Aquaculture International **1**, 20–46 (1993)

REVIEW

Feeding, growth and environmental requirements of Arctic charr: a review of aquaculture potential

Malcolm Jobling*, Even H. Jørgensen, Arne M. Arnesen and Einar Ringø

NFH, University of Tromsø, 9037 Tromsø, Norway

Interest in the cultivation of Arctic charr arose during the 1970s, and research into charr farming was instigated in the Nordic countries and in Canada. Most work has been conducted on fish from anadromous populations, although 'land-locked' freshwater populations of Arctic charr have also received attention. Research has also been carried out in the British Isles and in the alpine regions of central Europe, where land-locked populations of charr occur. Small-scale commercial farming is now carried out in several countries of northern Europe and North America, and charr are reared for restocking purposes in a number of countries.

Growth of charr is rapid during the early freshwater rearing stages, and quite good rates of growth can be achieved at low water temperatures. Growth may be submaximal if charr are reared in systems designed for other salmonids, and problems may arise when charr are held at low stocking densities. Growth and food conversion can be improved by exposing the fish to water currents, forcing them to swim at moderate speeds. Growth in seawater has been reported as being highly variable, probably as a result of the use of inappropriate rearing techniques and owing to the seasonal changes in the hypo-osmoregulatory ability of the charr.

Prospects for aquaculture development and areas requiring further research effort are briefly discussed.

KEYWORDS: Arctic charr, Feeding, Nutrition, Growth requirements

INTRODUCTION

In northern Europe, Canada and USA the farming of salmonids is concentrated on Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*) and various species of Pacific salmon (*Oncorhynchus* spp.), but other species have been produced for stock enhancement and sport fishery purposes. Several species of the genus *Salvelinus* have been reared for release, and during the 1970s and 1980s there was increased interest in the development of farming of a number of charr species, including the Arctic charr (*Salvelinus alpinus*). Because the Arctic charr appears to be in decline in certain geographic areas (Maitland, 1992), interest in rearing has arisen from the viewpoints both of restocking and of the development of commercial farming for the table.

Because much of the salmonid farming in northern regions is carried out in coastal fjords or sea lochs, the initial aim of commercial farming was the development of sea-cage rearing of Arctic charr, but early rearing trials gave variable, and often contradictory, results. Consequently, alternative rearing strategies have now been adopted, and in this paper we will present an overview of the developments that have

* Author to whom correspondence should be addressed.

occurred during the course of the past two decades. Particular emphasis will be given to studies aimed at the elucidation of the growth requirements of the charr, since these give information both about the rearing conditions required for the optimization of production in commercial farms and about factors that should be taken into consideration when stock enhancement and release programmes are envisaged.

SOURCES OF ARCTIC CHARR FOR GROWTH TRIALS

The Arctic charr has a northern circumpolar distribution, and anadromous populations are found in the northernmost part of the geographical range of the species e.g. Canada, Greenland, Iceland and northern Norway. Non-migratory and land-locked populations are found both in these northern areas and in parts of North America and Europe further to the south. Furthermore, given populations of charr may comprise both migratory and resident components (Nordeng, 1983), and certain water bodies have been found to contain charr of several different distinct 'ecotypes' or 'morphs' (Johnson, 1981; Maitland, 1992; Sandlund *et al.*, 1992).

Populations of charr in individual watercourses and lakes may have been isolated from each other for several thousands of years and have developed a variety of phenotypic characteristics. The differences are probably genetically based (Nyman, 1972) and, in some cases, are so large that Arctic charr from different populations were originally described as distinct species (Johnson, 1981).

Since it was hoped that Arctic charr could be developed as a new or alternative species for sea-cage culture in some Nordic countries and North America, fish from anadromous populations attracted interest in farming circles. In addition, charr from some anadromous populations grow up to several kilograms in weight and this was also considered advantageous from the commercial viewpoint.

In Norway, many of the experimental studies and commercial growth trials have been conducted on charr of the anadromous 'Hammerfest strain', and the majority of the Arctic charr in Norwegian commercial farms are descendants of broodstock fish collected during the early and mid 1970s. Charr of this anadromous population show annual migrations to and from Lake Storvannet, which lies within the municipal boundaries of the town of Hammerfest in northern Norway (70°30′ N). Experimental studies have also been carried out on charr from other sources, including fish from land-locked populations in both northern (e.g. Takvatn) and southern (e.g. Skogseidvann) Norway (e.g. Ringø and Nilsen, 1987; Holm, 1989; Jørgensen and Jobling, 1989).

Canadian workers have imported fish of the Hammerfest strain and have used these fish, along with those of Canadian origin (e.g. Fraser River, Labrador and Nauyuk Lake, Northwest Territories), in a series of growth trials (e.g. Tabachek, 1984). Charr from both anadromous and land-locked populations have been used in Canadian studies, whereas work carried out in other countries (e.g. Sweden, Britain and alpine regions of central Europe) has been conducted, predominantly, on non-migratory charr. Swedish workers have concentrated research effort on studies of the Arctic charr population from Lake Hornavan, northern Sweden (e.g. Brännäs and Alanärä, 1992) and much of the British work refers to Windermere charr (e.g. Swift, 1964, 1965), although studies have been carried out on other charr populations (e.g. Loch Rannoch).

There have been few attempts to make systematic interpopulation comparisons of growth characteristics with the aim of finding charr populations that may be particularly well suited for commercial cultivation. Some comparative studies have, however, been carried out in Norway, Sweden and Canada and a research programme is currently under way in Iceland.

Few studies have investigated intra- and interstrain genetic differences (de March, 1991a,b; Torrissen and Barnung, 1991; Torrissen and Shearer, 1992), but results suggest that these may be large. Thus, there may be considerable potential for stock improvement through selective breeding. Despite the success of selective breeding programmes for stock improvement of other salmonids, there has been little systematic genetic selection carried out on the Arctic charr populations held in captivity (Nilsson, 1990, 1992; de March, 1991a,b). Broodstocks of several populations (e.g. Hammerfest, Hornavan, Fraser River and Nauyuk Lake) have, however, been established in a number of research stations and commercial facilities (e.g. Papst and Hopky, 1984; Nilsson, 1990).

RESULTS OF THE EARLY REARING TRIALS

When growth trials were initiated in the mid 1970s, only a handful of the approximately 1000 papers in the international literature relating to Arctic charr gave information that could have direct application to cultivation of the species. At that time the majority of the work on charr referred to aspects of the ecology of a number of southern non-migratory populations. There was, however, a considerable body of information available about the farming of other salmonid species, particularly *Oncorhynchus* spp. (including the rainbow trout). This inevitably had a considerable influence on the choice of problems to be studied and the experimental design employed in the studies with Arctic charr. Hatchery and grow-out systems were available for some salmonid species and it was natural to adopt these systems when starting growth trials with charr. Similarly, experience gained during the development of rearing methods (e.g. with respect to feeding regimes, stocking densities etc.) for other salmonid species was incorporated into the trials with charr.

Growth of Arctic charr during the freshwater rearing phase appeared to be quite rapid (Swift, 1964; Gjedrem and Gunnes, 1978; Wandsvik and Jobling, 1982a) and this gave rise to optimism with regard to the development of commercial production. Despite the fact that good rates of growth were obtained, these trials also revealed a number of problems to be solved before commercial farming could become a reality. There were, for example, clear indications that the size range of the fish increased markedly with time. This would be considered disadvantageous in commercial farming because large differences in size between individuals within a rearing group create problems for rational management (e.g. with respect to food supply and harvesting strategy).

It was suspected that social interactions and aggressive behaviour played an important role in determining the rates of food acquisition and growth of individual fish, leading to the suppression of growth of some fish to levels well below their full potential (Wandsvik and Jobling, 1982a; Jobling and Wandsvik, 1983a). Therefore, it was suggested (Wandsvik and Jobling, 1982a) that the influences of different stocking densities, and the effects of size sorting, on growth performance merited further investigation.

During the course of laboratory growth trials, several charr were seen to develop symptoms of 'swimbladder stress syndrome' and this was considered to be an indication that rearing conditions were suboptimal. 'Swimbladder stress syndrome' is characterized, in the early stages, by the fish swimming at the water surface with the dorsal fin exposed, and later the fish may keel over and swim with belly uppermost. Fish which display such symptoms may, however, continue to feed and grow. The early growth experiments (Wandsvik and Jobling, 1982a) were conducted in commercially available hatchery tanks (1 × 1 m), in which water depth was maintained at 30–40 cm. Later studies revealed that the incidence of 'swimbladder stress syndrome' could be reduced by rearing charr in deeper water (Kolbeinshavn and Wallace, 1985).

Investigations to test the ability of Arctic charr to survive in the sea gave results that were less promising than those obtained during the freshwater rearing phase. Charr held in sea cages began to suffer mortality during the late summer/early autumn (August–September) and very few fish survived the winter (Gjedrem, 1975). Results from other studies also suggested that there was relatively poor survival in seawater during winter months (Wandsvik and Jobling, 1982b). This inability to survive exposure to full-strength seawater for extended periods of time was thought to be related to the Arctic charr having poor hypo-osmoregulatory ability, and there was a consensus that members of the genus *Salvelinus* had a lower salinity tolerance than most other salmonid species (Roberts, 1971; Saunders *et al.*, 1975; Sutterlin *et al.*, 1977). These reports obviously had negative consequences for the development of year-round sea-cage cultivation of the Arctic charr, and highlighted the necessity of investigating alternative rearing methods.

TEMPERATURE REQUIREMENTS AND GROWTH RATES

The Arctic charr is, in common with other salmonids, a relatively stenothermal cold-water species. Spawning occurs in freshwater lakes and streams during autumn or early winter, and the eggs remain buried in gravel, in areas called 'redds', throughout the winter months and hatch during the course of the spring. During the winter the eggs may be exposed to low water temperatures, and, under culture conditions, high rather than low rearing temperatures have been found to be most deleterious for egg development and survival.

Reproductive development, involving gametogenesis and vitellogenesis, is relatively protracted, and the increase in gonad size that precedes spawning is accompanied by marked changes in the plasma concentrations of sex steroid hormones (Mayer *et al.*, 1992). Ovulation may be delayed if broodstock are exposed to temperatures over 8 °C for prolonged periods and may be completely inhibited at temperatures in excess of 11 °C (Gillet, 1991). When water temperatures remain above 5 °C throughout the period prior to and during spawning, the quality of the eggs stripped from the females may be poor owing to the rapidity with which overripening occurs at elevated temperatures (Gillet, 1991).

