Atlantic Salmon, *Salmo salar*

6

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Introduction

Farming of Atlantic salmon (*Salmo salar*) began in Norway in the late 1960s. During the 1980s and 1990s the production spread, mainly to other north-western European countries and to Chile. In 1980 annual world production was less than 10,000 t and this increased to 850,000 t whole fish produced in 2000. It is projected to approach 2 million t in 2010.

The growth rate of the fish in the farms is continuously improving, due to genetic selection, improved diets and feeding and improved management. The improvement in growth ascribed to genetic selection can be as much as 15–20% per generation if the salmon are from a combined family–phenotype selection programme (Gjedrem, 1983). Recent Canadian results have shown that transgenic salmon, which express growth hormone receptor activity in muscle tissues, have a growth rate 2.6–2.9 times that of the control population, mainly because of increased feed intake (Cook *et al.*, 2000a). Selection or transgenic techniques may also influence the composition of the growth, result in improved feed conversion (Thodesen *et al.*, 1999; Cook *et al.*, 2000a) and change the rate of metabolism (Thodesen *et al.*, 1999; Cook *et al.*, 2000b,c). Economical feed conversions in Norwegian salmon farming have changed from more than 2 kg feed dry matter (DM) kg^{-1} gain in 1980 to approximately 1.15 kg kg^{-1} at the end of the 1990s. In salmon the biological feed conversion can vary from less than 0.6 to more than 1.3 kg intake kg^{-1} gain, and the proportion of protein and energy in diet partitioned into gain can vary from 25 to 60%, depending on the formulation of the diet and the size of the fish. Thus, requirement figures must be based on the requirements of the animal, related to growth, nutrient partitioning and the specific physiological processes in which the nutrient is required.

Requirements differ throughout the life cycle. This is especially important in salmon, which undergo physiological changes during smoltification and transfer from a life in fresh water to salt water. In addition to developing the ability to maintain the ion balance in the hyperosmotic salt water, the salmon also

 Nutrient Requirements and Feeding of Finfish for Aquaculture (eds C.D. Webster and C. Lim)

undergoes changes in connection with preferred substrates for energy metabolism. Furthermore, the composition of the growth becomes more fatty as the salmon grows larger. Sexual maturation is another life stage that may call for attention in respect of diet formulation. Initially, growth is stimulated by an increase in the levels of sex steroids. Later in the maturation process, nutrients are directed into gonads rather than somatic growth.

The freshwater stage of the salmon is characterized by a moderately fatty composition of the growth (Shearer *et al.*, 1994). During smoltification and immediately after transfer to salt water, the body fat content drops rapidly by around 0.1 kg of body weight. Thereafter, the growth becomes increasingly fatty as the salmon grows. During sexual maturation, gonadal development has priority, with a subsequent reduction in body fat. The growth rates are also much higher in juvenile than in on-growing salmon, when related to body weight (Austreng *et al.*, 1987), while reduced growth is often seen during smoltification.

In the 1970s, moist diets, consisting of minced trash fish, binder meal with micronutrients and canthaxanthin, crustacean by-products and fish-oil, were the ‘only feed which salmon in saltwater would accept’. Steam-pelleted, crumbled diets were only used in the freshwater stage. The process of developing diets especially for Atlantic salmon was largely started in 1972, with the work of Erland Austreng at the Department of Poultry and Fur Animal Science at the Agricultural University of Norway. Among the most significant initial findings was that increasing dietary lipid levels from 8–10%, a level commonly accepted at that time, up to 18% in steam-pelleted diets increased growth and survival (Austreng, 1976). The dietary protein level and the cost of gain decreased correspondingly. In the middle of the 1970s, the quality of ingredients in the dry feeds was so high that the salmon also accepted it in salt water. Since then, dietary lipid concentrations have increased and protein concentrations decreased, facilitated by the introduction of extruded diets in the 1980s and vacuum-coating techniques in the 1990s.

Nutrient Requirements

Protein and amino acids

Salmon digest protein efficiently, and more than half of the protein is hydrolysed and absorbed in the pyloric region (Krogdahl *et al.*, 1999). Digestion and absorption of protein are highly different from one feed ingredient to another, or even within feed ingredients processed by the same method. This is illustrated in Table 6.1. Salmon utilizes dietary protein from high-energy diets more efficiently for growth than from low-energy diets. Protein retention values higher than 50% are not uncommon (Table 6.2).

Requirements for only three essential amino acids – lysine, arginine and methionine – have been published for salmon (Table 6.3). The estimates of arginine requirements in post-smolts differ by more than 25%. The main differences in the two experiments were that Lall *et al.* (1994) obtained faster growth

Table 6.1. Apparent amino acid and crude protein digestibilities in various protein-rich feed ingredients.

	Capelin meal*†‡	Herring meal*†§	Herring meal‡‖	Menhaden meal‡‖	Anchovy meal*‡‖	Canola meal*	Soybean meal*	Wheat gluten¶	Bacterial meal**
Crude protein	81–87	74–83	81–85	78	77	74	71	100	82
Amino acids									
Ala	89–94	87–88	86–92	88	81	80	74	96	85
Arg	90–96	89–92	91–96	91	82	85	77	98	92
Asp	84–86	68–79	83–84	70	79	74	67	94	82
Cys	72	76				79		100	52
Glu	89–94	84–88	86–91	86	82	88	75	99	86
Gly	78–85	75–80	81–82	72	82	75	63	98	80
His	88–96	84–90	75–90	85	76	85	77	98	81
Ile	87–95	84–91	85–93	91	82	75	67	98	83
Leu	91–95	87–91	86–93	89	82	77	70	99	84
Lys	88–95	82–88	86–91	84	81	77	67	95	92
Met	89	86				89	71	98	83
Phe	88–94	84–90	84–92	89	80	78	70	99	77
Pro	86–89	84–80	83–89	84	74	81	77	100	84
Ser	90–94	84–86	90–90	86	81	77	73	99	80
Thr	88–93	79–87	81–89	85	81	75	62	97	82
Trp	84–85	53–93	84–88	73	81		45	98	
Tyr	89–97	83–82	89–97	86	87	76	68	99	74
Val	89–95	84–90	85–93	90	82	73	67	98	85

