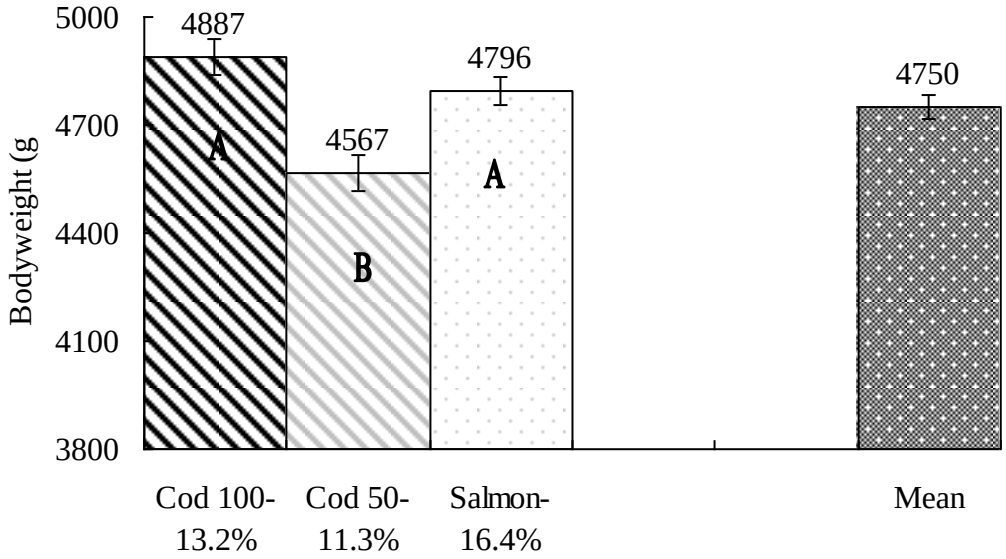

Figure 4.10 Body weight of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group were measured in December sampling period. Results are given as means ± standard error (SE). Significant variations were indicated between Cod 100- 13.2% group and Cod 50- 11.3% group ($P < 0.0005$) and between Salmon- 16.4% group and Cod 50- 11.3% group ($P = 0.004$).

Table 4.3 Relative growth rate (%) of Cod 100- 13.2% group, Cod 50- 11.3% group and Salmon- 16.4% group were calculated during different periods.

Relative growth rate (%)	Cod 100-13.2% group	Cod 50- 11.3% group	Salmon- 16.4% group	Mean
Aug-Oct	59.01	89.6	49.91	63.7
Oct-Dec	22.33	28.18	20.32	23.4

4.3.4 Block parameter

The overall SGR was strongly influenced by block (P = 0.001) (Figure 4.11). The overall SGR within block one and block two were 0.78 ± 0.15 and 0.75 ± 0.14 respectively. The SGR for Cod 100- 13.2% group and Cod 50- 11.3% group was significantly higher in block one compared with block two (P = 0.03 and P < 0.0005, respectively). No significant variation in SGR was observed in Salmon- 16.4% group. Significant differences in TGC and body weight were not observed within block one and block two.

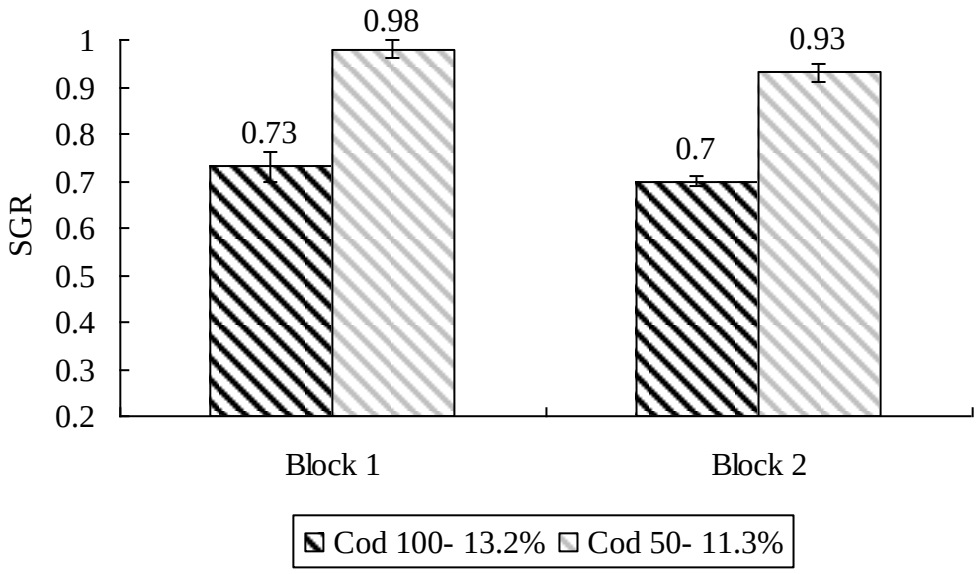

Figure 4.11 Specific growth rate (SGR) for Atlantic salmon in Cod 100- 13.2% group and Cod 50- 11.3% group. Results are given as means ± standard error (SE). Significant variations were indicated between block one and block two (P = 0.03 and P < 0.005, respectively).