Egg mortality in the period from fertilization to hatch may amount to 10–15% if the incubation temperature remains around 5 °C, but at temperatures over 10 °C rates of mortality can increase markedly (Swift, 1965; Jungwirth and Winkler, 1984; Steiner, 1984; Gillet, 1991). Thus, eggs from northern and alpine populations should be incubated at temperatures below 10 °C, with an incubation temperature in the range 4–6 °C giving satisfactory results with respect both to rate of development and to survival. Rate of development is temperature dependent, and the time taken between fertilization and hatch will decrease from over 100 days at 4 °C to approximately 55 days at 8 °C (Fig. 1) (Jungwirth and Winkler, 1984; Steiner, 1984).

During the period immediately following hatching, the young fish will be dependent

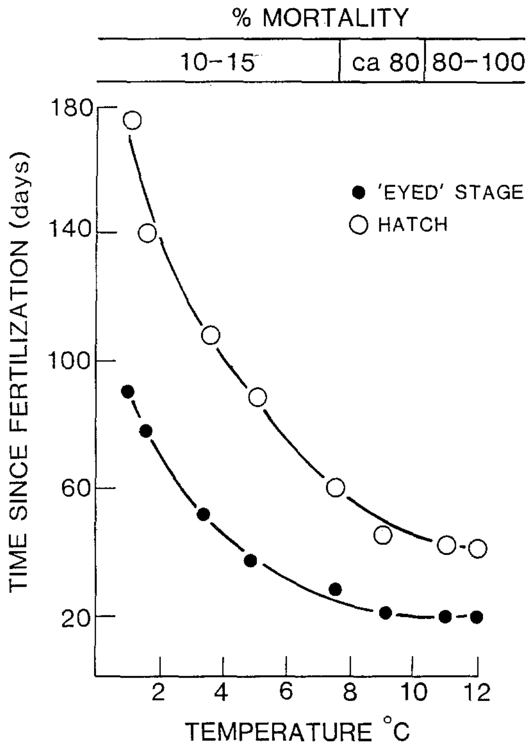

FIG. 1. The effects of different incubation temperatures on the developmental rates of the eggs of Arctic charr from the Hammerfest strain.

upon the yolk sac for nutrition, but later they begin to actively seek food. The active search for food commences when most of the yolk sac reserves have been depleted. Exogenous feeding coincides with the 'swim-up' stage, when approximately 30% of the yolk sac remains, and food should be supplied at this time. Depending upon temperature, swim-up occurs at various times after hatching, but at the ideal temperature to start feeding (6–8 °C), the time between hatch and swim-up is 40–45 days (Wallace and Aasjord, 1984).

Rates of growth of underyearling and yearling charr increase with increasing temperature, reach a maximum within the range 12–15 °C (Swift, 1964; Jobling, 1983) and then decline precipitously at higher temperatures (Fig. 2). Thus, there appear to be ontogenetic differences in thermal optima between juveniles, eggs and start-feeding fry, with the juveniles tolerating a wider range of temperatures and having higher temperature optima than the other developmental stages. To what extent thermal preferenda and optima change with further increases in age and/or size, or differ between populations of different geographic origin is not known. This is a topic worthy of investigation, because young fishes of some species have been found to select higher temperatures than do older and larger conspecifics (McCauley and Huggins, 1979).

As charr increase in size their rates of growth decrease (Fig. 3). Specific growth rates (G) are calculated as $[(\ln W - \ln w)/T] \times 100$, where w and W are fish weights at the start and completion of a growth period, respectively, and T is the time, in days, between

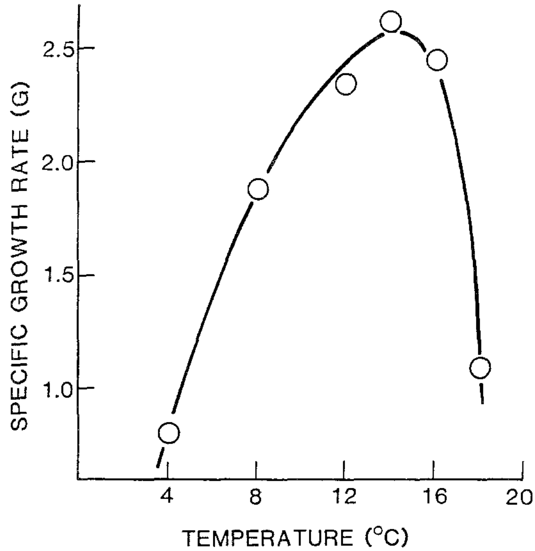

FIG. 2. Effects of temperature on growth rates of Hammerfest strain Arctic charr (50g) fed in excess.

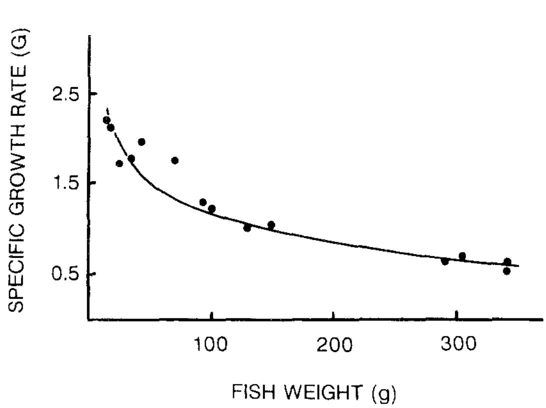

FIG. 3. Effects of body weight on growth rates of Hammerfest strain Arctic charr held at 10 °C and fed in excess.

weighings. The relationship between specific growth rate (G) and body weight (W) can be described by a power function. After logarithmic transformation the power function gives an equation of the form $\ln G = \ln a + \mathrm{b} \ln W$, where a represents the growth rate of a 1 g fish under the particular study conditions, and b is the exponent describing the relationship between growth rate and fish weight. The weight exponent found for charr is similar to that reported for other salmonids (Table 1), with values for the negative exponent usually being within the range -0.32 to -0.40. When growth rates of different salmonids, at their respective optimal temperatures, are compared it can be seen that Arctic charr would be expected to perform at least as well as the other species (Table 1).

By combining data about the effects of temperature and body size on growth rates of Arctic charr, it has been possible to predict rates of growth to be expected under

TABLE 1. Effects of fish weight (*W*, g) on maximum growth rates (*G*) of salmonid fish species. Maximum growth rate is achieved at the optimum temperature for growth, under conditions of unlimited food supply

Species	Temperature (°C)	$\ln G = \ln a + b \ln W$ Growth coefficient* (*a*)	Weight exponent (*b*)
Oncorhynchus nerka (Sockeye salmon)	15.5	5.42	−0.40
Oncorhynchus mykiss (Rainbow trout)	17	6.86	−0.32
Oncorhynchus gorbuscha (Pink salmon)	15	9.78	−0.45
Salmo trutta (Brown trout)	13	2.79	−0.32
Salvelinus alpinus (Arctic charr)	14	8.54	−0.35

* Growth rate of a 1 g fish.

different rearing conditions (Jobling, 1983). The descriptive growth model for Arctic charr of the Hammerfest strain was derived from studies carried out on immature fish during rearing in freshwater. Little information is available about the growth of large, mature charr in brackish or seawater.

Since its publication in 1983, Jobling's model has been adopted as the 'standard' against which the growth performances of Arctic charr derived from different populations and strains have been compared, and it has also been used by commercial farmers in the planning of production cycles. Whilst available information suggests that the growth rates displayed by charr from a number of different populations may be similar, the model may under–estimate growth at very low temperatures (below 1 °C) (Brännäs and Wicklund, 1992). Nevertheless, the growth model for the Hammerfest strain may provide a useful rule-of-thumb prediction of the growth rates to be expected under a wide range of different rearing conditions. The information given (Table 2) is restricted to the lower end of the temperature range, because there are few data about the growth of charr at supra-optimal temperatures (15 °C and over), and it should also be noted that growth rates refer to those displayed by immature fish.

FEEDING BEHAVIOUR AND FOOD INTAKE

A prerequisite for the optimal production of salmonid, and other, fish species is a knowledge about the size of food particles to be fed, because food particle size can affect acceptance, growth and feed efficiency. For example, the growth of juvenile Atlantic salmon (4–20 cm) is most rapid when they are fed particles having a diameter corresponding to 2.2–2.6% of the fork length (Wankowski and Thorpe, 1979). Tabachek (1988) investigated the effects of feed particle size on acceptance and growth in juvenile

TABLE 2. Effects of body weight and temperature on growth rates of Arctic charr. Values presented are specific growth rates (SGR) (in % body weight per day) for fish of different sizes fed in excess under different temperature conditions

Weight (g)	Temperature (°C)				
	2	4	6	8	10
10	0.559	1.045	1.531	2.017	2.503
20	0.438	0.819	1.200	1.582	1.963
30	0.380	0.711	1.041	1.372	1.702
50	0.318	0.594	0.870	1.147	1.423
100	0.249	0.466	0.682	0.899	1.116
150	0.216	0.404	0.592	0.780	0.968
200	0.195	0.365	0.535	0.705	0.875
250	0.181	0.338	0.495	0.652	0.809
300	0.169	0.317	0.464	0.611	0.759
400	0.153	0.286	0.419	0.553	0.686
500	0.142	0.265	0.388	0.511	0.634
750	0.123	0.230	0.336	0.443	0.550

Arctic charr (3–20 g). Growth of small fish (7–11 cm) was best when feed pellets corresponding to 1.5–1.8% of their fork length were offered. Feed particle sizes recommended for the promotion of best growth increased to approximately 2.4% of the fork length of charr of 12–13 cm (Tabachek, 1988). For larger charr (20–40 cm), feed particles having a diameter corresponding to 2–2.25% of the fish body length have been shown to promote good growth. Thus, Arctic charr appear to grow best when fed on pellets with particle sizes that are slightly smaller than those recommended for Atlantic salmon.

Commercial producers are interested in knowing how much food must be fed to their fish in order to sustain good rates of growth, whilst, at the same time, minimizing food wastage. Thus, quantitative information about the food intake of the fish is required, but the collection of such information has hitherto not been a particularly easy task.