* Anderson *et al.* (1992), in salt water.
† Norse LT-94. Low-temperature dried capelin meal with high hygienic quality of the fish.
‡ Anderson *et al.* (1995), in fresh water.
§ Flame-dried.
‖ Steam-dried.
¶ Vital wheat gluten. Storebakken *et al.* (2000a), in salt water.
** BioProtein. Skrede *et al.* (1998), in salt water.
Ala, alanine; Arg, arginine; Asp, aspartic acid; Cys, cystine; Glu, glutamic acid; Gly, glycine; His, histidine; Ile, isoleucine; Leu, leucine; Lys, lysine; Met, methionine; Phe, phenylalanine; Pro, proline; Ser, serine; Thr, threonine; Trp, tryptophan; Tyr, tyrosine; Val, valine.

and more efficient feed conversion than those of the salmon in the experiment by Berge *et al.* (1997), thus giving a more reliable result. Since requirement estimates are still lacking for most indispensable amino acids for salmon, dietary digestible amino acid profiles may be based on whole-body amino acid composition (Wilson and Cowey, 1985) or on amino acid requirements for other salmonids.

It is common practice to include 50–55% crude protein in diets for juvenile salmon and to reduce the dietary protein content to 40–45% in grower diets, provided the protein-rich feed ingredients are of high quality.

Lipids and fatty acids

The need for high fat content in the diet for Atlantic salmon reflects the body composition of the fish. The high dietary lipid level stresses the need to use

Table 6.2. Partitioning of dietary nitrogen into growth and excretion in salmon fed diets with fish-meal as the main protein source.

Life stage	Water	Fish weight (kg)	DP : DE (mg kJ^{-1})	N retention (%)	Faecal N loss (%)	Other N losses (%)	Reference
Parr	Fresh	0.08	16.7–27.9	55–47	8–6	37–46	Grisdale-Helland and Helland, 1997
During smoltification	Fresh	0.07	19.5–27.1	51–43	6–6	43–51	
Post-smolt	Salt	0.10		56–57	8–8	36–34	Helland and Grisdale-Helland, 1998a
Post-smolt	Salt	0.80	18.6	44	12	44	Thodesen *et al.*, 1999

DP, digestible protein; DE, digestible energy; N, nitrogen.

Table 6.3. Known essential L-amino acid requirements for salmon.

Amino acid	g kg^{-1} DM*	g kg^{-1} N × 6.25*	Fish size	Reference
Arginine	16	41	Post-smolt	Lall *et al.*, 1994
	21.2–21.6	50–51	Post-smolt	Berge *et al.*, 1997
Lysine	19.9	39.8	Fingerling	Anderson *et al.*, 1993
	16–18		Post-smolt	Berge *et al.*, 1998
Methionine	11†	24†	Fingerling	Rollin *et al.*, 1994

* Estimated by broken-line regression of growth on dietary amino acid concentration.
† Dietary cysteine level not specified.
DM, dry matter; N, nitrogen.

high-quality oils and to know the effects of the lipid source on growth and salmon health, as well as product quality. Lipids are sources of energy, essential fatty acids, eicosanoids and components of the cell membrane (phospholipids) and they assist in the uptake of lipid-soluble nutrients.

Salmon must have oil with a low melting-point, as saturated fats are poorly digested. The pyloric caeca and the proximal intestine are the main sites of fat digestion and absorption but some absorption also occurs in the distal portion of the intestine (Krogdahl *et al.*, 1999). The digestibility of fish-oil from fish-meal-based extruded diets ranges from 90 to 95% in salmon (Aksnes, 1995; Storebakken *et al.*, 1998a, 2000a). Most vegetable oils are digested at a similar or higher rate in rainbow trout (Austreng *et al.*, 1979).

Atlantic salmon, like other fish, are unable to synthesize fatty acids of the n-3 and n-6 families. These fatty acids must be provided in the diet. The main symptoms of essential fatty acid deficiency in salmon, in addition to reduced growth and increased mortality, is a decrease in the essential fatty acids in the blood and liver phospholipids and a subsequent increase in 20:3n-9 (Ruyter *et al.*, 2000a). The precursor fatty acids, 18:3n-3 (linolenic acid) and 18:2n-6 (linoleic acid) are desaturated and elongated into the longer polyunsaturated fatty acids (PUFA), such as 20:5n-3 (eicosapentaenoic acid (EPA)) and 22:6n-3 (docosahescaenoic acid (DHA)), typical 'marine' fatty acids, and 20:4n-6 (arachidonic acid) by the same enzyme systems.

In juvenile salmon fed semipurified diets with graded amounts of methyl esters of either 18:2n-6, 18:3n-3 or a 1 : 1 mixture of 20:5n-3 and 22:6n-3, increasing levels up to 1% of dietary DM improved growth and survival. Fry fed the mixture of fatty acids performed better than fish fed 18:3n-3 alone (Ruyter *et al.*, 2000b). The requirement for n-3 fatty acids is approximately 1% of dry feed for juveniles if the fatty acids are supplemented as 20:5n-3 and 22:6n-3. No requirement has been established for n-6 fatty acids. A requirement by larger salmon for essential fatty acids has not been published.

Fish-oils and fish-lipid residue of fish-meal are the two main sources of fat in salmon feed, but fluctuations in the fish-oil supply and an anticipated shortage of fish-oil during the first half of the 1990s made it increasingly necessary to substitute at least part of the fish-oil with vegetable oils. The effects of different combinations of fish-oils (high in n-3 PUFA) and vegetable oils (rich in 18:2n-6, 20:4n-6 and eventually 18:3n-3) on the growth and health of salmon have been evaluated. Generally, growth reductions or increased mortalities as a result of substituting half or more of the fish-oils with vegetable oils have not been observed with salmon, as long as the quantitative requirement for n-3 fatty acids is met (Thomassen and Røsjø, 1989; Dosanjh *et al.*, 1998).

