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CHARR

The Arctic charr story: development of subarctic freshwater fish farming in Sweden

Lars-Ove Eriksson · Anders Alanärä · Jan Nilsson · Eva Brännäs

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Abstract We present an overview of 27 years of experience of domestication and farming of Arctic charr (*Salvelinus alpinus*) in Sweden. The domestication process included an evaluation of suitable strains for farming, a breeding programme and the study of the biological and behavioural characteristics of the species. Traits of three different Arctic charr populations differing in ecology and appearance were compared during initial 2-year trials under farming conditions. The best-performing population with respect to the growth rate and the lowest frequency of early sexual maturation was a piscivore form and this became the foundation for a breeding programme intended to select for an Arctic charr strain suitable for farming. After 23 years and 7 generations, our selective breeding has resulted in a fast-growing, late-maturing strain much appreciated by farmers. The biological and behavioural characteristics studied included annual and diel locomotor activity, feeding, social and thermal behaviour. Applying our findings in these areas has greatly improved both profits and conditions for the fish. Other investigations have focused on the application and further evaluation of the results from research in practical farming trials, such as evaluation of growth at different farms with different temperature conditions, optimal time and stocking density for start-feeding and evaluation of different feeding schedules. In Sweden, Arctic charr is mainly farmed in net pens situated in nutritionally depleted and extremely unproductive water reservoirs formed by damming rivers to create electric power. Judicious farming of Arctic charr in such reservoirs can restore their nutritional and productivity state to that which existed before regulation. Site selection criteria for Arctic charr farming in such waters have been developed. The development of intensive farming of Arctic charr in Sweden is discussed together with current limitations and future possibilities.

Keywords Arctic charr · Domestication · Selective breeding · Social behaviour · Feeding · Farming

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L.-O. Eriksson (✉) · A. Alanärä · J. Nilsson · E. Brännäs
Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 90183 Umea, Sweden
e-mail: Lars-Ove.Eriksson@vfm.slu.se

Introduction

In Sweden, Arctic charr (*Salvelinus alpinus* L.) are native to the mountain region of the Scandinavian Peninsula from 56° to 69°N, but are also found in a few large, deep lakes in south Sweden (Johnson, 1980). The Scandinavian Arctic charr populations are typically polymorphic with a considerable variation in life history and behavioural traits amongst and within watersheds. In post-glacial lakes, the Arctic charr exists in 1–4 sympatric forms, a piscivorus form, a limnetic planktivore and one or two additional epibenthic zoobenthos feeders and, in addition, some of these may form anadromous populations (Jonsson & Jonsson, 2001). Also, there are size-structured populations mainly formed by differing competitive abilities, the formation of 'giants', 'losers' and 'victims' (Persson et al., 2003). The most competitive individuals become piscivores and grow fast (to become giants) and prey on the youngest juveniles (victims), whilst the less competitive individuals (losers) were unable to prey on the juveniles and instead have to compete with them for planktonic prey. In contrast to the Atlantic side of the Scandinavian Peninsula, there are no populations of anadromous charr in Sweden (Eriksson et al., 1993).

The culturing of Arctic charr in Sweden initially began at a small scale in natural ponds during the early 1900s and was designed to produce fry and juvenile fish for stocking. Since in 1950s, charr have been reared in hatcheries using intensive tank-rearing techniques developed for juvenile salmon and trout, enabling production of larger fish for stocking.

The domestication process, defined as human control of breeding, care and feeding of animals (Hale, 1962) was intensified in the early 1980s to produce Arctic charr for the table market. Domestication of fish is a comparably recent endeavour, but has already produced successful results (e.g. the family based selection programme of Norwegian salmon starting in the 1970s).

We initiated a programme designed to evaluate Arctic charr as a species for sub-arctic aquaculture along two lines of investigation: (a) one on evaluation of suitable populations for intensive farming (and a subsequent selective breeding programme as well as a study of the basic biological characteristics of the species), and (b) the other on the application and evaluation of results gained from research and practical farming trials. In later years, our activities have dealt with evaluation of alternative and sustainable feed sources and quality aspects of Arctic charr farming, biological bottle-necks for production and reducing the environmental impacts of charr farming. In the following, we will give an overview of our 27 years of experience of research on domestication and farming of Arctic charr in Sweden.