X-radiography has been used to study digestive physiology in fish (reviewed by Fänge and Grove, 1979; Talbot, 1985) and X-radiographic techniques (Talbot and Higgins, 1983) have been used to monitor the food intake of groups of Arctic charr of different sizes (year classes) held under a range of different rearing conditions (Jørgensen and Jobling, 1989, 1990; Christiansen and Jobling, 1990; Pálsson *et al.*, 1992).

Much of the variability in food intake by fish can be explained by taking into consideration the two factors fish size and water temperature (Elliott, 1975; Brett, 1979; Fänge and Grove, 1979), but some seasonal differences in food consumption may be observed for fish of a given size held under conditions of constant water temperature (Higgins and Talbot, 1985).

The relationship between food intake (*FI*) and body weight (*W*) can be described by a

TABLE 3. Effects of body weight and temperature on daily food intake of Arctic charr. Values presented are % of fish body weight per day for charr fed commercial dry pellet feed (approx. 23 kJ per g feed)

Weight (g)	Temperature (°C)				
	2	4	6	8	10
10	0.43	0.77	1.11	1.45	1.79
20	0.34	0.60	0.87	1.14	1.41
30	0.29	0.52	0.76	0.99	1.22
50	0.24	0.44	0.63	0.83	1.02
100	0.19	0.34	0.50	0.65	0.80
150	0.17	0.30	0.43	0.56	0.70
200	0.15	0.27	0.39	0.51	0.63
250	0.14	0.25	0.36	0.47	0.58
300	0.13	0.23	0.34	0.44	0.55
400	0.12	0.21	0.31	0.40	0.50
500	0.11	0.20	0.28	0.37	0.46
750	0.09	0.17	0.25	0.32	0.40

power function, and logarithmic transformation gives rise to an equation of the form $\ln FI = \ln a + b \ln W$, where a and b are constants. The constant a represents the food intake of a fish weighing 1 g, and the constant b is the weight exponent describing the relationship between fish weight and food intake. The regular monitoring of food consumption of Arctic charr using the X-radiographic method has shown that daily food intake is proportional to body weight raised to the power 0.651. This weight exponent (b) is in the mid-range (0.47–1.00) of those reported previously for other fish species (Brett, 1979; Fänge and Grove, 1979).

Food intake by fish increases with increasing temperature, reaches a peak and then falls dramatically at supra-optimal temperatures (Brett, 1979). The effects of temperature on food intake in charr have been studied for fish held at the lower end of the temperature range (0.6–10 °C). Within this temperature range, food consumption was found to increase with increasing temperature, but the effects of higher temperatures on food intake are not known.

By combining the data about body size and temperature effects on food intake, it has been possible to compile a table giving preliminary information about the daily food requirements of Arctic charr of different sizes held at different water temperatures (Table 3). The information presented in Table 3 refers to the relative food intake (% body weight per day) of Arctic charr fed on commercially available pellet feed (gross energy content approx. 23 kJ per g feed), and growing at rates similar to those indicated in Table 2.

Whilst the monitoring of daily food intake of fish fed in excess provides information about the feed requirements of the fish, this type of study does not give any information about the time of day at which food should be presented. By carrying out studies in which food intake is monitored over short time periods it is possible to gain an insight into how the feeding behaviour of a group of fish changes during the course of a 24 h cycle. Salmonid fishes are usually regarded as visual feeders that take food predomi-

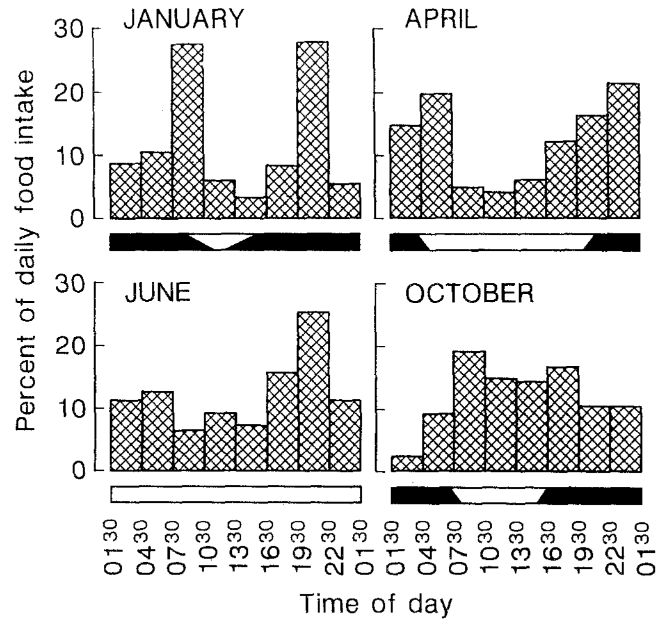

FIG. 4. Percentage of total daily (24 h) food intake consumed by hatchery-reared Hammerfest strain Arctic charr during successive 3 h periods. Measurements were made at different times of the year under simulated natural daylength conditions; horizontal bars indicate the light:dark cycle.

nantly during daylight, but feeding at night, and in total darkness, has been reported for some species (Hoar, 1942; Landless, 1976; Higgins and Talbot, 1985; Dervo *et al.*, 1991). Studies carried out with both Arctic charr (Jørgensen and Jobling, 1989) and rainbow trout (Landless, 1976) reveal that feeding patterns of salmonid fishes may be complex, such that fish cannot be simply classified as feeding actively either by day or by night. Feeding by Arctic charr is not evenly distributed throughout the entire 24 h cycle, and there is often a peak of feeding activity around either dusk or dawn. At certain times of the year (winter months) the Arctic charr appear to consume up to 70% of their daily food intake at night, whereas in the period between late spring and autumn the majority of feeding occurs during daylight hours. The original studies on feeding behaviour of charr (Jørgensen and Jobling, 1989) were conducted using wild-caught land-locked fish, but when experiments were repeated with charr of the Hammerfest strain that had been reared in captivity throughout their lives, the results obtained were similar (Fig. 4). Patterns of feeding behaviour of rainbow trout appear to resemble those of Arctic charr, but juvenile Atlantic salmon appear to feed during daylight hours irrespective of season, and larger salmon in sea cages seem to feed most actively during the early morning and late afternoon (Landless, 1976; Higgins and Talbot, 1985; Kadri *et al.*, 1991).

The finding that the Arctic charr often consumed a large proportion of their daily food intake at night (Jørgensen and Jobling, 1989) led to the suspicion that the fish may forage on the bottom rather than use vision to locate food in the water column. Whilst it is suspected that charr may be able to visually locate and catch prey at lower light intensities than other salmonids (Dervo *et al.*, 1991), the fact that Arctic charr are able to feed in complete darkness suggests that senses other than sight may also be employed for the location of food (Jørgensen and Jobling, 1990). Foraging on the bottom was shown to be an important feeding mode both under conditions of darkness and whilst fish were feeding during daylight hours (Jørgensen and Jobling, 1990; Brännäs and Alanärä, 1992).

These studies were conducted on groups of charr held in tanks with relatively little water flow, and to consider the Arctic charr as a bottom-feeding species would be erroneous. It is known that there are differences in feeding behaviour between charr 'ecotypes' or 'morphs', with the different morphs tending to be distinctly segregated with respect to foraging habitat (Malmquist, 1992; Sandlund *et al.*, 1992). In addition, there may be ontogenetic changes, with charr moving from benthic to limnetic habitats at various stages in their life-history (Klemetsen *et al.*, 1989). A series of subjective observations made under laboratory conditions suggest that when juvenile charr are exposed to water currents they display changes in feeding behaviour and foraging mode. Fish held in standing water spend much of their time resting on the tank bottom, and they tend to forage on or near the bottom, seldom taking food close to the water surface. By contrast, charr that are forced to swim against a water current hold station in the water column, and feed either in mid-water or close to the surface (Christiansen and Jobling, 1990). Thus, the Arctic charr may be flexible in its feeding behaviour, adopting different feeding modes depending upon the rearing conditions to which it is subjected.

NUTRITIONAL REQUIREMENTS

Few studies have been carried out in order to elucidate the nutritional requirements of Arctic charr, possibly because the results of the earliest trials indicated that charr generally showed good rates of growth when fed on dry pellet diets similar to those developed for other salmonid species (Gjedrem and Gunnes, 1978; Wandsvik and Jobling, 1982a; Papst and Hopky, 1983; Tabachek, 1984).

Dietary protein requirements of charr appear to be similar to those of other salmonids (Jobling and Wandsvik, 1983b), and, in a study of protein and energy utilization in charr, Tabachek (1986) found that greatest weight gain was achieved on a diet containing 54% protein and 20% lipid. Lowest feed cost per weight gain was, however, obtained using a 44% protein, 20% lipid diet. Commercially produced start- and grower-feeds for salmon and trout span this range of dietary protein and lipid contents, so these feeds would appear to meet the gross nutritional requirements of charr.

Fish, in common with other animals, are known to be incapable of the *de novo* synthesis of certain amino acids, and these must be included in the diet if the fish are to survive and grow. Whilst a dietary requirement for 10 amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, valine) has been demonstrated, there is comparatively little information available regarding the quantitative requirements for the various essential amino acids by fish species (Wilson, 1989, 1991). Quantitative amino acid requirements are determined by conducting a series of growth trials in which the fish are fed diets containing graded levels of the amino acid of interest, but few detailed studies of this nature have been carried out (Wilson, 1989, 1991).

For species in which essential amino acid requirements have not been determined in growth trials, an analysis of the amino acid composition of body tissues may provide valuable information about the dietary requirement for the various essential amino acids (Wilson, 1989). The muscle of Arctic charr has been analysed with regard to essential

TABLE 4. Essential amino acid (EAA) content of the muscle tissue of Arctic charr in comparison with the dietary requirement for EAAs in Chinook salmon and the amino acid compositions of body tissues in a range of other salmonids. Values are presented on a percentage of protein basis. CHS, Chinook salmon (*Oncorhynchus tshawytscha*); AC, Arctic charr (*Salvelinus alpinus*); AS, Atlantic salmon (*Salmo salar*); RT, Rainbow trout (*O. mykiss*); COS, Coho salmon (*O. kisutch*); n.a., not analysed

Amino acid	Growth	Body tissue composition			
	CHS	AC	AS	RT	COS
Arginine	6.0	4.6	6.6	6.4	6.0
Histidine	1.8	2.2	3.0	3.0	3.0
Isoleucine	2.2	4.6	4.4	4.4	3.7
Leucine	3.9	8.3	7.7	7.6	7.5
Lysine	5.0	8.7	9.3	8.5	8.6
Methionine	4.0	3.0	1.8	2.9	3.5
Phenylalanine	5.1	3.6	4.4	4.4	4.1
Threonine	2.2	5.3	5.0	4.8	5.1
Tryptophan	0.5	n.a.	0.9	0.9	1.4
Valine	3.2	6.3	5.1	5.1	4.3

amino acid content, and the composition of this tissue is shown in Table 4 along with the information available for several other salmonid species. The composition of the Arctic charr muscle is similar to that of other salmonids with regard to essential amino content, and there are generally only minor differences between the requirements determined from growth trials and those found by analysing body tissues. Consequently, the information given in Table 4 may provide a useful guideline about the dietary essential amino acid requirements of the Arctic charr.