The fatty acid composition of the salmon fillet largely reflects that of the dietary oil, with some enrichment of n-3 PUFA (Hardy *et al.*, 1987; Thomassen and Røsjø, 1989; Polvi and Ackmann, 1992; Dosanjh *et al.*, 1998). This may also affect the quality of the farmed salmon. However, Hardy *et al.* (1987) did not obtain any significant differences in flavour or texture traits when a sensory panel evaluated salmon gaining from 36 to 52% weight on low-fat (18–20%) diets. The dietary lipids tested were herring or menhaden fish-oils, soybean oil and tallow. However, when 0.25 kg salmon were fed low-fat diets consisting of capelin fish-oil, high- or low-erucic acid rape-seed oil or soybean oil, the fish fed either of the rape-seed oils had lower 'salmon odour' than the group fed the fish-oil (Thomassen and Røsjø, 1989). Furthermore, the fish fed the soybean oil had significantly less 'salmon taste' than those fed the low-erucic acid rape-seed oil.

During the last two decades, the understanding of the term 'high-energy' salmon grower diet has shifted from 25–30% fat to 35–40% fat. Johnsen *et al.* (1993) and Hillestad *et al.* (1998) did not find any significant effects on growth by increasing dietary fat concentrations from 23 to 30% in diets for salmon with a start weight of 0.2 and 0.3 kg, respectively. Einen and Roem (1997) observed a reduction in growth for the highest fat content when gradually increasing dietary fat levels from 26 to 39%, and suggested that digestible protein : digestible energy (DP : DE) ratios around 19 g MJ^{-1} are optimal for salmon weighing from 1 to 2.5 kg, decreasing to 16–17 g MJ^{-1} for fish weighing from 2.5 to 5 kg. In support of these findings, Refstie *et al.* (2000) obtained an increase in growth by increasing dietary fat from 32 to 39%, with a corresponding decrease in DP : DE from 21 to 17 g MJ^{-1}, in salmon with a final weight of 2.7–2.8 kg.

Dietary fat content also influences the chemical composition of the fish. The proportion of fat in the viscera increases significantly with increasing dietary fat content (Einen and Roem, 1997; Hillestad *et al.*, 1998; Refstie *et al.*, 2000). The fat content of the fillets is less influenced by dietary fat content than that of the viscera, even with an increase in dietary fat content from 20 to 40% (Einen and Skrede, 1998), but increased fillet fat deposition has been observed in salmon fed diets with increased dietary fat content from 32 to 39% (Refstie *et al.*, 2000). Smoked fillets from salmon fed diets with a range of dietary fat concentrations from 26 to 39% were also presented to an expert panel, and the only significant difference found was a slightly elevation in fattiness in the fillets with the highest fat content. Other traits, such as hardness, juiciness and various measures for odour, flavour and colour, were not significantly affected by dietary fat level (Einen and Skrede, 1998). Similarly, no significant differences were found when salmon fed diets with 32 or 39% fat were subjected to sensory evaluation (Bjerkeng *et al.*, 1998). Thus, the effects on the quality of the edible parts of the salmon of increasing the dietary fat content from 20 to 35–40% seems to have been small.

The 'high-energy' grower diets do not just affect growth rates and body composition, but also have positive effects on feed conversion and release of nutrients from the fish farm. Johnsen *et al.* (1993) found that the nitrogen load to the environment was reduced by 35% kg^{-1} salmon produced by increasing the dietary fat content from 22 to 30%. This is ascribed both to an overall more efficient feed conversion and to a reduction in deamination of protein because of reductions in the protein intake per kg gain. The same authors also calculated a parallel reduction in organic-matter load to the environment by 22% and a reduction of phosphorus load by 22%.

Carbohydrates

Atlantic salmon have no specific requirement for dietary carbohydrates, since they can synthesize sufficient amounts of glucose by gluconeogenesis. There are mainly two types of carbohydrates in commercial salmon diets: starches and non-starch polysaccharides (NSP). Starches are added to the diet mainly for binding and expansion during extrusion. NSP come from vegetable feed ingredients such as grains or legumes.

The starches must be gelatinized to improve availability, but salmon still have a limited ability to hydrolyse gelatinized starch. One reason may be that salmon have low, if any, detectable activity of α-amylase in the intestine (Sørensen, 1995). Thus, the amylose chain is not hydrolysed into oligo- and disaccharides before they are subjected to the disaccharidases. Intestinal brush-border disaccharidases are active in salmon, and maltase has the highest activity. Most of the disaccharidase activity is found in the pyloric caeca and the proximal part of the intestine, which is also the main site of starch hydrolysis (Krogdahl *et al.*, 1999).

Starch digestibility in salmon appears to be higher in fresh or brackish water than in salt water. Figure 6.1 illustrates that starch digestibility is reduced with increasing dietary concentrations, and that this reduced digestibility of starch is accompanied by reduced digestibility of fat. This necessitates extra precaution to avoid excessive use of starch in salmon feeds. Atlantic salmon also has a poor ability to regulate blood glucose when the dietary carbohydrate load is excessive (Hemre and Hansen, 1998). However, the salmon regulates blood glucose fairly efficiently when the load is more moderate (Hemre *et al.*, 1996). Small salmon regulate blood glucose less efficiently than larger fish (Waagbø *et al.*, 1993), and the ability to regulate is higher at optimal water temperature than at low temperature (Hemre *et al.*, 1995b).