4.4 Production date within autumn dietary groups during the second period

4.4.1 Specific feed ratio (SFR)

No significant differences were observed between the three dietary treatments during the whole experimental period (Figure 4.12). Numerically, the SFR for marine diet group, protein diet group and control diet group were 0.79 ± 0.03, 0.82 ± 0.03 and 0.79 ± 0.02 respectively. The mean SFR of all net-pens was 0.8 ± 0.01.

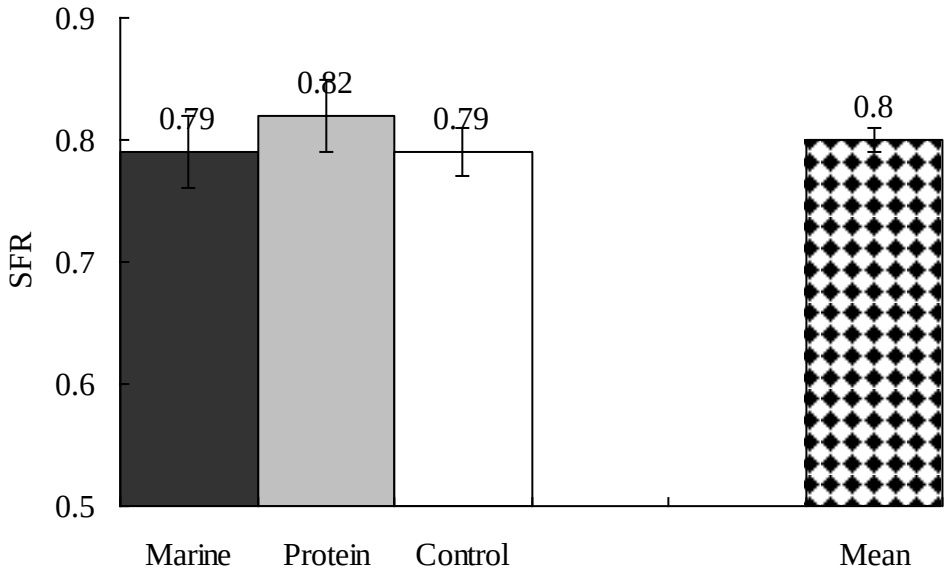

Figure 4.12 Specific feed ratio (SFR) in Atlantic salmon fed marine diet, protein diet – protein supplemented diet and control diet. Results are given as means ± standard error (SE). No difference was observed between three dietary treatments.

4.4.2 Feed conversion ratio (FCR)

No significant differences were observed between the three dietary treatments during the whole experimental period (Figure 4.13). The FCR for marine diet group, protein diet group and control diet group were 1.08 ± 0.02, 1.14 ± 0.02 and 1.08 ± 0.02 respectively. The mean FCR of all net-pens was 1.1 ± 0.01.

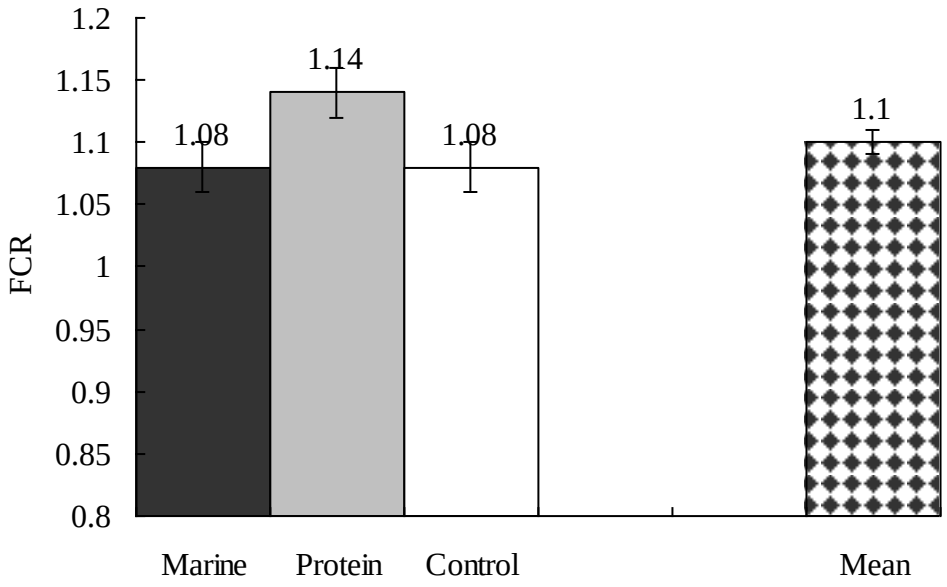

Figure 4.13 Feed conversion ratio (FCR) in Atlantic salmon fed marine diet, protein diet – protein supplemented diet and control diet. Results are given as means ± standard error (SE). No difference was observed between three dietary treatments.