Normal development and growth are not possible unless the diet contains certain essential fatty acids (EFAs) which the fish are unable to synthesize *de novo*. Fish have an essential dietary requirement for fatty acids of the (n−3) series, and are also incapable of *de novo* synthesis of (n−6) fatty acids (Wilson, 1991). In common with other salmonid species, Arctic charr possess the desaturase and elongase enzymes required for the transformation of the medium-chain polyunsaturated fatty acids (PUFAs) (18:2 (n−6) and 18:3 (n−3)) into highly unsaturated fatty acids (HUFAs) (20:3 (n−6), 20:4 (n−6), 20:5 (n−3) and 22:6 (n−3)) (Olsen and Ringø, 1992), and the medium-chain PUFAs may, therefore, have essential fatty acid activity (Olsen *et al.*, 1991; Olsen and Ringø, 1992).

Amongst the 18C PUFAs, 18:3 (n−3), which has three double bonds in the carbon chain, is preferred over 18:2 (n−6) as the substrate for elongation and desaturation. This preference for fatty acids with several double bonds is a feature common to the enzyme systems of a wide range of animal species, including humans (Sardesai, 1992a). The HUFAs formed through desaturation and elongation of the shorter-chain fatty acids may then be incorporated into phospholipids, especially phosphatidylcholine (PC) and phosphatidylethanolamine (PE), which are the major phospholipid components of cell membranes. The HUFAs, which contribute to the maintenance of cell membrane fluidity, may, therefore, either be synthesized from 18C PUFAs or they may be obtained directly through the diet. In addition to being integral components of the phospholipids, the 20C HUFAs are the precursors from which the eicosanoids (prostanoids, leukotrienes and lipoxins) are formed. The eicosanoids are a series of biologically active compounds with important roles in the regulation of a range of physiological functions. Certain of these compounds are, for example, known to have marked influences upon the reproductive, respiratory and circulatory systems, or upon the organs involved in salt and water balance (Sardesai, 1992a,b).

Whilst it is clear that charr must obtain certain fatty acids, especially those of the (n−3) series, in the diet, the quantitative essential fatty acid requirement is not known with any degree of certainty (Olsen *et al.*, 1991; Olsen and Ringø, 1992). In those species of fish for which quantitative information about EFA requirements is available, it seems that the amounts of EFA that must be included in the diet to ensure good growth increase as the overall lipid content of the diet is increased (Wilson, 1991). Thus, it is becoming increasingly common to express the EFA requirements of fish as a proportion of the total fatty acids present in the diet, rather than as a percentage of the diet *per se.* Information available for salmonids suggests that the EFA requirements will be met if diets are formulated to contain 10% of the fatty acid content as (n−3) HUFAs, or 20% as 18:3 (n−3), along with small amounts of fatty acids of the (n−6) series (Wilson, 1991).

In common with other salmonids, the Arctic charr deposits large quantities of storage lipid in the swimming muscle, and the fatty acid composition of these neutral lipid reserves is largely determined by the fatty acid composition of the diet (Olsen *et al.*, 1991). Wild-caught land-locked charr, which feed on freshwater invertebrates, have muscle storage lipids dominated by 16:0, 16:1 and 18:1 fatty acids (Ringø and Nilsen, 1987), and the neutral lipids of start-feeding fry of farmed charr may also contain large proportions of 16:0 and 18:1, along with 20:1 fatty acids (Christiansen *et al.*, 1989). When Arctic charr, of either wild or hatchery origin, are weaned on to formulated feeds, the neutral lipid fatty acid profiles change, and may gradually come to resemble those of the diet (Ringø and Nilsen, 1987; Olsen *et al.*, 1991).

It is important that commercial producers realize the influence that the dietary fatty acid supply has upon the composition of the storage lipids, especially because there has been a recent focus of attention on the value of fish and fish products as sources of fatty acids in human nutrition (Pigott, 1989). The (n−3) series of fatty acids that are derived from aquatic plants and animals have been shown to have important functions vital to human health and well being, with the HUFAs 20:5 (n−3) and 22:6 (n−3) conferring the greatest health benefits (Sardesai, 1992a).

Thus, if farmed salmonids in general, and charr in particular, are to be marketed as being of especial nutritional value, it must be clearly demonstrable that the edible portion of the fish (fillet) contains a high proportion of (n−3) series fatty acids. Farmed salmonids fed on diets in which plant oils and terrestrial animal fats have been used as the main lipid sources will have storage lipids dominated by 18:2 (n−6), monoenes and saturated fatty acids, something which is obviously undesirable from a human health, and marketing, point of view. On the other hand, if the fish are fed diets formulated to include marine fish oils as the major lipid source, the storage lipids in the fillet may be expected to contain relatively high levels of the (n−3) series fatty acids. Because many commercially available salmonid feeds contain marine fish oils, the neutral lipids of farmed charr may contain relatively high levels of 18:1, 20:1, 22:1 and the (n−3) series of fatty acids (Olsen *et al.*, 1991), and there would seem to be few arguments in favour of replacing marine oils with either plant oils or other lipids of terrestrial origin.

The muscle of wild-caught charr often looks redder than that of other salmonids, and it appears that the carotenoid content of charr muscle may be towards the higher end of the salmonid range (Scalia *et al.*, 1989; Torrissen *et al.*, 1989). The red flesh coloration is deemed desirable by the consumer, and salmonid flesh should contain at least 4 mg pigment per kg in order to meet consumer preference (Torrissen *et al.*, 1989). Since the carotenoids may fade during processing and storage, compensation must be made for this by producing farmed salmonids with flesh carotenoid concentrations elevated above the minimum acceptable level. Pigments supplied in the diet are, however, relatively poorly retained (2–10%) in the flesh of salmonids, and poor pigment retention appears to be a particular problem in the case of Arctic charr. For example, muscle tissue of 2+ Arctic charr contained only 2 mg pigment per kg following feeding for nine weeks on a diet containing 40 mg canthaxanthin per kg feed (Christiansen and Wallace, 1988). The digestibility (18% for 1+ and 39% for 2+ fish) of the synthetic pigment reported for the Arctic charr (Christiansen and Wallace, 1988) appears to be lower than that found in studies with other salmonids (Torrissen *et al.*, 1989), so this may partially explain why there is particularly poor retention of pigment by charr.

Attempts have been made to compensate for the poor digestibility and retention of pigment by incorporating higher levels of pigment (80–100 mg astaxanthin per kg feed) into dry feeds destined for charr production, than is usual for salmon and trout feeds (40–60 mg pigment per kg feed). Because pigment is one of the most expensive ingredients in the diet, the need for high levels of inclusion in charr diets increases the cost of the diet substantially compared with production diets for other salmonids. Thus, it is expected that research aimed at improving pigment deposition and retention in Arctic charr would pay economic dividends.

SIZE-SORTING AND GROWTH

Results of some of the early growth trials revealed considerable disparity in growth rates between individual fish, which led to increasingly marked differences in size between fish as time progressed (Wandsvik and Jobling, 1982a; Papst and Hopky, 1983). Whilst there could have been many root causes of the size disparity, it was suggested that the establishment of dominance hierarchies may have been a major factor influencing the growth of individual fish.

The rearing of salmonids in small groups can lead to the establishment of dominance hierarchies which results in the suppression of growth of subordinate individuals (Yamagishi, 1962; Li and Brocksen, 1977). Arctic charr are often overtly aggressive, displaying quite high rates of agonistic encounters even after a hierarchy has been established (Noakes, 1980). Consequently, it seemed likely that social rank could influence the growth of individual fish, and that the overall level of social interactions within a group of charr could be an important factor determining gain in total biomass.

In commercial farming of salmonids, size-sorting is carried out in order to ensure good husbandry practice with respect to feeding regimes and feed particle size, and to enable a rational harvesting strategy. Size-sorting would also have the effect of disrupting established dominance hierarchies, and it is widely believed that size-sorting results in greater gain in biomass because the suppressive effect of larger fish on the growth of smaller individuals is removed at regular intervals. There is, however, little evidence that frequent size-sorting gives any marked advantage in terms of increased gain of biomass in Arctic charr when they are reared together in large groups (Papst and Hopky, 1983; Jobling and Reinsnes, 1987; Wallace and Kolbeinshavn, 1988). Under some conditions, charr reared in size-sorted groups may even suffer a growth disadvantage when compared with those reared in groups containing fish of a wider range of sizes (Baardvik and Jobling, 1990).

EFFECTS OF STOCKING DENSITY ON GROWTH

Many of the growth trials conducted with charr have been carried out at stocking densities (5–25 kg m^{-3}) within the range recommended for the routine rearing of other salmonid species. Rearing at these densities has resulted in large differences in size between individuals (Wandsvik and Jobling, 1982a; Jobling and Wandsvik, 1983a; Papst and Hopky, 1983; Papst *et al.*, 1992), possibly owing to the effects of social interactions on growth, and charr reared at low stocking densities often show external signs of having been involved in aggressive encounters (Christiansen and Jobling, 1990).

There are a number of ways in which changes in social behaviour can be affected, including by the manipulation of stocking densities (Brown *et al.*, 1992) or by rearing charr in duoculture with other salmonids (Holm, 1989; Nortvedt and Holm, 1991). When Arctic charr are held at stocking densities in excess of 20 kg m^{-3} the fish tend to form distinct schools in the water column, rather than congregate in a loose group close to the tank bottom (Wallace *et al.*, 1988; Jørgensen *et al.*, 1993). There also appears to be a marked decrease in the incidence of agonistic interactions as stocking density is increased, which may serve to reduce metabolic expenditure and thereby contribute to the improved growth that has been observed at higher stocking densities (Brown *et al.*, 1992).