A small inclusion of starch in the diet is beneficial, since a protein-sparing effect of starch has been observed in salmon in the freshwater stage (Hemre *et al.*, 1995a; Grisdale-Helland and Helland, 1997). With larger salmon in salt water, replacement of protein with starch did not result in protein-sparing (Helland and Grisdale-Helland, 1998a). Currently, it is common practice to use 6–15% gelatinized starch in salmon diets, depending on fish size and feed processing. This level of inclusion does not impair salmon growth (Hemre *et al.*, 1995a; Aksnes,

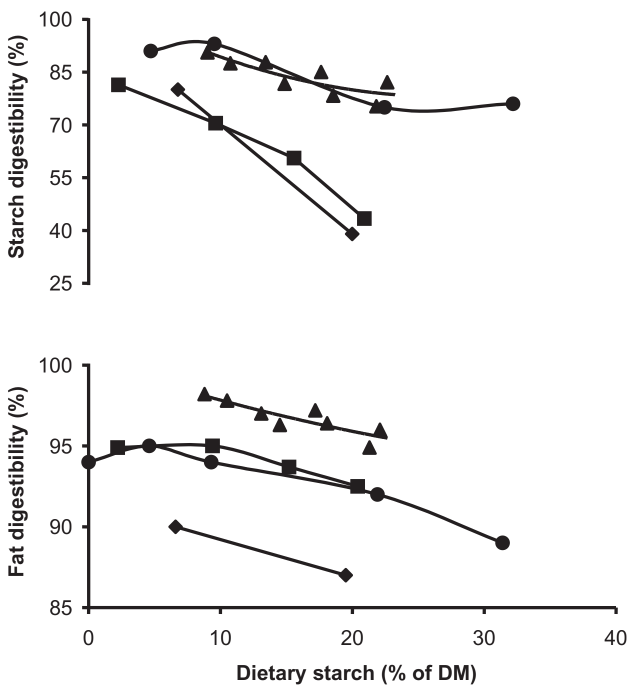

Fig. 6.1. Apparent digestibility of starch and fat in salmon fed diets with different dietary starch concentrations. ■, Aksnes (1995), 0.6 kg salmon in salt water; ●, Hemre *et al.* (1995a), 80 g post-smolt in brackish water (20 g l^{-1}); ▲, Grisdale-Helland and Helland (1997), 80 g fingerlings in fresh water; ◆, Krogdahl *et al.* (1999), 1.9 kg salmon in salt water; DM, dry matter.

1995). A further increase in dietary starch reduces growth and feed conversion (Helland and Grisdale-Helland, 1998a).

Insoluble NSP, such as cellulose, mainly act as fillers in the stomach and intestine and do not affect uptake of nutrients (Mundheim and Opstvedt, 1990). Soluble NSP, such as mixed β-glucans and arabinoxylans in grains, and pectic and acidic polysaccharides in legumes, increase the viscosity of the digesta and the water content of the faeces and reduce digestibility of fat- and lipid-soluble components. Refstie (2000) has estimated that, if fish-meal were substituted with 30% soybean meal in a high-energy (40% fat) salmon diet, 35 g less fat would be absorbed per kg feed intake, mainly due to soluble NSP in the soybean.

Energy

Lipid, protein and carbohydrates are converted into energy. The energy utilization is improved by reducing dietary protein and increasing dietary fat, thereby decreasing the DP : DE ratio. The energy expenditures in faecal losses normally account for 10% or less if the quality of the feed ingredients is high and dietary carbohydrate is kept at a tolerable level (Grisdale-Helland and Helland, 1997; Helland and Grisdale-Helland, 1998a,b). However, in post-smolts newly transferred to sea water, faecal energy losses were elevated due to low fat digestibility (Helland and Grisdale-Helland, 1998a). Ammonia and urea represent a minor loss in energy, and the heat increment accounted for only 9% of gross energy intake of post-smolts newly released to the sea (Helland and Grisdale-Helland, 1998b). Maintenance and activity can account for a considerable amount of the energy budget. Activity inflicted by stress and too high a water current in tanks may represent unnecessary energy expenditure.

In a salmon that is genetically selected against early sexual maturation and against excessive adipose deposition, the following DP : DE ratios may be considered optimal:

Fingerlings:	23 g MJ^{-1}
Smoltification:	20 g MJ^{-1}
Grower:	
Up to 2.5 kg	19 g MJ^{-1}
Over 2.5 kg	16–17 g MJ^{-1}

Vitamins

In this chapter, only mechanisms and symptoms confirmed in experiments with Atlantic salmon will be described. Among the lipid-soluble vitamins (A, D, E, K), vitamins A and E have received most attention in salmon. Vitamin C is the water-soluble vitamin that has been subject to most investigation in salmon, while requirements are established for only a few of the B vitamins.

Lipid-soluble vitamins

It is common practice to add a supplement of 2000 to 2500 IU of vitamin A to salmon feeds. However, fish-meal and fish-oil normally contain considerable amounts of vitamin A, and unsupplemented practical diets have been reported to contain more than 70,000 IU vitamin A kg^{-1} (Grisdale-Helland *et al.*, 1991). In view of this, the justification for adding a supplement of vitamin A to salmon diets based on fish-meal (full meal from pelagic, fatty species) may be questioned. In addition to reduced vitamin A stores in the liver, salmon parr respond to diets depleted in vitamin A (1300 IU kg^{-1}) by a reduction in both humoral and cell-mediated immune responses (Thompson *et al.*, 1994). Vitamin A is toxic when fed in high doses, but even juvenile salmon can tolerate diets with more than 75,000 IU vitamin A kg^{-1} without pronounced reductions in growth or increased mortality (Grisdale-Helland *et al.*, 1991). Vitamin A and astaxanthin are closely related in salmon, since astaxanthin is provitamin A and is capable of supporting the need for vitamin A, even in juvenile salmon (Christiansen *et al.*, 1995). The quantitative requirement for vitamin A has not been established in Atlantic salmon.

It is common practice to add a supplement of between 1500 and 2500 IU of vitamin D_3 to salmon feeds. Also, commonly used feed ingredients, such as fish-meal and fish-oil, are rich in this vitamin. No differences in growth, survival or plasma calcium level were observed when salmon fingerlings were fed three different levels (0.04, 2.21 and 26.7 mg kg^{-1}) of vitamin D_3 for 11 weeks (Horvli *et al.*, 1998). However, tissue levels of vitamin D_3 were elevated in accordance with the increase in dietary dose. Plasma concentration of 25-OH D_3 was significantly elevated in the fish fed the highest dose of D_3, while the concentration of 1,25-di-OH D_2 decreased. The requirement for vitamin D has not been established in Atlantic salmon.

The main function of vitamin E is as a lipid-soluble antioxidant. Vitamin E is also important for a normal reproductive result in warm-blooded animals. α-Tocopherol has a considerably higher vitamin E effect than the β, δ and γ forms. Only α-tocopherol is abundant in marine fish, and fish-oils normally contain approximately 300 mg kg^{-1}.