4.4.3 Thermal growth coefficient (TGC)

No significant differences were observed between the three dietary treatments during the whole experimental period (Figure 4.14). The TGC for marine diet group, protein diet group and control diet group were 3.14 ± 0.01, 3.13 ± 0.05 and 3.15 ± 0.03 respectively. The mean TGC of all net-pens was 3.14 ± 0.02.

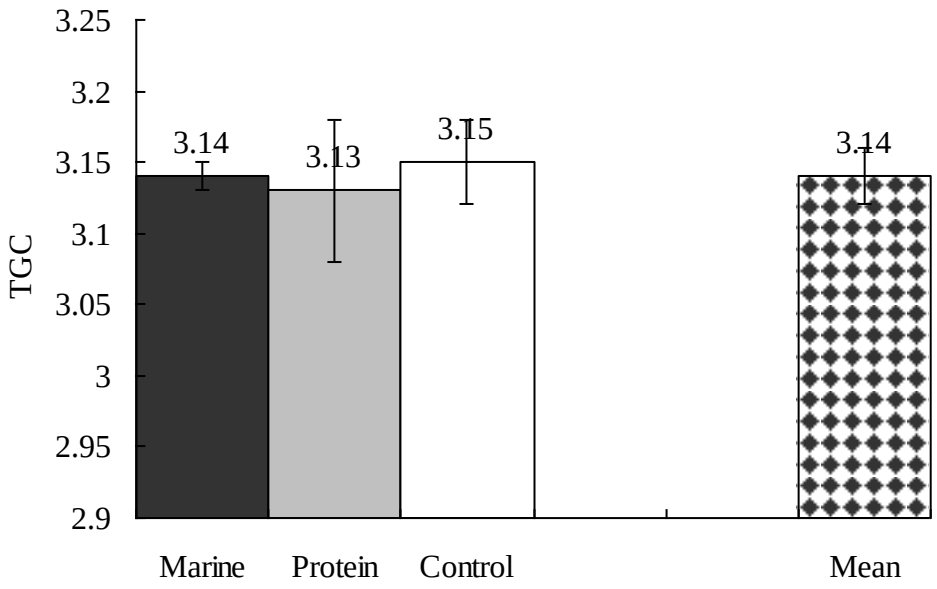

Figure 4.14 Thermal growth coefficient (TGC) in Atlantic salmon fed marine diet, protein diet – protein supplemented diet and control diet. Results are given as means ± standard error (SE). No difference was observed between three dietary treatments.

4.4.4 Body weight and growth

The growth in body weight from 27th August 2011 to 9th December 2011 (Figure 4.15) showed no significant different between the dietary treatments in August sampling and December sampling, but in October sampling (Figure 4.16) the marine diet group (3912 g ± 23) had a significantly higher body weight (P = 0.038) than protein diet group (3765 g ± 40). The mean body weight of Atlantic salmon within the present experiment increased from 2350 ± 29 g in August 2011 to 4750 ± 29 g in December 2011. No significant effect of block was observed during the experimental period.

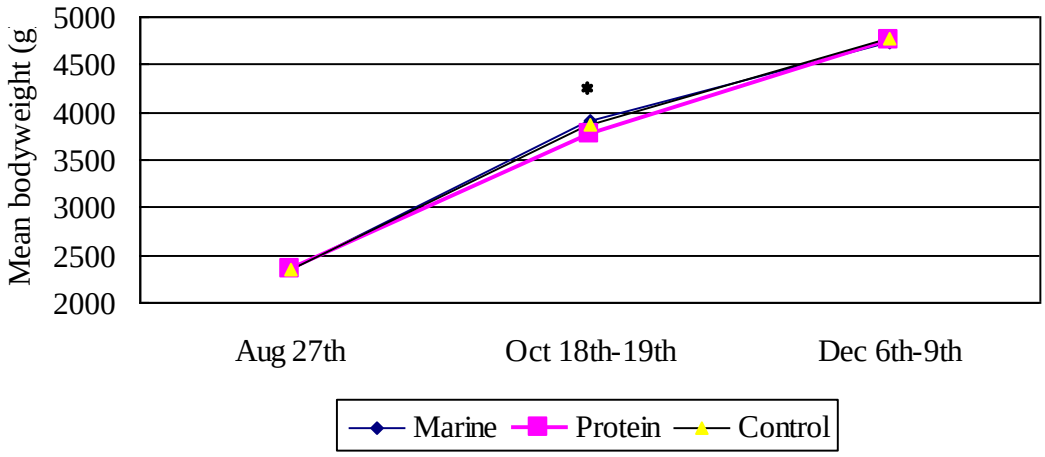

Figure 4.15 Development of body weight during the experimental period (from 27th August 2011 to 9th December 2011). Atlantic salmon were fed marine diet, protein diet – protein supplemented diet and control diet, where significant differences were observed between the three dietary groups are indicated by *. Results are given as means ± standard error (SE).