Growth of Arctic charr is poor when fish are held at stocking densities of 5–15 kg m^{-3}, and weight gain can be significantly increased by stocking the fish at higher densities. Rates of gain improve markedly as stocking density is increased from 15 to approximately 40 kg m^{-3}, but then growth rate reaches a plateau. When stocking densities exceed approximately 70 kg m^{-3}, growth rates may begin to decline (Baker and Ayles, 1990), but high rates of weight gain may be achieved at stocking densities in excess of 100 kg m^{-3} (Wallace *et al.*, 1988; Baardvik and Jobling, 1990; Pálsson *et al.*, 1992; Jørgensen *et al.*, 1993) provided that good water quality can be maintained.

Thus, there are clear benefits to be gained in rearing Arctic charr at quite high stocking densities, and growth rates of charr appear to be maximized when they are held at densities within the range 50–70 kg m^{-3}. Above this range, there may be some decline in rates of gain, but stocking densities in excess of 100 kg m^{-3} are not particularly detrimental to growth provided that the increase in fish biomass is not allowed to lead to a deterioration in water quality.

SUSTAINED EXERCISE AND THE ENHANCEMENT OF GROWTH PERFORMANCE

There can be no denying that swimming is an energetically expensive process, and metabolic rates (assessed by monitoring the oxygen consumption of fish forced to swim against water currents in tunnel respirometers) tend to increase exponentially with increasing swimming speed (Brett, 1964; Beamish, 1980, 1990). It has, therefore, been widely believed that exposure to water currents may be detrimental to the growth performance of farmed salmonids, but this belief is not supported by the results obtained in growth trials.

There is now a large body of evidence indicating that growth rates of salmonids can be improved by forcing the fish to swim against moderate water currents for prolonged periods of time (reviewed by Davison, 1989; Christiansen and Jobling, 1990), and the beneficial effects of sustained exercise may be mediated through the fish displaying both behavioural and physiological changes.

Arctic charr exposed to water currents exhibit schooling behaviour, distribute themselves evenly in the water column, and appear to show much lower levels of agonistic behaviour than fish held in standing water (Christiansen and Jobling, 1990). Charr reared at low stocking density ($10\,kg\,m^{-3}$) in static water may display differing levels of spontaneous activity, ranging from almost complete passivity whilst resting on the tank bottom to bursts of high-speed swimming when engaged in aggressive encounters. Under some circumstances, rates of oxygen consumption of spontaneously active salmonids held in groups may equal, or exceed, those of fish forced to swim at moderate speeds (Brett, 1964, 1973; Christiansen *et al.*, 1991). This clearly suggests that the energetic costs of engaging in agonistic activity may be substantial.

The results of these metabolic studies demonstrate that forcing a group of fish to swim against a moderate water current does not necessarily impose a greater energetic load than rearing in standing water. Thus, exposure of the fish to the current should not be detrimental to growth performance. These observations cannot, however, explain why growth rates and food conversion of exercised fish are better than those of conspecifics reared in standing water (Christiansen and Jobling, 1990).

Expressions of growth rates are synonymous with rates of weight gain, and in discussions of food conversion it is common practice to provide information about the amount of food required to produce a given live weight gain. In other words, neither growth rates nor expressions of food conversion usually take into account the possible changes in fish body composition that may occur under different rearing conditions. Prolonged swimming at moderate speeds can give rise to marked changes in the swimming muscles of salmonids (Davison, 1989) and, because these muscles represent approximately 60% of the body weight, any changes here will have a considerable influence on body growth as a whole.

Prolonged swimming is known to induce muscle hypertrophy (Davison, 1989) and there are also marked changes in rates of protein synthesis and deposition in the body tissues of exercised salmonids (Houlihan and Laurent, 1987). Thus, it is suspected that it is the combination of the behavioural and physiological changes induced by prolonged exercise that lead to the improvements in rates of weight gain and food conversion (Christiansen and Jobling, 1990).

From the marketing viewpoint it is desirable that the harvested fish be of uniform size, and there is some evidence that exposure of the fish to water currents ensures an even distribution of food, resulting in relatively homogenous growth rates of fish within the group. For example, data presented by Christiansen and Jobling (1990) show that variability in food intake, assessed in terms of the coefficient of variation ($CV = 100 \times SD/mean$) decreased from 64% for charr reared in static water to less than

50% in groups exposed to water currents. This was reflected in the CVs of growth rates, which were 40–55% for exercised groups but over 130% for the fish held in static water.

Thus, it appears that exercise regimes can be used to increase rates of weight gain, improve food conversion and reduce interindividual variability in charr held under hatchery conditions.

EFFECTS OF SEXUAL MATURATION ON RATES OF GROWTH

Early maturation is considered disadvantageous in the commercial farming of salmonids, because maturation is often accompanied by a slowing of growth rate, increased mortality and a reduction in flesh quality. Consequently, efforts have been directed towards producing late-maturing strains of some salmonid species through selective breeding programmes. Age at maturation may, however, also be under considerable environmental influence, and rearing under good growth conditions may promote early maturation, particularly amongst the males, in several salmonid species (McCormick and Naiman, 1984; Thorpe, 1989).

When charr are held under conditions of abundant food supply, a large proportion of the males may mature at a comparatively young age, and at a smaller body size than females (Nordeng, 1983). Under farming conditions, many male charr will mature at 2+, and there may be few immature male fish over 3+, but the exact proportions maturing at different ages will depend both on the strain of charr and on the rearing environment (Nilsson, 1990; de March, 1991a,b).

The growth rates of mature charr are lower than those of immatures, and Jobling and Baardvik (1991) found that four-year-old Hammerfest charr were divisible into distinct groups on the basis of body size. The smallest fish were males that matured at 2+, those of intermediate size were the males that matured at 3+, and the largest fish were the last to mature, with females generally maturing later than the males.

Accordingly, there would appear to be benefits to be gained in rearing monosex cultures of all-female fish. Sex reversal of fish can be induced by the administration of various steroids to incubating eggs and to the diet of juveniles. Oestrogens can be used to feminize salmonid fishes (Yamazaki, 1983; Dunham, 1990) but the direct use of sex steroids is not recommended for use in the feminization of salmonids destined for use as food fish.

Sex reversal can also be achieved by treating young salmonid fish with male steroids, and this is usually accomplished by administering the steroid in the diet at the time of first feeding (Dunham, 1990). Masculinization procedures will result in a proportion of the fish being genetic females, but phenotypic males, and, if these fish are held until they mature, they will produce sperm bearing only the female sex chromosome. If the sperm produced by these sex-reversed fish (genotypic females/phenotypic males) are used to fertilize the eggs from normal females, the resulting offspring will all be female. These monosex, female progeny are one generation removed from hormone treatment, and there is therefore no risk of steroid residues remaining in the flesh, nor is there any damaging stigma attached to these fish that could have negative effects upon marketing (Bye and Lincoln, 1986).

All-female stocks of several salmonids, most notably rainbow trout, are now in commercial production, and a similar production strategy would seem to have applications in the farming of Arctic charr. The combination of the production of all-female stocks with procedures (temperature or pressure shocking of newly fertilized eggs) that lead to triploidy is another avenue worthy of investigation, although triploid stocks of other fish species have not always performed as well as expected (Dunham, 1990; Blanc *et al.*, 1992; Johnstone, 1992).

It is probable that genetic selection for late maturation would meet with some success (Nilsson, 1992). Selective breeding would, therefore, seem to offer a viable long-term alternative to the production of all-female stocks, but the two approaches to solving the problem of early maturation should not be viewed as mutually exclusive.

SALINITY TOLERANCE AND GROWTH IN SALTWATER

In the wild, anadromous Arctic charr migrate to the sea during the late spring or early summer, and they remain in coastal waters throughout the summer months. The duration of the stay in the marine environment rarely exceeds 50 days, and re-migration to freshwater occurs during late summer. Therefore, increases in mortality that have been observed in charr held in sea cages during autumn (August–September) (Gjedrem, 1975) have occurred at the time when the fish would, in the wild, have already returned to freshwater.

Problems of overwinter survival of charr in seawater might, therefore, be associated with seasonal changes in hypo-osmoregulatory ability. Salinity tolerance and hypo-osmoregulatory ability of charr, from both anadromous and land-locked stocks, have been found to increase during the spring and early summer (Finstad *et al.*, 1989a; Schmitz, 1989, 1992; Arnesen *et al.*, 1992; Staurnes *et al.*, 1992) and then decline during late summer and early autumn. Both hypo-osmoregulatory ability and saltwater tolerance remain low during the winter months (Finstad *et al.*, 1989a; Schmitz, 1989, 1992). The increase in hypo-osmoregulatory ability of the charr occurs during the course of the spring whilst the fish are still in freshwater and seems, therefore, to represent a preadaptation to survival in the marine environment (Arnesen *et al.*, 1992; Halvorsen *et al.*, 1993). The change in photoperiod that occurs during the spring appears to have an important influence on the development of hypo-osmoregulatory ability, because charr held in the laboratory under conditions of natural daylength showed better hypo-osmoregulatory ability and salinity tolerance than did fish exposed to continuous light (Arnesen *et al.*, 1992).

Whilst Arctic charr from land-locked populations may display improvements in seawater tolerance during the course of the spring and early summer, the development of hypo-osmoregulatory ability may differ between fish of land-locked and anadromous populations (Staurnes *et al.*, 1992), and charr from some land-locked populations may not be able to tolerate prolonged exposure to full-strength (35‰) seawater (Roberts, 1971; Finstad *et al.*, 1989a,b; Schmitz, 1989, 1992). It has generally been found that salinity tolerance declines during the autumn and winter, but charr of some stocks may be able to survive, and continue to grow, when held in seawater throughout the winter (DeLabbio *et al.*, 1990). Clearly, possible differences in salinity tolerances and hypo-osmoregulatory abilities of Arctic charr from different geographic areas merit further investigation if year-round cage culture in seawater is to be developed.