Major symptoms of vitamin E deficiency in addition to reduced growth and increased mortality are: skeletal muscle degenerations due to lacking antioxidant protection of the cell membranes, anaemia and increased erythrocyte fragility, ceroid accumulation in the liver and a response to handling characterized by transitory fainting with interruption in swimming (Poston *et al.*, 1976; Lall *et al.*, 1988; Hamre *et al.*, 1994). The immune response is only moderately affected by vitamin E deficiency, and the response of vitamin E-deficient salmon fingerlings to bacterial infection has been inconsistent (Lall *et al.*, 1988; Hardie *et al.*, 1990). In juvenile salmon (from first feeding) the minimum requirement of α-tocopheryl acetate has been estimated as 60 mg kg^{-1} dry feed (Hamre and Lie, 1995a). This requirement figure is higher than that found in other salmonids. Hamre *et al.* (1997) suggested that this was influenced by a low tissue ascorbic acid level in the fish, limiting regeneration of oxidized tocopherol. In salmon fingerlings, Lall *et al.*

(1988) found that the requirement for vitamin E was about 30 mg α-tocopheryl acetate kg^{-1} dry feed. Vitamin E supplementation cannot be seen independently from the quantity and quality of the dietary oil. Vitamin E deteriorates rapidly when oils become oxidized (Koshio *et al.*, 1994). The level of dietary n-3 PUFA seems to be of minor importance for the accumulation of vitamin E in salmon tissues (Hamre and Lie, 1995b), but there are examples showing that the beneficial effects of high-n-3 PUFA fish-oils on fish growth and health at low sea temperatures are only seen when the dietary level of vitamin E is high (Waagbø *et al.*, 1993). Furthermore, a combination of high dietary vitamin E concentration and a high-n-3 PUFA fish-oil has been shown to facilitate efficient carotenoid pigmentation (Christiansen *et al.*, 1993). Tocopherols are not only antioxidants *in vivo* but also protect the salmon fillet against oxidation during storage (Sigurgisladottir *et al.*, 1994; Hamre *et al.*, 1998; Parazo *et al.*, 1998). In order to improve the oxidative stability of the fish during storage and to ensure efficient pigmentation, it is not uncommon to supplement high-energy diets for salmon growers with several times the vitamin E requirement, as high as 150 mg kg^{-1} or more.

There are three forms of vitamin K, K_1 (phytomenadione, synthesized from plants), K_2 (menaquinone, synthesized by bacteria) and K_3 (menadione, the form commonly obtained by chemical synthesis). The effect and toxicity of the three forms differ among various animal species. It is common practice to add approximately 0.04 g vitamin K_3 kg^{-1} feed. In juvenile salmon fed diets with a high concentration of vitamin A, growth was inferior when K_3 was fed compared with K_1 (Grisdale-Helland *et al.*, 1991). This questions the present use of K_3 in salmon feeds. Menadione is unstable during extrusion of fish feeds (Marchetti *et al.*, 1999). The requirement for vitamin K in salmon is not known.

Water-soluble vitamins

The information on most water-soluble vitamins for Atlantic salmon is limited, and only two requirement figures have been established for B vitamins.

Pyridoxine deficiency in salmon fingerlings is characterized by increased mortality, 'shock syndrome' behavioural changes, degenerative changes in kidneys, ovary and liver, paucity of the thyroid colloid and hyperplasia of haematopoietic tissue in the kidney (Herman, 1985). In addition, Albrektsen *et al.* (1994a) showed that deficient fingerlings had reduced lipid content in the muscle, reduced n-3 PUFA in liver phosphatidylethanolamine and phosphatidylcholine and reduced activity of aspartate aminotransferase in the liver. The requirement for pyridoxine in juvenile salmon is covered by adding 5 mg kg^{-1} to a practical fish-meal-based diet (Albrektsen *et al.*, 1994a).

In biotin-deficient fry, growth is decreased and mortality increased. In addition, increased liver glycogen and reduced activity of pyruvate carboxylase in the liver, hypertrophy and hyperplasia of the gill tissue and extensive fusions of the secondary gill lamellae have been observed in deficient salmon. The requirement for biotin is covered by 0.3 mg biotin kg^{-1} feed for juvenile salmon (Mæland *et al.*, 1998).

The requirement for inositol is no higher than 300 mg kg^{-1} of feed for juvenile salmon (Waagbø *et al.*, 1998). The requirement should be covered by the inositol content of the feed ingredients in most practical diets. Waagbø *et al.* (1998), however, recommended a supplementation of starter diets with 200 mg kg^{-1} to compensate for fluctuations in inositol content in the ingredients, leaching loss and the eventual increased requirement in the fry.

Based on growth, survival and body composition in an experiment where salmon fingerlings were fed diets with different amounts of choline chloride and soya lecithin, Poston (1991) suggested that the choline requirement in salmon fingerlings is between 430 and 1300 mg kg^{-1}. Hung *et al.* (1997) did not observe improved growth or changes in whole-body fat and protein in fingerlings when supplementing the diets with more than 880 mg choline kg^{-1}. This indicates that the higher range of the requirement estimate is 880 mg kg^{-1} or less.

Ascorbic acid is a dietary essential in Atlantic salmon (Mæland and Waagbø, 1998). Crystalline ascorbic acid is unstable, especially during extrusion, even with coated vitamin C preparations (Gadient and Fenster, 1994). Thus, more stable forms of vitamin C, such as ascorbyl-2-sulphate, ascorbyl-2-monophosphate or polyphosphate, are currently used in today's salmon feeds. Ascorbyl-2-sulphate does not seem equivalent to ascorbic acid as a dietary vitamin C source in Atlantic salmon (Sandnes *et al.*, 1990), but ascorbyl-2-monophosphate has high vitamin C activity in salmon (Sandnes and Waagbø, 1991). Mixtures of ascorbyl mono-, di- and triphosphates or mono- and diphosphates showed similar, high stability during feed production and storage, and are equally bioavailable (Roem and Oines, 1993). Lall *et al.* (1989) found that giving a supplement of 50 mg of ascorbic acid kg^{-1} was sufficient for growth and feed conversion for juvenile salmon. The absence of vitamin C caused deficiency symptoms such as lethargy, scoliosis, lordosis, broken back and anaemia. Sandnes *et al.* (1992) estimated the need for a supplement of vitamin C in a fish-meal-based practical diet to 10–12 mg ascorbic acid equivalents kg^{-1} in salmon from first feeding to 23 g of weight.