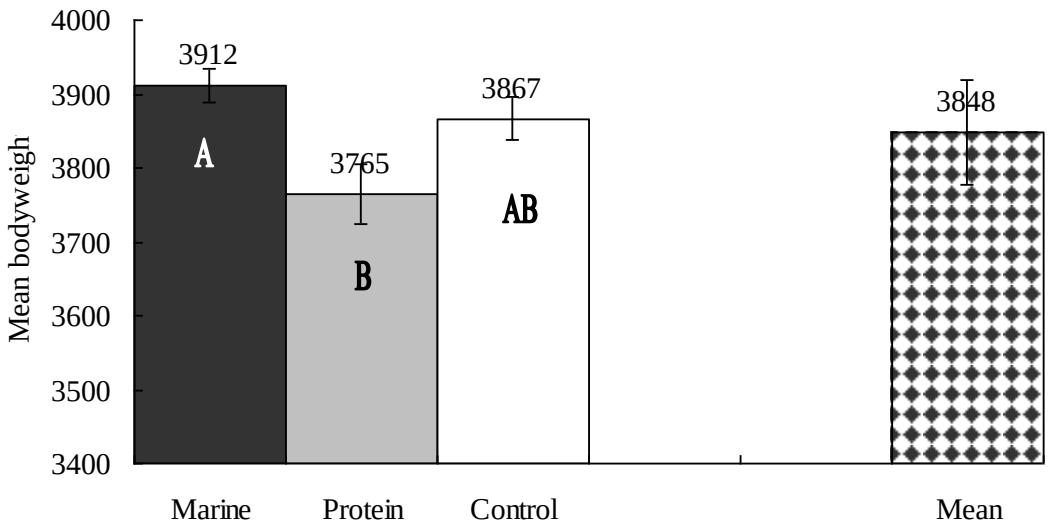

Figure 4.16 Body weight for Atlantic salmon fed marine diet, protein diet – protein supplemented diet and control diet in October sampling period. Results are given as means ± standard error (SE). Significant variations were indicated between marine diet group and protein diet group (P = 0.038).

4.4.5 Block parameter

The overall SFR was strongly influenced by block (P = 0.001) (Figure 4.17). The overall SFR within block one was 0.84 ± 0.03, and the overall SFR within block two was 0.76 ± 0.02. The SFR for marine diet group, protein diet – protein supplemented diet group and control diet group were significantly higher in block one compared with block two (P = 0.005, P = 0.006 and P = 0.027, respectively).

Significant differences in FCR and TGC for marine diet group, protein diet – protein supplemented diet group and control diet group were not observed within block one and block two (Table 4.4).

Table 4.4 Feed conversion ratio and thermal growth coefficient for marine diet group, protein diet group and control diet group within two blocks during the whole experimental period. Results are given as means ± standard error (SE). No significant

variations were indicated within two blocks.

Parameter	Block	Marine	Protein	Control
Feed conversion ratio (FCR)	Block 1 Block 2	1.11 ± 0.00 1.05 ± 0.01	1.17 ± 0.06 1.11 ± 0.01	1.10 ± 0.04 1.07 ± 0.03
Thermal growth coefficient (TGC)	Block 1 Block 2	3.14 ± 0.04 3.13 ± 0.02	3.07 ± 0.08 3.19 ± 0.11	3.14 ± 0.11 3.16 ± 0.00