Because Arctic charr develop an improved hypo-osmoregulatory ability during the course of the spring, it seems reasonable to assume that they could be held in seawater throughout the summer without experiencing mortality or marked depressions in growth

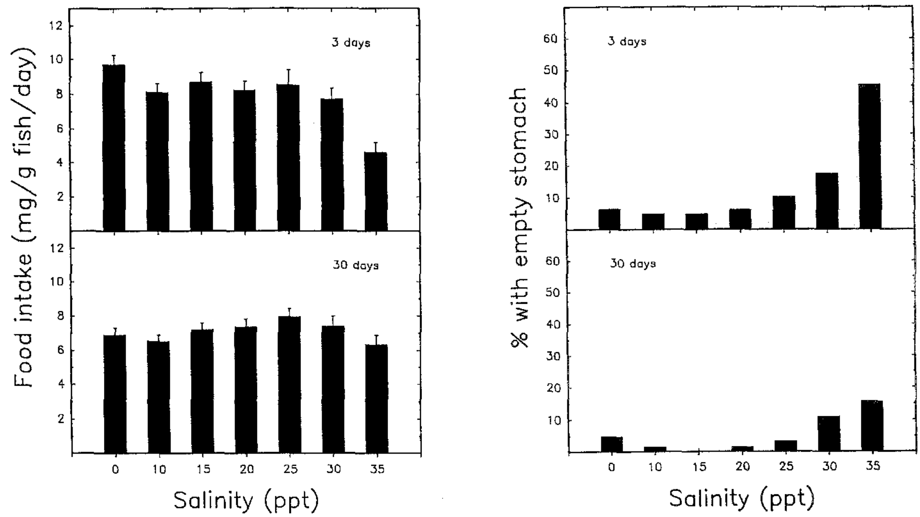

FIG. 5. Food intake in groups of Arctic charr (150 g) estimated 3 and 30 days after abrupt transfer from freshwater to waters of different salinities (0–35‰). Water temperature was maintained at 8 °C. On day 3, food intake in all salinity treatments, with the exception of 15‰, was significantly lower than that recorded in fresh water. Food intake recorded for fish exposed to 35‰ was significantly lower than that for all other treatment groups. There were no significant differences in food intake between treatment groups on day 30.

rate. An abrupt transfer of groups of charr (20–24 cm fork length) from freshwater to waters of increased salinity led to a depression of feeding, a decrease in food intake being recorded when measurements were made three days following the time of transfer (Fig. 5) (Arnesen *et al.*, 1993). The proportions of non-feeding fish also tended to increase with increasing salinity (Fig. 5). When measurements of food intake were repeated 30 days after the time of transfer, no significant differences were recorded between groups (Fig. 5), and growth rates of the fish exposed to the different salinities were similar (Arnesen *et al.*, 1993). Thus, exposure to increased salinity appeared to have had an acute, but short-lived, depressive effect upon food intake in the charr, this being of insufficient duration to have a marked effect upon growth. These results for charr differ from those reported for Atlantic salmon smolts, in which appetite and growth were found to be suppressed for a period of at least 30 days following transfer from freshwater to seawater (Usher *et al.*, 1991).

Whilst these results clearly demonstrate that charr may feed and grow well in seawater during the summer months, there is little information about possible seasonal changes in feeding and growth that may occur when charr are exposed to waters of different salinities. In a recent study (Arnesen *et al.*, unpublished data), Arctic charr (initial weight 150 g) were held in freshwater, brackish water, and seawater, both winter and summer, to examine the effects of salinity on feeding, growth and survival. Fish exposed to fresh and brackish water (20‰) continued to feed and grow well irrespective of season, but charr held in seawater during the winter fed little and many of the fish lost weight. Whilst there was evidence that gradual acclimation of the charr to seawater during winter alleviated some of the negative effects of seawater exposure, growth of these fish was also

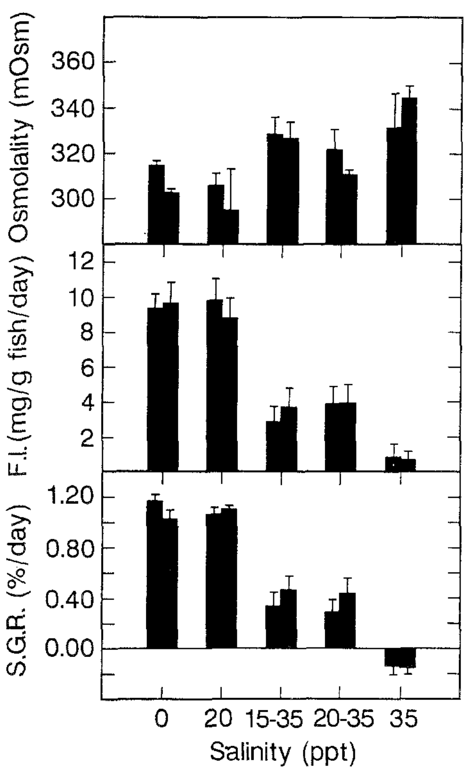

FIG. 6. Effects of rearing in fresh, brackish and seawater on plasma osmolality, food intake and growth of Arctic charr (150 g) during the winter months. Fish were held under conditions of natural photoperiod in fresh water prior to the start of the experiment and then either acutely transferred to brackish (20‰) and seawater (35‰), or gradually acclimated to seawater over a period of several days. Water temperature was maintained at 8 °C. Data are presented for two replicate groups under each of the rearing conditions. Top panel, plasma osmolality of fish sampled at day 60. Middle panel, food intake (FI) measured on day 60. Bottom panel, growth rates (SGR) of charr for the duration of the trial.

substantially poorer than that of fish held continuously at lower salinities (freshwater or 20‰) (Fig. 6). Measurement of blood osmolality suggested that the charr exposed to full-strength seawater during the winter did not experience severe osmoregulatory problems (Fig. 6), a finding which appears to contrast with the results reported by Finstad *et al.* (1989a).

Finstad *et al.* (1989a) recorded high mortalities in Arctic charr exposed to seawater at low temperature (1 °C), but rates of mortality were much lower for charr tested at 8 °C. In the most recent study (Arnesen *et al.*, unpublished data), water temperature was held at 8 °C. Thus, from the limited information available, it appears that water temperature, in addition to the seasonal changes that occur in hypo-osmoregulatory ability, may be a factor influencing the ability of the charr to survive the winter in seawater. Some circumstantial evidence in support of this idea is given by Wandsvik and Jobling (1982b), who found that rates of mortality increased markedly during the latter part of the winter when seawater temperatures were at their lowest.

Current evidence suggests that Arctic charr exhibit marked seasonal changes in hypo-osmoregulatory ability, and such changes may be responsible for the poor survival of fish held in seawater over winter. Whilst it appears that charr of some strains can be kept in seawater throughout the winter without suffering mortality (DeLabbio *et al.,* 1990), knowledge about interstrain differences in salinity tolerance and growth in saltwater is meagre. Thus, on the balance of available evidence it is recommended that Arctic charr be held in fresh or brackish water during the winter, whilst transfer to somewhat higher salinities may be possible for the duration of the summer.

PROSPECTS AND CONCLUDING REMARKS

The opinion that Arctic charr has potential as a 'new' species for aquaculture has been voiced on a number of occasions during the course of the 1970s and 1980s, and growth trials are currently being conducted in several countries within the northern temperate zone. Early trials suggested that growth could be rapid during the freshwater rearing phase, and these findings gave rise to optimistic prognoses with respect to the development of commercial production. Arctic charr has also been found to have other attributes that would be deemed desirable in an aquaculture species, and particularly so in one destined to be farmed in cold regions:

1. The Arctic charr is a hardy fish that can be reared at high stocking densities.
2. Growth rates of juvenile Arctic charr are high and, provided that care is taken with feeding and rearing procedures, excellent food conversion can be achieved.
3. Egg incubation and development occur at low temperatures, and larger fish continue to feed and grow reasonably well even when water temperatures fall below 5 °C.
4. The Arctic charr has a very attractive appearance that can be exploited when marketing the farmed product.

Against these attributes, however, must be balanced a number of negative factors that can reduce the suitability of charr for farming under some conditions:

1. Reduced hypo-osmoregulatory ability during the winter months has been reported to lead to mortality of charr held in sea-cages throughout the winter.
2. The high rate of early maturation, at small body size, that may occur in male charr held under intensive farming conditions is considered undesirable.
3. Poor retention of pigment in the flesh requires diets to be over-fortified with carotenoids, making diets for charr more expensive than those formulated for other salmonids.

Initially, the poor overwinter survival of charr in seawater was considered to be a major stumbling block for the development of commercial sea-cage culture. Alternative rearing methods have been developed, with rearing both in onshore tanks and in enclosed floating systems (either cages or raceways) containing either fresh or brackish water giving satisfactory results with regard to growth and survival.

Enclosed systems permit greater control of rearing conditions than do the traditional open cage, and this can be considered to have a number of advantages. The physical environment (e.g. salinity, temperature) can be controlled to some extent, enabling conditions to be held within the range producing good rates of growth. The use of enclosed systems also permits the generation of the water currents found to have beneficial effects on growth performance. Since most of the wastes produced within an enclosed system are collected and treated, the pollution loads from these systems should be low. The risk of disease transfer between rearing units may also be lower than in traditional open sea-cage systems. Despite the potential advantages, the high levels of initial investment required for the establishment of enclosed systems may deter many commercial producers.

Early maturation of a proportion of the male fish, followed by poor post-maturational growth, is a problem in the culture of all salmonid species and may be of particular significance in the cultivation of Arctic charr. Selective breeding and the production of all-female stocks may, however, offer solutions to the problems associated with early age at maturation.

Because red or pink flesh is a characteristic that the consumer associates with salmonids, the problem of poor pigment retention in the muscle of the charr remains a real one. Fish with pale flesh are thought to be of inferior quality and achieve low market prices. Thus, if farmed Arctic charr are to have the image of being an exclusive fish of top quality, producers will have to produce fish having well-pigmented flesh of the characteristic salmonid red.

Despite the early set-backs, and problems that remain, commercial farming of charr has been started in some areas (e.g. Nordic countries and North America), and there is growing interest in commercial development elsewhere. Charr farming must, however, still be considered as being a small-scale enterprise, and annual production in most countries amounts to no more than a few hundred tonnes. Prospects for the future are promising, but development is likely to be limited by the availability of sites having adequate supplies of good-quality, fresh and salt water. It is not possible to envisage that levels of production will approach those of rainbow trout and Atlantic salmon. If the farming of Arctic charr is to become a successful venture, it seems most likely that production will have to be maintained at relatively low levels (no more than a few thousand tonnes per year), and the product aimed at the top end of the market so that the charr becomes accepted as being an exclusive fish of excellent quality.