Minerals

The requirement for essential minerals varies with the life-cycle stage and growth rate, while the need for supplementation of the feeds varies with the mineral composition of the water and diet composition. This is due to the salmon's ability to take up minerals from the water and physiological changes in connection with smoltification and sexual maturation. There is also significant genetic variation in the apparent absorption of several minerals (potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn) and iron (Fe)) (Thodesen *et al.*, 2001), indicating a potential to select salmon genetically for improved utilization of essential minerals. There is often a poor relationship between the mineral profile of the diet and the amounts of various elements that are available to the fish. In general, fish-meal-based diets contain higher amounts of available macrominerals than vegetable-protein-based diets, while the adequacy of many of the microminerals remains to be determined.

Calcium is abundant in both hard fresh water and salt water. Salmon actively take up calcium, unless the ammonium ion concentration is too high (Vinogradov *et al.*, 1987). Thus, salmon can partially or fully satisfy their requirement for calcium by uptake from hard fresh water or salt water (Flik *et al.*, 1995). In contrast to what is often found in warm-blooded animals, excess dietary calcium does not inhibit the uptake of phosphorus (P) in Atlantic salmon (Vielma and Lall, 1998). The requirement for calcium has not been established in Atlantic salmon.

For salmon in fresh water, it is important to supplement the diets to cover the phosphorus requirement, but not in excess, since phosphorus is the first limiting factor for plant growth in fresh water. Practical experience has shown that the combination of regulatory limitations for phosphorus supplementation to the feed and the use of feed ingredients with low phosphorus availability makes phosphorus one of the most limiting essential nutrients in salmon production. The availability of phosphorus to the salmon is highly variable depending on the form in which it is fed. For example phytic acid phosphorus in vegetable-feed ingredients has low availability to salmon, while some inorganic phosphorus salts are almost 100% available (Nordrum *et al.*, 1997; Storebakken *et al.*, 1998b). Typically the availability of phosphorus from fish-bone is half of that from sodium phosphate, while the availability of phosphorus from mono- and dibasic calcium phosphates is intermediate between the sodium salt and fish-bone (Nordrum *et al.*, 1997). Previous studies indicate that the phosphorus requirement is around 6 g total P kg^{-1} dietary DM for juvenile salmon in fresh water (Ketola, 1975) and for salmon in salt water (Lall and Bishop, 1977). More recently, Åsgård and Shearer (1997) found that the requirement was 10–11 g total P kg^{-1} DM or 9 g digestible P kg^{-1} DM for rapidly growing juvenile salmon.

Salmon take up magnesium from the water. In addition to deficiency symptoms generally found in fish, magnesium deficiency results in insufficient osmoregulation in salmon smolts. Whole-body, serum and vertebrae magnesium concentrations are better indicators of subclinical deficiency than growth (El-Mowafi and Maage, 1998). The requirement for dietary magnesium remains to be established for salmon in soft fresh water. With salmon kept in fresh water supplemented with some salt water (54 mg Mg l^{-1}), El-Mowafi and Maage (1998) found that 196 mg Mg kg^{-1} resulted in a lower magnesium content in serum, vertebrae and the whole body of salmon parr than diets with 325 mg Mg kg^{-1} or more.

Manganese (Mn) can also be taken up from the water. Experiments with salmon parr in water with a salinity of 2.5 p.p.t. indicate that a total concentration of 15 mg total dietary Mn kg^{-1} was necessary to maintain a normal level of manganese in vertebrae and whole fish (Lorenzen *et al.*, 1996). More recent studies (Maage *et al.*, 2000) have shown that growth and mortality in salmon fry were not affected over a range of dietary manganese concentrations exceeding 1.1 mg kg^{-1}. However, 7 mg total Mn kg^{-1} was required to maintain the normal activity of superoxide dismutase in the liver, and 7.5–10 mg kg^{-1} was needed for normal mineralization. Whole-body Mn levels in salmon parr are also reduced by excessive supplementation of iron to the diet (Andersen *et al.*, 1996).

It is advisable to include salt in smoltification diets, as this increases Na–K adenosine triphosphatase activity (Basulto, 1976). Requirements for sodium and potassium and their nutritional interactions have not been published with respect to Atlantic salmon.

The availability of iron depends on the dietary source; haem iron is about twice as available as Fe from iron sulphate, while elemental iron (Andersen *et al.*, 1997) and ferric oxide (Fe_2O_3) (Maage and Sveier, 1998) are not available to salmon. High dietary doses of iron are metabolically stressful to the salmon, and they do not seem to adequately downregulate iron uptake when the body stores are high (Kvingedal *et al.*, 1996). Thus, precautions should be taken to avoid overdosing of iron in diets for salmon. There are discrepancies concerning the iron requirement of salmon. Andersen *et al.* (1996) estimated the dietary iron requirement to be between 60 and 100 mg kg^{-1} in salmon parr. However, when re-evaluating the same data, Shearer (2000) suggested that the dietary Fe requirement in juvenile salmon may be as high as 200 mg kg^{-1}.

In studies dealing with copper (Cu) toxicity in salmon parr, growth declined with increasing dietary supplementation above 35 mg Cu kg^{-1}, while there was no increase in mortality when the diets were supplemented up to 1750 mg Cu kg^{-1} (Berntssen *et al.*, 1999). No copper requirement has been established in salmon. However, no differences in growth or haematology were observed when parr were fed a basal diet with 3.5 mg kg^{-1}, or supplemented with from 5 to 100 mg Cu kg^{-1} from copper sulphate ($CuSO_4$). The only significant difference in tissue Cu concentration was that the salmon supplemented with 5 mg kg^{-1} had a slightly elevated liver Cu concentration (Lorenzen *et al.*, 1994).