Evaluation of different strains

In our first evaluation of candidate strains suitable for intensive farming in 1982, we assessed the growth and maturation patterns of typical representatives of three common morphs under net-pen farming conditions; a pelagic plankton-feeding morph (from Lake Torrön), a benthic, invertebrate feeding morph (Lake Tinnsjön) and a predatory morph (Lake Hornavan). In general, we found that all populations showed that a high incidence of early pre-market size maturation and grew at a slow rate (Eriksson et al., 1993; Fig. 1). In addition, the feed conversion ratio was poor, which probably was an effect of using feed management originally developed for salmon and trout (Eriksson et al., 1993). However, the predatory morph type from Lake Hornavan grew considerably faster and matured prior to market size at 3 years of age at a somewhat lower rate (73%) than other morphs (100%; Fig. 1). In addition, in a later trial, the Hornavan predatory strain was found to have higher growth capacity than other strains of charr in Sweden (Näslund & Henriksson, 1996). For these reasons, in 1986, we choose the predatory morph from Lake Hornavan to be the starting population for a selective breeding programme.

Selective breeding

The selective breeding programme was carried out according to the model with a combined family/

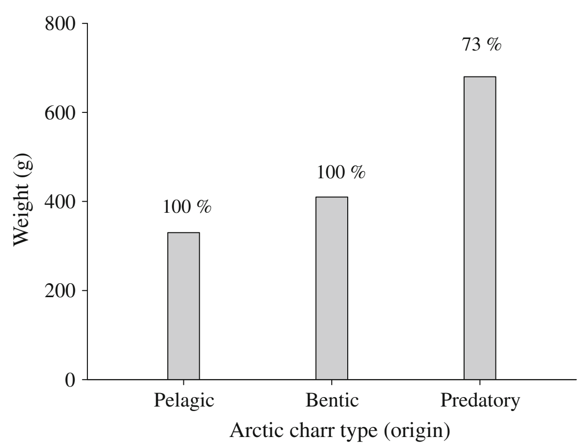

Fig. 1 Average final weight (*staples*) and incidence of early maturation (%) in farmed 3-year-old Arctic charr of different origin after 2 years in net pens (from Brännäs et al., 2010)

Table 1 Farming improvements after 20 years of farming Arctic charr in Sweden

Arctic charr farming 1985	Arctic charr farming 2008
Farming cycle 3–4 years	Farming cycle 1.5–2 years
Relatively slow growth, poor feed utilization	Fast growth, efficient feed utilization
Early maturation (70–100% before 500 g)	Late maturation (<5% before 800 g)
Variable quality	Improved flesh coloration and quality
Production costs 50–60 Swedish krona (4.3–5.6 Euro)	Production costs 35 Swedish krona (3.3 Euro)

Source: Eriksson et al. (1993), Nilsson et al. (2010); Assn. Fish Farmers of Northern Sweden, Mr. Josef Nygren, pers. comm

individual selection, developed for rainbow trout (*Onchorhyncus mykiss*) and Atlantic salmon (*Salmo salar*) in Norway (Gjedrem et al., 1987). Details on the outline of the selective breeding programme, the quantitative genetic characteristics of Arctic charr, and the progress in performance is presented elsewhere in this issue by us (Nilsson et al., this issue). In summary, seven generations of pedigree-based selective breeding has, along with improvements of rearing techniques, resulted in an at least a doubling of growth performance, and in a reduction of the incidence of maturation to <5% in fish smaller than 1 kg. The production cycle to achieve 600–900 g carcass weight of Arctic charr has been reduced from 3.5 to about 1.5 years in Swedish fish farms using the selected strain (Table 1).

Basic biological characteristics

By adjusting the rearing environment and feeding routines to the behavioural ecology of the fish, aggressive interactions between individuals can be reduced (Huntingford et al., 2006). Studies of basic characteristics of Arctic charr, such as the diel and annual locomotor activity, social behaviour, feeding behaviour and thermal behaviour have been performed, and have also contributed to the development of species-specific farming techniques for Arctic charr.