ACKNOWLEDGEMENTS

We should like to thank colleagues and students, both past and present, who have assisted in the collection of the Hammerfest charr data which form the backbone of this review. The work would not have been possible without the financial support provided by the Norwegian Council for Fisheries Research (NFFR).

REFERENCES

Arnesen, A. M., Halvorsen, M. and Nilssen, K. J. (1992) Development of hypoosmoregulatory capacity in Arctic charr (*Salvelinus alpinus*) reared under either continuous light or natural photoperiod. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 229–337.

Arnesen, A. M., Jørgensen, E. H. and Jobling, M. (1993) Feed intake, growth and osmoregulation in Arctic charr, *Salvelinus alpinus* (L.), following abrupt transfer from freshwater to more saline water. *Aquaculture* (in press).

Baardvik, B. M. and Jobling, M. (1990) Effect of size-sorting on biomass gain and individual growth rates in Arctic charr, *Salvelinus alpinus* L. *Aquaculture* **90**, 11–16.

Baker, R. F. and Ayles, G. B. (1990) The effects of varying density and loading level on the growth of Arctic charr (*Salvelinus alpinus* L.) and rainbow trout (*Oncorhynchus mykiss*). *World Aquaculture* **21** (1), 58–62.

Beamish, F. W. H. (1980) Swimming performance and oxygen consumption of the charrs. In: *Charrs, Salmonid Fishes of the Genus* Salvelinus, (ed E. K. Balon) Dr. W. Junk: The Hague. pp. 739–748.

Beamish, F. W. H. (1990) Metabolism and photoperiod in juvenile lake charr and walleye. *Environmental Biology of Fishes* **29**, 201–207.

Blanc, J.-M., Poisson, H. and Vallée, F. (1992) Survival, growth and sexual maturation of the triploid hybrid between rainbow trout and Arctic charr. *Aquatic Living Resources* **5**, 15–21.

Brännäs, E. and Alanärä, A. (1992) Feeding behaviour of the Arctic charr in comparison with the rainbow trout. *Aquaculture* **105**, 53–59.

Brännäs, E. and Wiklund, B.-S. (1992) Low temperature growth potential of Arctic charr and rainbow trout. *Nordic Journal of Freshwater Research* **67**, 77–81.

Brett, J. R. (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* **21**, 1183–1226.

Brett, J. R. (1973) Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. *Journal of the Fisheries Research Board of Canada* **30**, 1799–1809.

Brett, J. R. (1979) Environmental factors and growth. In: *Fish Physiology, VIII*, (eds W. S. Hoar, D. J. Randall and J. R. Brett) Academic Press: London. pp. 599–675.

Brown, G. E., Brown, J. A. and Srivastava, R. K. (1992) The effect of stocking density on the behaviour of Arctic charr (*Salvelinus alpinus* L.). *Journal of Fish Biology* **41**, 955–963.

Bye, V. J. and Lincoln, R. F. (1986) Commercial methods for the control of sexual maturation in rainbow trout (*Salmo gairdneri* R.). *Aquaculture* **57**, 299–309.

Christiansen, J. S. and Jobling, M. (1990) The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. *Canadian Journal of Zoology* **68**, 2185–2191.

Christiansen, J. S. and Wallace, J. C. (1988) Deposition of canthaxanthin and muscle lipid in two size groups of Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture* **69**, 69–78.

Christiansen, J. S., Jørgensen, E. H. and Jobling, M. (1991) Oxygen consumption in relation to sustained exercise and social stress in Arctic charr (*Salvelinus alpinus* L.). *Journal of Experimental Zoology* **260**, 149–156.

Christiansen, J. S., Ringø, E. and Jobling, M. (1989) Effects of sustained exercise on growth and body composition of first-feeding fry of Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture* **79**, 329–35.

Davison, W. (1989) Training and its effects on teleost fish. *Comparative Biochemistry and Physiology* **94A**, 1–10.

DeLabbio, J. L., Glebe, B. D. and Sreedharan, A. (1990) Variations in growth and survival between two anadromous strains of Canadian Arctic charr (*Salvelinus alpinus*) during long-term saltwater rearing. *Aquaculture* **85**, 259–270.

Dervo, B. K., Hegge, O., Hessen, D. O. and Skurdal, J. (1991) Diel food selection of pelagic Arctic charr, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* L., in Lake Atnsjø, SE Norway. *Journal of Fish Biology* **38**, 199–209.

Dunham, R. A. (1990) Production and use of monosex or sterile fishes in aquaculture. *CRC Critical Reviews in Aquatic Science* **2**, 1–17.

Elliott, J. M. (1975) Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, *Salmo trutta* L. *Freshwater Biology* **5**, 287–303.

Fänge, R. and Grove, D. (1979) Digestion. In: *Fish Physiology, VIII*, (eds W. S. Hoar, D. J. Randall and J. R. Brett) Academic Press: London. pp. 161–260.

Finstad, B., Nilssen, K. J. and Arnesen, A. M. (1989a) Seasonal changes in sea-water tolerance of Arctic charr (*Salvelinus alpinus*). *Journal of Comparative Physiology B* **159**, 371–378.

Finstad, B., Nilssen, K. J. and Gulseth, O. A. (1989b) Sea-water tolerance in freshwater resident Arctic charr (*Salvelinus alpinus*). *Comparative Biochemistry and Physiology* **92A**, 599–600.

Gillet, C. (1991) Egg production in an Arctic charr (*Salvelinus alpinus* L.) brood stock: effects of temperature on the timing of spawning and the quality of eggs. *Aquatic Living Resources* **4**, 109–116.

Gjedrem, T. (1975) Survival of Arctic charr in the sea during fall and winter. *Aquaculture* **6**, 189–190.

Gjedrem, T. and Gunnes, K. (1978) Comparison of growth rate in Atlantic salmon, pink salmon, Arctic charr, sea trout and rainbow trout under Norwegian farming conditions. *Aquaculture* **13**, 135–141.

Halvorsen, M., Arnesen, A. M., Nilssen, K. J. and Jobling, M. (1993) Osmoregulatory ability of anadromous Arctic charr, *Salvelinus alpinus* (L.), migrating towards the sea. *Aquaculture and Fisheries Management* (in press).

Higgins, P. J. and Talbot, C. (1985) Growth and feeding in juvenile Atlantic salmon (*Salmo salar* L.). In: *Nutrition and Feeding in Fish*, (eds C. B. Cowey, A. M. Mackie and J. G. Bell) Academic Press: London. pp. 243–263.

Hoar, W. S. (1942) Diurnal variations in feeding activity of young salmon and trout. *Journal of the Fisheries Research Board of Canada* **6**, 90–101.

Holm, J. C. (1989) Mono- and duoculture of juvenile Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 697–704.

Houlihan, D. F. and Laurent, P. (1987) Effects of exercise training on the performance, growth and protein turnover of rainbow trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1614–1621.

Jobling, M. (1983) Influence of body weight and temperature on growth rates of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **22**, 471–475.

Jobling, M. and Baardvik, B. M. (1991) Patterns of growth of mature and immature Arctic charr, *Salvelinus alpinus*, in a hatchery population. *Aquaculture* **94**, 343–354.

Jobling, M. and Reinsnes, T. G. (1987) Effect of sorting on size-frequency distributions and growth of Arctic charr, *Salvelinus alpinus* L. *Aquaculture* **60**, 27–31.

Jobling, M. and Wandsvik, A. (1983a) Effect of social interactions on growth rates and conversion efficiency of Arctic charr, *Salvelinus alpinus* L. *Journal of Fish Biology* **22**, 577–584.

Jobling, M. and Wandsvik, A. (1983b) Quantitative protein requirements of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **22**, 705–712.

Johnson, L. (1981) The Arctic charr, *Salvelinus alpinus*. In: *Charr: Salmonid Fishes of the Genus* Salvelinus, (ed E. K. Balon) Dr. W. Junk: The Hague. pp. 15–92.

Johnstone, R. (1992) Production and performance of triploid Atlantic salmon in Scotland. *Scottish Aquaculture Research Report* **2** (1992), 1–10.

Jørgensen, E. H. and Jobling, M. (1989) Patterns of food intake in Arctic charr, *Salvelinus alpinus*, monitored by radiography. *Aquaculture* **81**, 155–160.

Jørgensen, E. H. and Jobling, M. (1990) Feeding modes in Arctic charr, *Salvelinus alpinus* L. : the importance of bottom feeding for the maintenance of growth. *Aquaculture* **86**, 379–385.

Jørgensen, E. H., Christiansen, J. S. and Jobling, M. (1993) Effects of stocking density on food intake, growth performance and oxygen consumption in Arctic charr (*Salvelinus alpinus*). *Aquaculture* **110**, 191–204.

Jungwirth, M. and Winkler, H. (1984) The temperature dependence of embryonic development of grayling (*Thymallus thymallus*), Danube salmon (*Hucho hucho*), Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta fario*). *Aquaculture* **38**, 315–327.

Kadri, S., Metcalfe, N. B., Huntingford, F. A. and Thorpe, J. E. (1991) Daily feeding rhythms in Atlantic salmon in sea cages. *Aquaculture* **92**, 219–224.

Klemetsen, A., Amundsen, P. A., Muladal, H., Rubach, S. and Solbakken, J. I. (1989) Habitat shifts in a dense, resident Arctic charr, *Salvelinus alpinus*, population. *Physiological Ecology, Japan. Special Volume* **1**, 187–200.

Kolbeinshavn, A. G. and Wallace, J. C. (1985) Observations on swim bladder stress syndrome in Arctic charr (*Salvelinus alpinus*) induced by inadequate water depth. *Aquaculture* **46**, 259–263.

Landless, P. J. (1976) Demand feeding behaviour of rainbow trout. *Aquaculture* **7**, 11–25.

Li, H. W. and Brocksen, R. W. (1977) Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *Journal of Fish Biology* **11**, 329–341.

McCauley, R. W. and Huggins, N. W. (1979) Ontogenetic and non-thermal seasonal effects on thermal preferenda of fish. *American Zoologist* **19**, 267–271.

McCormick, S. D. and Naiman, R. J. (1984) Some determinants of maturation in brook trout, *Salvelinus fontinalis*. *Aquaculture* **43**, 269–278.