The availability of zinc is highly affected by dietary composition. For example the availability of Zn is strongly reduced by phytic acid from vegetable-feed ingredients (Storebakken *et al.*, 1998b). Other protein ingredients, such as wheat gluten, have been shown to enhance zinc absorption in salmon (Storebakken *et al.*, 2000a), while the dietary oil source has no effect on the zinc status of the fish (Maage and Waagbø, 1990). Increased dietary ash content may also result in a reduced uptake of zinc (Shearer *et al.*, 1992). The Zn requirement during first feeding is high, and deficiency symptoms, such as retarded growth, high condition factor and elevated iron levels, appear rapidly. Supplementation of 37–57 mg Zn kg^{-1} in the feed was needed to avoid deficiency symptoms, while as much as 57–97 mg kg^{-1} was needed to sustain whole-body Zn levels in fast-growing fry (Maage *et al.*, 1993). In larger (40 g) fingerlings, 17 mg Zn kg^{-1} was sufficient to avoid deficiency symptoms, while 67 mg Zn kg^{-1} was needed to maintain whole-body and serum Zn concentrations within a normal range (Maage and Julshamn, 1993).

Selenium (Se) is important for the glutathione peroxidase system. Deficiency symptoms in juvenile salmon other than reduced tissue selenium levels are: reductions in growth and packed blood-cell volume, reduced vitamin E concentrations in liver, blood and brain, lost integrity of the endoplasmic reticulum in pancreatic tissue, reduction in glutathione peroxidase activity in the liver and plasma, and increased hepatic glutathione-*S*-transferase, plasma pyruvate kinase and kidney glutathione levels (Poston *et al.*, 1976; Bell *et al.*, 1987). The availability of Se varies among dietary sources. In smolts Se-methionine was efficiently digested, while the availability of Se from Na_2SeO_3, Se-cystine and fish-meal was lower. However, selenium from Na_2SeO_3 and Se-cystine is much more efficiently incorporated into plasma glutathione peroxidase than Se from the other two sources (Bell and Cowey, 1989). The requirement for selenium has not been established in salmon.

Carotenoid pigments

Astaxanthin (3, 3′-dihydroxy-β, β-carotene-4, 4′-dione) or canthaxanthin (β, β-carotene-4, 4′-dione) are added to the diet of salmon mainly to give a pink colour to the flesh. Astaxanthin is the major carotenoid in wild Atlantic salmon (Khare *et al.*, 1973), is more efficiently utilized for flesh pigmentation (Storebakken *et al.*, 1985) and gives a redder hue to the flesh colour than canthaxanthin (Skrede and Storebakken, 1986). Thus, astaxanthin is the most commonly used carotenoid in salmon production today. Astaxanthin is metabolized by the salmon (Schiedt, 1998). The first step in reductive metabolism of astaxanthin metabolism is formation of idoxanthin (3, 3′, 4′-trihydroxy-β, β-carotene-4, 4-one). Idoxanthin is found in the blood and accumulated in the flesh of Atlantic salmon. Accumulation of idoxanthin may be high in the flesh of small salmon but decreases as the fish grows larger. Astaxanthin is taken up from the intestine as free astaxanthin. It is not unusual for the salmon to lose as much as 40–60% of the dietary astaxanthin unabsorbed in faeces. The rate of astaxanthin deposition is low in Atlantic salmon compared with other salmonid species (Storebakken *et al.*, 1986). The salmon rarely accumulates more than 10–12 mg astaxanthin kg^{-1} flesh, and 10–15% of dietary astaxanthin is normally recovered. Astaxanthin is not only a donor of pigment in salmon, as Christiansen *et al.* (1994, 1995) found that dietary astaxanthin was essential for growth and survival in salmon fry during first feeding. Based on their results, they recommended that first-feeding diets should contain a minimum of 5 mg astaxanthin kg^{-1}. The capacity to deposit carotenoids develops as the salmon grows, and the utilization of dietary carotenoid first starts getting efficient when the fish has reached a certain weight, around 1 kg. Generally, the response to increasing the dietary astaxanthin concentration beyond 50–60 mg kg^{-1} is marginal (March and MacMillan, 1996). The carotenoid uptake in salmon is facilitated by dietary lipid, since carotenoid uptake and pigmentation increase with increasing dietary fat content (Torrissen *et al.*, 1994; Bjerkeng *et al.*, 1998).

Astaxanthin represents a major proportion of the feed cost – more than 15% if the dietary astaxanthin concentration is 50–60 mg kg^{-1}. Thus, it is of crucial importance for the salmon farmer to use a pigmentation regime that results in satisfactory pigmentation at minimum cost. The target carotenoid concentration in the salmon fillet depends on the preference in the market. Generally, the demands for pigmentation are satisfied with 6–8 mg total carotenoid kg^{-1} flesh. As a consequence of the low capacity to utilize dietary carotenoid and the long time required to reach satisfactory pigmentation, salmon should receive pigmented feed throughout the salt-water period in order to ensure a satisfactory pigmentation. One pigmentation strategy that has proved useful is to start with a moderate astaxanthin concentration (25–35 mg kg^{-1}) in the feed once the smolts are transferred to the sea pens. The dietary concentration is then increased to 45–60 mg kg^{-1} when the salmon grows and the capacity to take up dietary astaxanthin is improved, at approximately 1 kg. Thereafter, sampling at least every 2 months must carefully monitor pigmentation to determine if the dietary carotenoid concentration may be reduced or increased. An alternative strategy, which has also been practised, is to start out with a high dietary astaxanthin concentration (50–60 mg kg^{-1}) in order to saturate the tissues with astaxanthin. At 1.5 to 2 kg body weight the carotenoid concentration is reduced to 35–45 mg kg^{-1}, and the concentration is maintained at this level until slaughter.