Thermal behaviour and growth in cold water

Together with research groups in Norway and Great Britain, thermal behaviour in Arctic charr was studied with respect to the potential effects of global warming on fish populations. Arctic charr appear to have some unusual characteristics in their thermal behaviour (Larsson & Berglund, 2005). It is a cold-stenothermic species that grows remarkably well at temperatures below 4°C (Brännäs & Wiklund, 1992), but it has a high optimum temperature for growth (16.4°C; Larsson & Berglund, 2005). However, in a laboratory preference tests, Arctic charr preferred temperatures around 11°C (Larsson, 2005) and charr also tended to select temperatures of around 11°C in net pens if they are deep enough to offer this temperature (Larsson & Eriksson, 2009). These results deviate strongly from what has been observed for other fish species, including salmonids, where preferred temperature coincides with optimal temperature for growth. This finding has resulted in the introduction of deep net pens in several Arctic charr farms, allowing the charr to access favoured temperatures below the thermocline during warm summer periods.

Arctic charr have the capacity to grow in excess of predictions by growth models (Jobling, 1983) in temperatures below 4°C (Brännäs & Wiklund, 1992). Towards the end of the summer and autumn, their appetite decreases dramatically, and during winter, they become more or less anorectic (Jobling, 1987; Jobling et al., 1998). Temporal cycling in food intake has been described in several animals, and it appears that species living at high altitudes may exhibit the greatest seasonal fluctuations (Bairlein & Gwinner, 1994; Loudon, 1994). We have data showing a very strong effect of selective breeding on winter growth (Fig. 2). The increase in thermal growth coefficient (TGC) for winter conditions is 2.4 times higher for the 2001-year class than the 1986-year class. TGC is a thermal unit growth coefficient that reduces the problem of growth data from groups of different sizes and temperatures (which is a problem when using specific growth rate (SGR), the most commonly used estimate of fish growth). As temperature is included, TGC data are assumed to reflect real differences in growth potential at different times of the year (Cho &

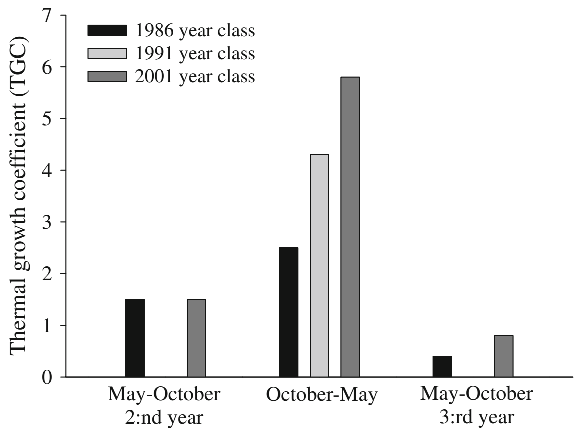

Fig. 2 Thermal growth coefficient (TGC) during summer second year, intermediate winter and summer third year of three consecutive generations in the Arctic charr breeding programme. TGC is expressed as: TGC = $(W_t^{(1/3)} - W_i^{(1/3)})/(T \cdot \Delta t) \cdot 1000$, where W_t is the group average weight at time t (g), W_i is the group average initial weight (g), T is the water temperature (°C) and Δt is the duration of the experiment (number of days). Data of the 1991-year class were only available from October to May (from Brännäs et al., 2010)

Bureau, 1998; Bailey & Alanärä, 2006). Thus, an important part of the improvement in growth achieved in the selective breeding programme stems from improved growth at temperatures below 4°C. The improved winter growth not only an effect of increased growth potential at low temperatures, but also an effect of a shorter 'winter depression' in appetite and growth.

Social behaviour

The issues of behaviour and welfare in farmed fish are receiving increased public and scientific attention, and there are several recent reviews on this topic (e.g. Huntingford et al. 2006; Brännäs & Johnsson 2008). Several of our studies have focused on the social behaviour of Arctic charr and the effect of rearing conditions on intraspecific aggression and competition. In situations, where dominance hierarchies exist in Arctic charr, we classified individuals as dominant, subdominant and subordinate according to Symons (1970). We developed methods for studying behaviour of fish: first, by assessing social ranks of individual fish in small groups of Arctic charr using aggressive interactions, food intake and position relative to a defendable food source as visible indicators (Bailey et al., 2000). Second, we set up a system where individual fish in small as well as large groups could be automatically monitored using PIT-tag systems (Brännäs et al., 1994). This technique has made it possible to study individual behaviour within groups of fish without having to rely on visual observations. For instance, using demand feeders where food is released only when a fish bites on a trigger in the water in combination with the individual recognition system, it is possible to identify several interesting aspects of differences in competitive ability as well as feeding strategies (Brännäs & Alanärä, 1993; 1994, 1996; Alanärä & Brännäs, 1997). In groups of self-fed Arctic charr, the dominant individuals had the highest self-feeding activity, the highest growth rates, and show little sign of stress as measured by levels of stress hormone. Subdominant fish had an intermediate growth rate and low levels of stress hormones. The subordinate fish showed that very low swimming and feeding activity. They suffered from weight loss and displayed elevated levels of stress hormones (Alanärä et al., 1998).