Maitland, P. S. (1992) The status of Arctic charr, *Salvelinus alpinus* (L.), in southern Scotland: a cause for concern. *Freshwater Forum* **2**, 212–27.

Malmquist, H. J. (1992) Phenotype-specific feeding behaviour of two Arctic charr *Salvelinus alpinus* morphs. *Oecologia* **92**, 354–61.

de March, B. G. E. (1991a) Genetic, maternal and tank determinants of growth in hatchery-reared juvenile Arctic charr (*Salvelinus alpinus*). *Canadian Journal of Zoology* **69**, 655–660.

de March, B. G. E. (1991b) Hatchery growth of pure strains and intraspecific hybrids of juvenile Arctic charr, *Salvelinus alpinus* (Canadian × Norwegian charr). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1109–16.

Mayer, I., Schmitz, M., Borg, B. and Schultz, R. (1992) Seasonal endocrine changes in male and female Arctic charr (*Salvelinus alpinus*) 1. Plasma levels of 3 androgens, 17α-hydroxy-20β-dihydroxyprogesterone and 17β–estradiol. *Canadian Journal of Zoology* **70**, 37–42.

Nilsson, J. (1990) Heritability estimates of growth-related traits in Arctic charr (*Salvelinus alpinus*). *Aquaculture* **84**, 211–217.

Nilsson, J. (1992) Genetic parameters of growth and sexual maturity in Arctic charr (*Salvelinus alpinus*). *Aquaculture* **106**, 9–19.

Noakes, D. L. G. (1980) Social behaviour in young charrs. In: *Charrs: Salmonid Fishes of the Genus* Salvelinus, (ed E. K. Balon) Dr. W. Junk: The Hague. pp. 683–701.

Nordeng, H. (1983) Solution to the 'charr problem' based on Arctic charr (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1372–1387.

Nortvedt, R. and Holm, J. C. (1991) Atlantic salmon in duoculture with Arctic charr: decreased aggression enhances growth and stocking density potential. *Aquaculture* **98**, 355–361.

Nyman, L. (1972) A new approach to the taxonomy of the *Salvelinus alpinus* species complex. *Report of the Institute of Freshwater Research, Drottningholm* **52**, 103–131.

Olsen, R. E. and Ringø, E. (1992) Lipids of Arctic charr, *Salvelinus alpinus* (L.) II. Influence of dietary fatty acids on the elongation and desaturation of linoleic and linolenic acid. *Fish Physiology and Biochemistry* **9**, 393–399.

Olsen, R. E., Henderson, R. J. and Ringø, E. (1991) Lipids of Arctic charr, *Salvelinus alpinus* (L.) I. Dietary induced changes in lipid class and fatty acid composition. *Fish Physiology and Biochemistry* **9**, 151–164.

Pálsson, J. Ö., Jobling, M. and Jørgensen, E. H. (1992) Temporal changes in daily food intake of Arctic charr, *Salvelinus alpinus* L., of different sizes monitored by radiography. *Aquaculture* **106**, 51–61.

Papst, M. H. and Hopky, G. E. (1983) Growth of Arctic charr (*Salvelinus alpinus* L.) in a pilot commercial rearing system. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1182**, iv + 16 pp.

Papst, M. H. and Hopky, G. E. (1984) Development of an Arctic charr (*Salvelinus alpinus* L.) brood stock. *Aquaculture* **43**, 323–332.

Papst, M. H., Dick, T. A., Arnason, A. N. and Engel, C. E. (1992) Effect of rearing density on the early growth and variation in growth of juvenile Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture and Fisheries Management* **23**, 41–47.

Pigott, G. M. (1989) The need to improve omega-3 content of cultured fish. *World Aquaculture* **20**(1), 63–68.

Ringø, E. and Nilsen, B. (1987) Hatchery-reared landlocked Arctic charr, *Salvelinus alpinus* (L.), from Lake Takvatn, reared in fresh and sea water. I. Biochemical composition of food, and lipid composition of fish reared in fresh water. *Aquaculture* **67**, 343–351.

Roberts, R. A. (1971) Preliminary observations on the ionic regulation of the Arctic charr, *Salvelinus alpinus*. *Journal of Experimental Biology* **55**, 213–222.

Sandlund, O. T., Gunnarsson, K., Jonasson, P. M., Jonsson, B., Lindem, T., Magnusson, K. P., Malmquist, H. J., Sigurjonsdottir, H., Skulason, S. and Snorrason, S. S. (1992) The Arctic charr, *Salvelinus alpinus* in Thingvallavatn. *Oikos* **64**, 305–351.

Sardesai, V. M. (1992a) Nutritional role of polyunsaturated fatty acids. *Journal of Nutritional Biochemistry* **3**, 154–166.

Sardesai, V. M. (1992b) Biochemical and nutritional aspects of eicosanoids. *Journal of Nutritional Biochemistry* **3**, 562–579.

Saunders, R. L., Muise, B. C. and Henderson, E. B. (1975) Mortality of salmonids cultured at low temperature in sea water. *Aquaculture* **5**, 243–252.

Scalia, S., Isaksen, M. and Francis, G. W. (1989) Carotenoids of the Arctic charr, *Salvelinus alpinus* (L.) *Journal of Fish Biology* **34**, 969–970.

Schmitz, M. (1989) Annual variations in seawater adaptability and rheotactic behaviour in Arctic charr (*Salvelinus alpinus* L.). *Physiological Ecology, Japan. Special Volume* **1**, 509.

Schmitz, M. (1992) Annual variations in rheotactic behaviour and seawater adaptability in landlocked Arctic charr (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 448–452.

Staurnes, M., Sigholt, T., Lysfjord, G. and Gulseth, O. A. (1992) Difference in the seawater tolerance of anadromous and landlocked populations of Arctic charr (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 443–447.

Steiner, V. (1984) Experiments towards improving the culture of Arctic charr (*Salvelinus alpinus*). In: *Biology of the Arctic charr*, (eds L. Johnson and B. Burns) University of Manitoba Press: Winnipeg. pp. 509–521.

Sutterlin, A. M., McFarlane, L. R. and Harmon, P. (1977) Growth and salinity tolerance in hybrids within *Salmo* spp. and *Salvelinus* spp. *Aquaculture* **12**, 41–52.

Swift, D. R. (1964) The effect of temperature and oxygen on the growth rate of the Windermere charr (*Salvelinus alpinus willughbii*). *Comparative Biochemistry and Physiology* **12**, 179–183.

Swift, D. R. (1965) Effect of temperature on mortality and rate of development of the eggs of the Windermere charr (*Salvelinus alpinus*). *Journal of the Fisheries Research Board of Canada* **22**, 913–917.

Tabachek, J. L. (1984) Evaluation of grower diets for intensive culture of two strains of Arctic charr (*Salvelinus alpinus* L.). *Canadian Technical Report of Fisheries and Aquatic Sciences* **1281**, iv + 21 pp.

Tabachek, J. L. (1986) Influence of dietary protein and lipid levels on growth, body composition and utilization efficiencies of Arctic charr, *Salvelinus alpinus* L. *Journal of Fish Biology* **29**, 139–151.

Tabachek, J. L. (1988) The effect of feed particle size on the growth and feed efficiency of Arctic charr [*Salvelinus alpinus* (L.)]. *Aquaculture* **71**, 319–330.

Talbot, C. (1985) Laboratory methods in fish feeding and nutritional studies. In: *Fish energetics: new perspectives*, (eds P. Tytler and P. Calow) Croom Helm: London. pp. 125–154.

Talbot, C. and Higgins, P. J. (1983) A radiographic method for feeding studies on fish using metallic iron powder as a marker. *Journal of Fish Biology* **23**, 211–220.

Thorpe, J. E. (1989) Developmental variation in salmonid populations. *Journal of Fish Biology* **35** (Supplement A), 295–303.

Torrissen, K. R. and Barnung, T. N. (1991) Genetic difference in trypsin-like isozyme pattern between two strains of Arctic charr (*Salvelinus alpinus*). *Aquaculture* **96**, 227–231.

Torrissen, K. R. and Shearer, K. D. (1992) Protein digestion, growth and food conversion in Atlantic salmon and Arctic charr with different trypsin-like isozyme patterns. *Journal of Fish Biology* **41**, 409–415.

Torrissen, O. J., Hardy, R. W. and Shearer, K. D. (1989) Pigmentation of salmonids – carotenoid deposition and metabolism. *CRC Critical Reviews in Aquatic Sciences* **1**, 209–225.

Usher, M. L., Talbot, C. and Eddy, F. B. (1991) Effects of transfer to seawater on growth and feeding in Atlantic salmon smolts (*Salmo salar* L.). *Aquaculture* **94**, 309–326.

Wallace, J. C. and Aasjord, D. (1984) The initial feeding of Arctic charr (*Salvelinus alpinus*) alevins at different temperatures and under different feeding regimes. *Aquaculture* **38**, 19–33.

Wallace, J. C. and Kolbeinshavn, A. G. (1988) The effect of size grading on subsequent growth in fingerling Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture* **73**, 97–100.

Wallace, J. C., Kolbeinshavn, A. G. and Reinsnes, T. G. (1988) The effects of stocking density on early growth in Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture* **73**, 101–110.

Wandsvik, A. and Jobling, M. (1982a) Observations on growth rates of Arctic charr, *Salvelinus alpinus* (L.), reared at low temperature. *Journal of Fish Biology* **20**, 689–699.

Wandsvik, A. and Jobling, M. (1982b) Overwintering mortality of migratory Arctic charr, *Salvelinus alpinus* (L.), reared in salt water. *Journal of Fish Biology* **20**, 701–706.

Wankowski, J. W. J. and Thorpe, J. E. (1979) The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* **14**, 351–370.

Wilson, R. P. (1989) Amino acids and proteins. In: *Fish Nutrition (2nd edition)*, (ed J. E. Halver) Academic Press: London. pp. 111–151.

Wilson, R. P. (ed.) (1991) *Handbook of Nutrient Requirements of Finfish*, CRC Press: Boca Raton, FL. pp. 196.

Yamagishi, H. (1962) Growth relation in some small experimental populations of rainbow trout fry, *Salmo gairdneri* Richardson, with special reference to social relations among individuals. *Japanese Journal of Ecology* **12**, 43–53.

Yamazaki, F. (1983) Sex control and manipulation in fish. *Aquaculture* **33**, 329–354.