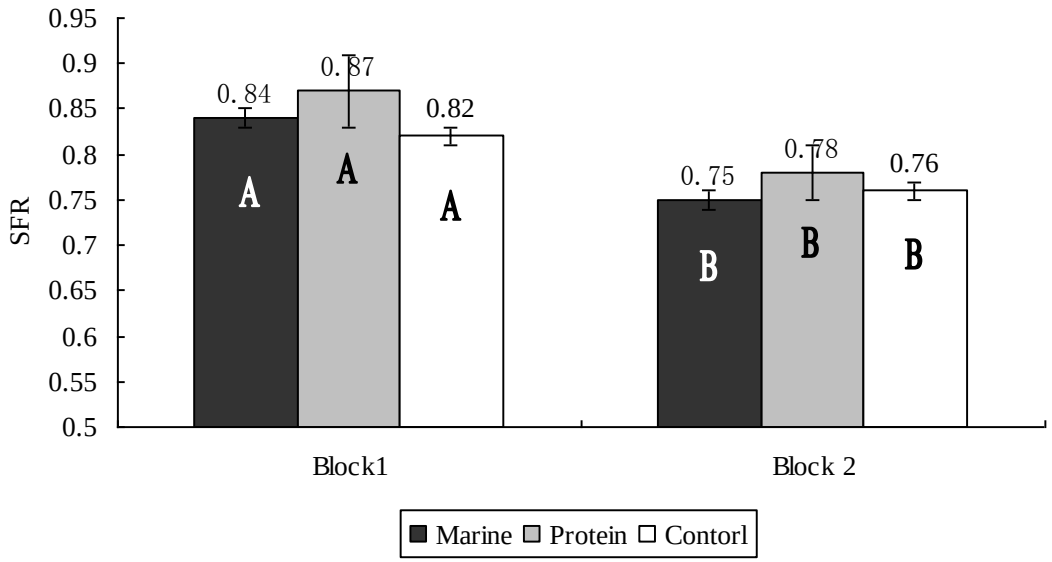

Figure 4.17 Specific feed ratios (SFR) for Atlantic salmon fed marine diet, protein diet – protein supplemented diet and control diet. Results are given as means ± standard error (SE). Significant variations were indicated between block one and block two (P = 0.005, P = 0.006 and P = 0.027, respectively).

5 Discussion

5.1 Production performances of the build-up phase

During the build-up phase, numerical differences in muscle fat content and body weight were observed between different dietary treatments (Figure 4.1 and Figure 4.2). With same initial fat level of 12.2% ± 0.2 and original body weight of 1085 g ± 2, fish fed Cod 50 diet group had the lowest muscle fat content and body weight at the ending of the build-up period, due to the food restriction in half ration. Additionally, a slight reduction in muscle fat content was shown from 12.2% to 11.3% in Cod 50 diet group. Thorpe et al. (1990) also suggested that fish undergoing feeding ration restriction duration have a low growth comparison to other groups. In Atlantic salmon production, fat concentrations of fish represent the fat level of the diet directly. Obviously, fish fed Salmon diet group had a high muscle fat content and body weight than Cod 100 diet group, due to the low fat content of commercial cod feed which ranges from 13% to 20% (Rosenlund et al. 2004). This corresponds to the results obtained by Johansen et al. (2002, 2003) that during the build-up phase fish fed low-fat concentrations feed construct a low body fat storage and achieve a depressed growth. Similar body weight between Salmon diet group and Cod 100 diet group might also indicate that cod dietary induces responses in Atlantic salmon that increase the appetite. Therefore, fish fed the high-fat feed is significantly fatter than fish given the low-fat feed.

5.2 Production parameters within pre-dietary groups

In the second experimental period, the overall specific growth rate (SGR) and thermal growth coefficient (TGC) ($P < 0.0005$) was found to be significantly higher in the Cod 50- 11.3% group, and lowest values ($P < 0.0005$) of that were observed in the Salmon-

16.4% group (Figure 4.6 and Figure 4.7). According to the lipostatic model of feed intake regulation, feed consumption has been considered to be inversely correlated to adipose tissue mass (Kennedy 1953; Jobling & Johansen 1999; Johansen et al. 2001; Johansen et al. 2002). Even through the specific values are not available to measure in the present study, with lowermost muscle fat concentration the Cod 50- 11.3% group fish are expected to have a higher feed intake, and the high-fat fish in Salmon- 16.4% group are thought to achieve a low feeding intake. Meanwhile, the Cod 100- 13.2% group should stand at medium position. Additionally, these results have indicated that growth is regulated in accordance with the size of the body fat deposition: fish with low adiposity have higher growth rate once fish have been transferred to a high fat concentration feeding available condition which is manipulated by negative feedback signals that inhibit feeding.

During the second experimental period (Table 4.1 and Table 4.2), the fish were found to have a decreasing in the growth rate (SGR and TGC) from the first 6 weeks feeding to second 6 weeks feeding and commenced to construct a convergence between groups. In particular, significant differences between Cod 100- 13.2% group and Salmon- 16.4% group were seen to diminish, where SGR and TGC were only reported having slightly numerical high statistical values in Cod 100- 13.2% group. These data strongly suggest that elevated adiposity to a certain concentration would lead to reducing the growth rate, which is in agreement with those of previous studies (Kennedy 1953; Johansen et al. 2003). Significant difference between Cod 50- 11.3% group and Salmon- 16.4% group was additionally reported having a weakening tendency. The specific growth rate during the second experimental period was also powerfully influenced by block ($P = 0.001$) (Figure 4.11), which elucidate that additional parameters at the experimental areas may strongly influence the growth and appetite.