According to Grant (1997), the significance of social dominance is reduced or diminished in conditions where it becomes unfavourable for the dominant or most competitive individuals to defend a favourable area or food resource. Increased stocking density is one such rearing condition where intraspecific aggression and the growth variance decrease (Alanärä & Brännäs, 1996; Brännäs & Linnér, 2000). Other rearing conditions where intraspecific aggression and growth rate variance decrease is when there are high reward levels (when using demand feeders; Brännäs & Alanärä, 1994), and a third is when the daily feed allotment is well-distributed in time and space (i.e. it is non-defendable; Linnér & Brännäs, 2001).

Consequently, the variation in growth will be much higher in situations that promote the formation of dominance hierarchies, such as feeding the fish with a demand feeder (a defendable food source) than when the same number of fish are given the same amount of feed, but by spreading the daily meal in time and space (a non-defendable food source). Also, social status had a pronounced effect on growth rate if the food source was defendable, and dominant individuals had a higher growth rate than subdominants which in turn had a higher growth rate than subordinates (Brännäs & Johnsson, 2008). However, with a non-defendable food source, there was no effect of social status on growth rate (Fig. 3).

Diel and annual locomotor activity

Each month of a full 12-month cycle, the activity pattern as well as swimming direction of five fish at a time was automatically recorded during 2 weeks in a stream tank equipped with photocells. The set up was supplied with a water temperature monitor and maintained in day length conditions that varied with the natural one at 63°35′N, 19°50′E. Swimming activity was linked to sunrise and sunset and decreased sharply during winter. Of the total activity,

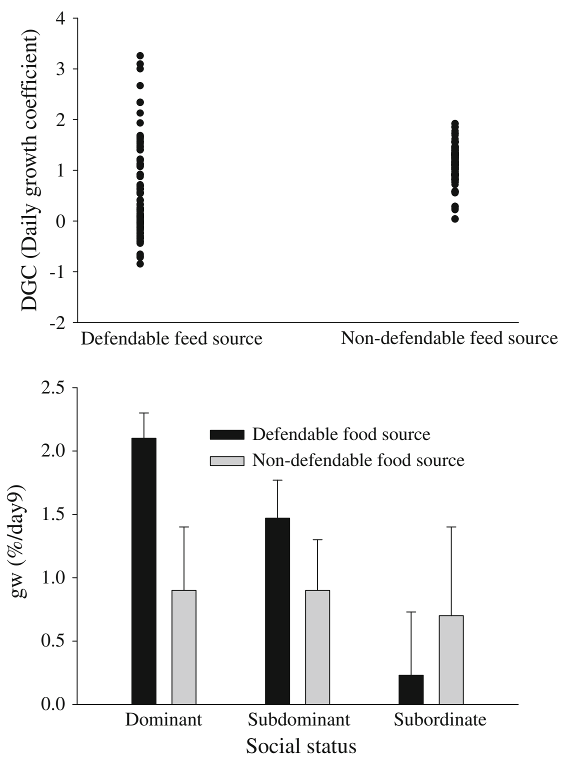

Fig. 3 The effect on variation of individual growth rate by providing the same amount of food to similar sized groups of Arctic charr by demand feeding (defendable food source) and were the food is distributed in time space (non-defendable food source; *upper figure*). The effect of feeding the fish with defendable or non-defendable food source on the mean growth rate of dominant, subdominant and subordinate fish (*lower figure*; Brännäs, unpublished results). Each individual was socially screened in smaller groups (five fish) prior to the test according to Bailey et al. (2000) and then merged into groups of 20 fish each forming six experimental groups in total, three for each treatment

75% occurred from July to November when the majority of all movements were directed against the current, whilst there was no preference for direction during the rest of the year (Linnér et al., 1990). Similar studies on rheotactic behaviour in combination with seawater adaptability showed that Arctic charr exhibited an increased seawater adaptability during spring and early summer, but a rapid decrease in autumn that coincides with the increase swimming movements against the current (Schmitz, 1992). The directed swimming direction in summer and fall and reduced seawater adaptability is probably related to an innate habitat change from the sea in anadromous populations. Landlocked populations also perform seasonal habitat shifts to temporally richer habitats (Näslund, 1990).