Practical Diets

Early findings (Austreng, 1977) in experiments replacing fish-meal with graded amounts of fish-oil and maize meal to parr with a starting weight of 1 g indicate that the optimal crude protein content with respect to growth and survival is around 44% in pelleted feeds. Increasing the dietary fat of a 60% protein diet to 12.6 and 16.0% caused a linear increase in growth and the number of fish becoming smolts after 15 months (Austreng, 1976). These findings resulted in commercially produced salmon diets containing 45–50% crude protein and 17–18% fat. With the introduction of extruded feeds came the possibility to further increase the dietary fat content, and salmon at the end of the freshwater stage grow rapidly on a diet containing 30% fat, 55% crude protein and 10.5% starch (Grisdale-Helland and Helland, 1997). The growth rates of salmon during smoltification appear to be little affected by dietary macronutrient composition, but both carcass and visceral fat contents decrease with decreasing dietary fat content (Helland and Grisdale-Helland, 1998b).

Currently, most diets for Atlantic salmon are produced by extrusion. Salmon feeds should sink. A range of compositions for practical salmon diets is presented in Table 6.4. Whole steam-dried fish-meal is the predominating protein source. Defatted or full-fat soybean is used to a limited extent in grower diets, but not in diets for juveniles due to inherent antinutrients (Storebakken *et al.*, 2000b). Wheat gluten is used mainly for feed technical reasons, while maize-gluten meals are commonly used as a supplementary source of protein. At the end of the 1990s it became increasingly common to substitute part of the fish-oil with soybean or canola oil, mainly because of the limited availability of fish-oil in the market.

Table 6.4. Typical ranges for formulation and chemical composition of diets for different size classes of Atlantic salmon.

	Starter	Fingerling	Smolt	Grower	Finishing	Brood stock
Ingredients (%)						
Fish-meal	35–60	35–60	35–60	25–50	25–50	25–50
Soy products	0	0–5	0–5	0–15	0–15	0–15
Gluten products	0–15	0–15	0–15	5–20	5–20	5–20
Cereal grains	8–15	8–15	8–15	10–18	10–18	10–18
Oils	10–15	10–20	10–20	20–30	10–30	10–30
Others*	3–5	3–5	3–5	3–5	3–5	3–5
Composition of DM (%)						
Crude protein	50–60	50–60	50–55	35–55	35–55	50–60
Crude fat	18–25	18–30	18–30	30–40	20–40	20–355
Starch	6–12	6–12	6–12	7–15	7–15	7–15

* Vitamin and micromineral premixes, macrominerals, pellet binders, carotenoids, other additives.
DM, dry matter.

Feeding Practice

It is of crucial importance for both the growth, feed conversion and health of the salmon, and the economy of the fish farmer that the fish receives the right amounts of feed at correct feeding frequency. The feeding should also be carried out in a manner that enables the salmon to eat all that is fed. The optimal particle diameter for juvenile salmon is 2.5% of 'fork-length' (Wànkowski, 1979). Similar experiments have not been published for salmon in salt water, but practical experience indicates that this value is also useful for larger fish.

When feeding salmon, it is important to spread the feed so that dominant individuals are prevented from driving other fish away from where the feed is dropped. This is achieved by utilizing the water current when automatic feeders are used in tanks and spreading the feed before it reaches the water in pens. Feeding in pens is carried out by several methods, such as manual shovelling or the use of air- or water-driven distributors. Optimal feeding frequency reflects the energy requirement of the fish and the rate of passage through the gastrointestinal tract. Thus, optimal feeding frequency depends on the fish size and water temperature: most frequent feeding is required for small fish and when the water temperature is optimal for growth. Starter diets float for some time, and frequent feeding results in continuous access to feed during this stage. Even though rapid growth can be obtained by less frequent feeding, it is common practice to feed juvenile salmon at least every half-hour. It is common practice also to feed salmon in marine pens every 0.5–2 h during daylight when using automatic feeders. However, maximum growth can be obtained by three to four meals a day in summer if sufficient time is used when feeding fish in each pen. It is important that sufficiently large amounts are fed at once, so that competition over the feed is avoided.

Salmon should be fed according to appetite for rapid growth and efficient feed conversion. Underfeeding should be avoided, especially for juvenile fish, as hunger-induced aggression results in excessive fin erosion and bimodality in growth (Storebakken and Austreng, 1987). Overfeeding is not necessary for rapid growth; it negatively affects the economy and may also pollute the fish farm. The correct amount to feed in a day mainly depends on fish size and water temperature, and it is possible to control feeding of juvenile salmon successfully based on these two variables and known feed efficiency (Austreng *et al.*, 1987; Storebakken and Austreng, 1987). One efficient method of predicting growth is to calculate growth factors, corrected for fish size and water temperature (based on Iwama and Tautz, 1981):

$$\text{Growth factor (GF)} = 1000 \times (W_t^{1/3} - W_0^{1/3})/dd$$

where W_t and W_0 are fish weights at days 0 and t, and dd is the product of average temperature and feeding days. W_t can be calculated as $(W_0^{1/3} + (\text{GF}/1000) \times dd)^3$. Thus, the estimated feed requirement is $(W_t - W_0)/\text{FE}$, where FE is feed efficiency (kg gain kg^{-1} fed). The GF is not independent of fish size, and typical values for salmon are (Einen and Mørkøre, 1997):

		GF
First feeding	(0.15–1 g)	1.0 (0.6)
Parr	(1–10 g)	1.5 (0.9–1.4)
Parr	(> 10 g)	2.0 (0.6–1.9)
Salmon in salt water		3.5 (2.5–2.7)

The values were relevant for Norwegian fish farms in the mid-1990s, while the values in parentheses are calculated from Austreng *et al.* (1987). The appetite of the fish and the optimum daily ration of the salmon, however, also depend on factors such as genetic selection, time of the year, sexual maturation and composition of the diets. It is still not feasible to incorporate such information into sufficiently accurate feeding management models. Appetite feeding based on observations of feeding activity in the surface of deep net pens will result in underfeeding. Thus, it is increasingly common to control automatic feeding based on detection of uneaten feed in the bottom of the pen, by the use of a collector attached to detectors. Once a certain amount of uneaten feed particles is detected, feeding is reduced or delayed. In spite of the labour costs involved, it is common to combine computer-controlled automatic feeding with manual feeding, mainly to check that the salmon is behaving normally in the pens.

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