Significant differences in body weight were observed between different dietary treatments at October sampling and December sampling (Figure 4.8). A trend in body

weight same as SGR and TGC has been acquired that differences are greatest at beginning of the second experimental period and ablate gradually and thus a convergence has been achieved between groups at the final sampling. This may indicate that as time progressed the semblable body compositions are found between different treatment groups. Furthermore, at both sampling points, Cod 100- 13.2% group and Salmon- 16.4% group had significantly higher body weight than Cod 50- 11.3% group (Figure 4.9 and Figure 4.10). Under the control of a similar environment, manipulation and repetitious treatments, the differences are therefore mostly induced by the different initial body weight at the onset of the trial. Fish in Cod 50- 11.3% group has low body weight may additionally could be illustrated as such, with half ration Cod feed treatment during build-up phase fish requires amounts of energy for organizing the body structure. Although there was no significant different in body weight between Cod 100- 13.2% group and Salmon- 16.4% group, Cod 100- 13.2% group had numerical higher body weights at October sampling of 12 g and at December sampling of 91 g than Salmon- 16.4% group. This not only refers to a higher growth but also represents that there is an over-compensation in Cod 100- 13.2%, which has also been reported by Johansen et al. (2001). On the other hand, high adiposity of Salmon- 16.4% group is probably thought to generate the growth impairment in fish since considering the relative growth rate. Very few literatures are documented that increased adiposity could result in growth reducing (Johansen et al. 2002, 2003). Relative growth rate of fish was reduced from 63.7% of the first 6 weeks to 23.4% of the second 6 weeks during the second period (Table 4.3). As mentioned before, growth is defined to regulate body fat deposition. Consequently, high relative growth rate appears in the first 6 weeks due to the low adiposity, while as treatments progressing the fat reserves enhance and negative feedback signals are regulated to normal level to determine a low relative growth rate in the second 6 weeks. The reduction was extremely pronounced in the Cod 50- 11.3% group, which had been recorded to drop from 89.6% of the first 6 weeks to 28.18% of the second 6 weeks (Table 4.3).

5.3 Fat deposition within pre-dietary groups

In the first 6 weeks, muscle fat content increased rapidly in three different dietary groups. While in the second 6 weeks a slight enhancing has obtained in Cod groups and a 0.3% decreasing was found in Salmon- 16.4% group. According to lipostatic model (Kennedy 1953) of regulation of negative feedback signals, with lower initial fat deposition fish drop negative feedback signals more and result in thirsting for feeds. Accordingly, fish with low fat reserves in the first 6 weeks have a higher developing rate in fat storage compared to that of second 6 weeks in the experiment. Since there are tremendous variations among the original fat content of the three groups, changes within the first 6 weeks in fat content are observed to be enormous as well especially for Cod 50- 11.3% group. A tendency for convergence of muscle fat content has been achieved at the end of first 6 weeks treatments, and more precise and accurate results appear at the ending sampling, where the difference in fat storage is 0.9%. These findings suggest that fat deposition increase fleetly once fish in compensation stage are transferred to a suitable condition and arrive at a certain point (around 18.5% - 19.2% in the present study). Whereafter the increasing rate slows down. The slope turns down abruptly from the first 6 weeks to second 6 weeks (Figure 4.3). Additionally, results found in the present study also detect that the lowest fat deposition fish desire feeding more strongly and thus enhance fat deposition speedy than their counterparts. Within the first 6 weeks treatment, a good correlation was found between muscle fat content and body weight. The slighter increasing in muscle fat content in Cod groups and the 0.3% reduction in muscle fat content of Salmon- 16.4% group (Figure 4.3 – 4.5) are effect of the negative feedback regulation, which leads to a low relative growth rate in body weight (mentioned before) during second 6 weeks period compared to first 6 weeks and reduces the differences between Cod 50- 11.3 % group and Salmon- 16.4% group. Seasonal variation in temperature may also partially affect appetite and growth at the final stage of the trial.

Although Cod 100- 13.2% group had a high growth rate in muscle fat content, significant differences between Salmon- 16.4% group and Cod 100- 13.2% group had been achieved. This may chiefly be affected by the initial fat content. Within Cod feeding groups, fish in Cod 50 -11.3% group had a high numerical muscle fat content at October sampling. After 6 weeks feeding, significant difference within Cod feeding groups acquired. It suggests that lower initial muscle fat content has a positive effect on feed intake and induces the higher growth rate of muscle fat content. Moreover, Cod feeding groups are expected to increase the muscle fat content in a slight level once trial persists.

5.4 Parameters within autumn dietary groups

No significant differences in specific feed ratio (SFR), feed conversion ratio (FCR) and thermal growth coefficient (TGC) (Figure 4.12, Figure 4.13, Figure 4.14) were found between autumn dietary groups. Results achieved in the present study thus suggest that feeding a diet partially replaced by rapeseed oil and supplemented with arginine/glutamate have no significant influence on the feeding rate, feed utilization and growth in Atlantic salmon reared in sea water during the period from August to early December (grown from 2350 g to 4750 g). These findings are in agreement with results obtained in previous studies with rapeseed oil (Torstensen et al. 2004a, b; Jordal et al. 2007). Results reported in trials with arginine/glutamate by Oehme et al. (2010) show that significant different in SFR, FCR and TGC did not obtain during the first experimental period but achieve in the second experimental period. Nevertheless, an interesting finding was found in the present study that in October sampling the arginine/glutamate supplemented group has a significantly low body weight compared to the Marine group (Figure 4.16). The lower body weight was a combined effect of lower growth and lower marine oil capacity in feeds, and only Block 1 was measured in October sampling which may also partially affect the ultimate results. The overall SFR within Block 1 was significantly high than Block 2 ($P = 0.001$) (Figure 4.17) and

the numerical higher results in FCR were obtained in Block 1 (Table 4.4), which elucidate that other parameters at the experimental areas may strongly influence the feed intake and growth.

5.5 Sexual maturation parameters

Studies have indicated that the levels of fat storage and energy content in the fish body during the late winter and spring may play a critical role in the onset of sexual maturation (Kadri et al. 1996; Thorpe et al. 1990). As mentioned before, both mature and immature fish show seasonal variations in fat growth, mature fish however obtain a higher fatty content than their immature counterparts (Figure 2.2-b). Furthermore, the greatest difference of the fat content appears in June, which is considered as the certain threshold point. However, the threshold of fat and energy deposition might be achieved earlier since the significantly high body fat content in the mature group emerges in December.

A triumphant spawning in autumn in Atlantic salmon reproduction requires adequate energy storage during winter and spring (Figure 5.1). The present study show that fish prepares the fat and energy reserves for certain threshold point and may also for preventing the natural outbreaks of diseases (Rørvik et al. 2007), which was commenced one year before. During the period from late summer to early autumn (first 6 weeks), fish reared in a suitable environment with abundant feeds obtains a significantly high growth and accumulates fat rapidly. Subsequently, during the second 6 weeks fish drop down the efficiency and capacity but still deposit fat and energy for the threshold point preparation. As described in section 5.3, these fat deposition procedure could be considered as consequences of lipostatic regulation. It furthermore suggests that fish accumulates plentiful fat during summer and autumn in order to reach sufficient energy reserves for reproduction of Atlantic salmon. A presumption could be introduced that fish will accumulate certain fat and energy

reserves in the autumn before sexual mature during following autumn. The present study show that certain fat and energy reserves are achieved in the early autumn where muscle fat content does not show significantly increase afterwards.

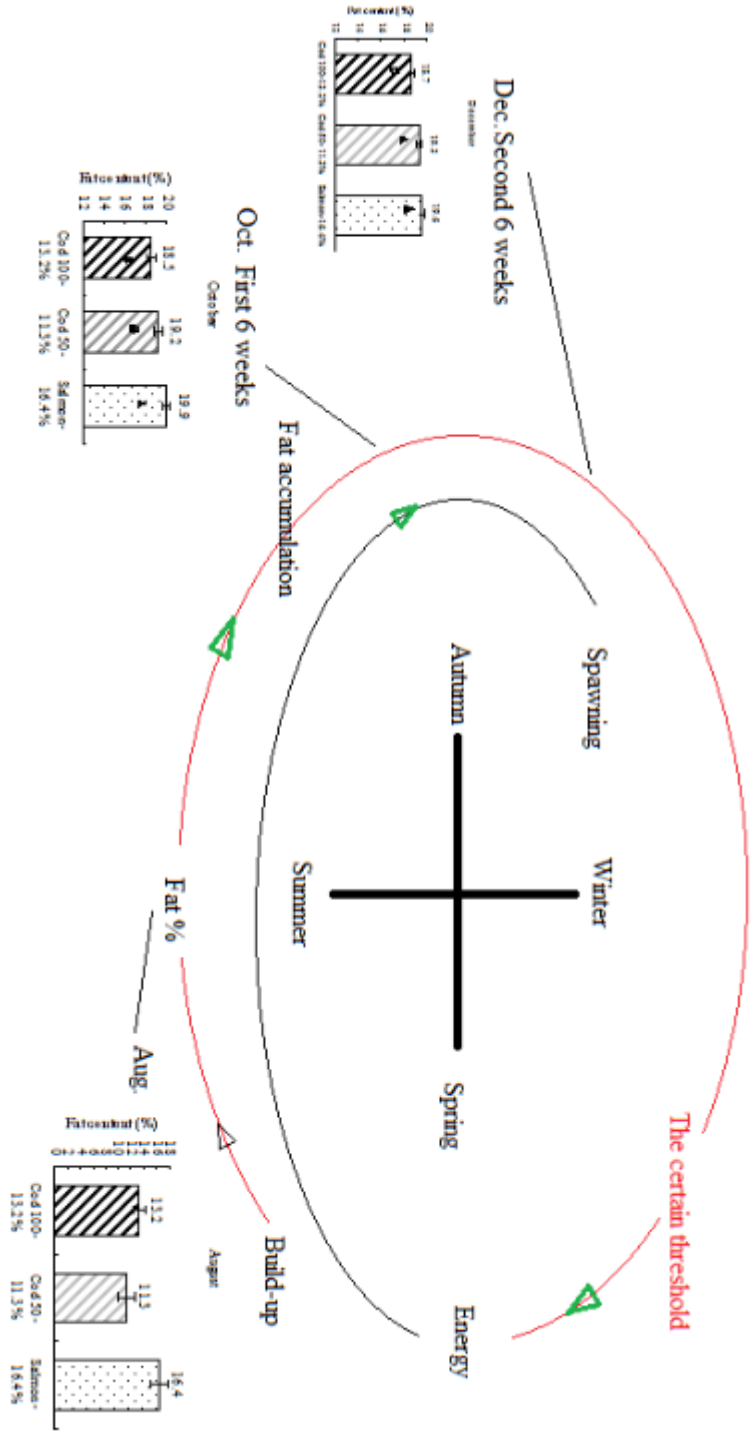

Figure 5.1 Variation in muscle fat accumulation in salmon reproduction. The build-up phase was designed to provoke the varied muscle fat content in the early summer.

6 Conclusion

The main findings in the present study were that different initial muscle fat concentrations in the early summer significantly affect the growth of Atlantic salmon in the following autumn. Fish with low initial muscle fat content obtained a significantly higher growth (SGR and TGC) than their counterparts. Both partial compensation and over-compensation had been achieved in the study. The observed results could be considered as partial evidences in supporting the lipostatic hypothesis. Regardless of lipostatic model, fat accumulation in the summer and/or autumn may be closely linked to the sexually mature preparation. We further observed that glutamate/arginine and rapeseed oil supplemental diets had no significant effect on growth rate and feed utilization.

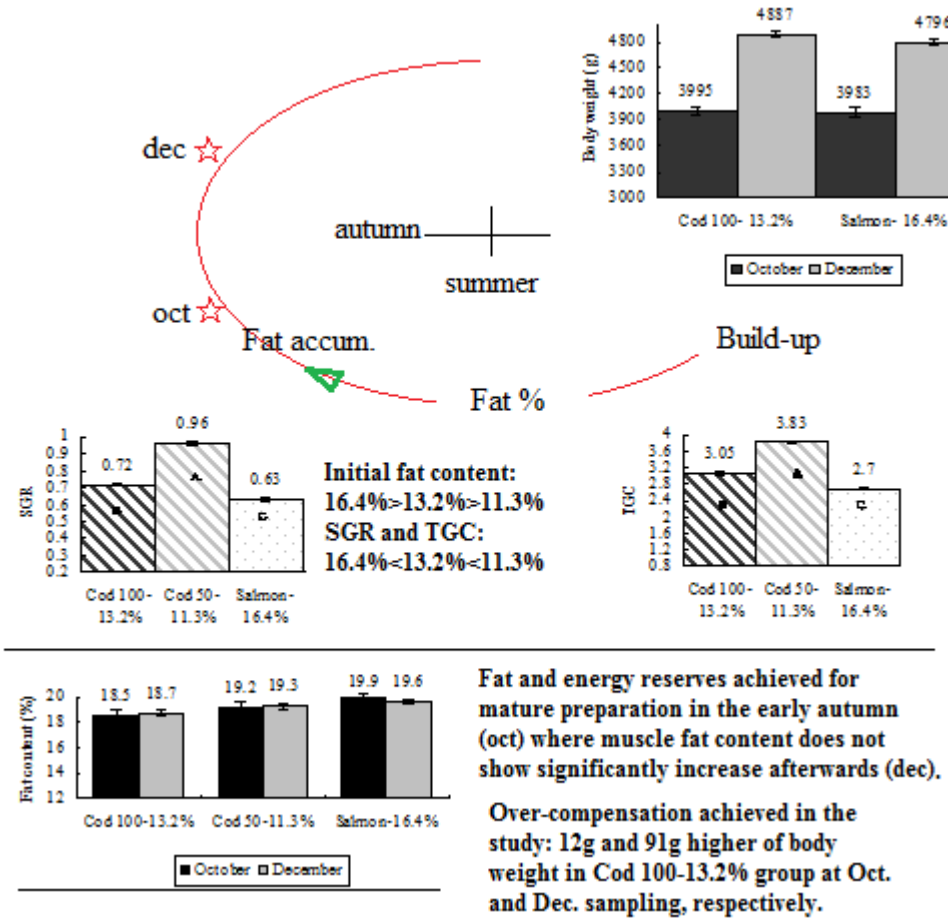

Figure 6.1 Different growth patterns provoked by varied initial muscle fat concentration in the early summer and main findings observed in the present study.

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