From February until June, the charr exhibit a bimodal diurnal activity pattern. In July, the activity is evenly spread over the whole 24-h period with a constant daylight and in August and September activity was mainly diurnal again with a biomodal pattern. Later in fall and winter, activity was mainly nocturnal (Linnér et al., 1990).

Feeding behaviour

The annual variation in diel self-feeding activity of Arctic charr groups kept in fish rearing tanks with a single demand feeder corresponds to the annual variation in diel activity pattern; a bimodal activity in spring and autumn with peaks at dawn and dusk, a free-running rhythm during summer and mainly diurnal during the short winter days (Brännäs, unpublished results). Using a combined PIT-tag system and demand feeders we found that Arctic charr also appear to have a plastic behaviour regarding their diel feeding patterns. They can show both a stable diurnal as well as a stable nocturnal activity pattern (Brännäs & Alanärä, 1996; Alanärä & Brännäs, 1997) and can easily learn when a temporally restricted feed source is available and adapt their activity to it (Eriksson & Alanärä, 1992; Brännäs et al., 2005). This plasticity in diel timing of feeding and social behaviour appears to be interrelated, since dominant fish or fish kept at very low densities were always found to be diurnal, whilst subordinate fish were nocturnal. The interrelation is further demonstrated by another study were differences in individual movements into a feeding area could be related to

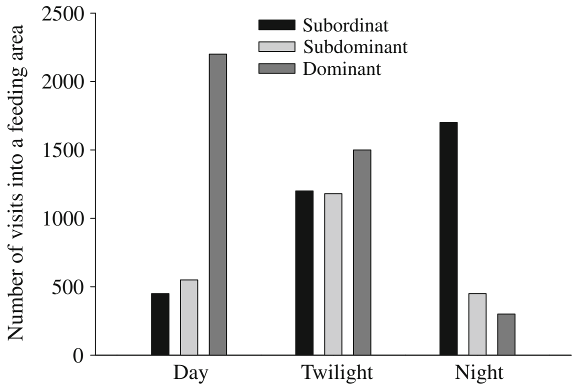

Fig. 4 The total number of visits during different times of the day into a separate feeding site from a resting/hiding site in group of socially screened Arctic charr (modified from Brännäs, 2008)

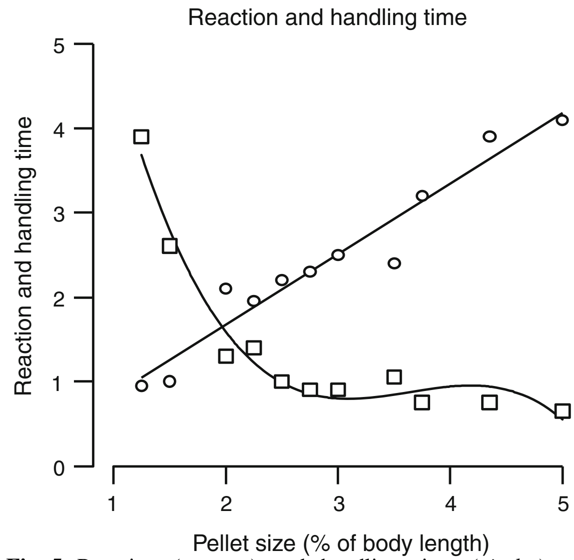

Fig. 5 Reaction (*squares*) and handling time (*circles*) of pellets caught be single Arctic charr of different sizes and in relation with pellet size in percent of fork length (from Linnér & Brännäs, 1994)

competitive rank (Fig. 4). Dominants, subdominants and subordinates all feed at a similar rate during twilight, dominant fish take most of their meals during day-time, whilst subordinates take most of their meals during darkness. Subdominants feed to a large extent during dawn and dusk only (Brännäs, 2008).

The importance of optimal pellets size for farmed Arctic charr was investigated by observing when single Arctic charr of different sizes fed on pellets of different sizes and recording the reaction and handling time before the pellet was swallowed. The handling time increases with increasing pellet size, whilst the time taken for the fish to catch the pellet increases with decreasing pellet size (Fig. 5). The fish caught most of the pellets at the point when the two lines crossed which corresponds to a pellets size of just over 2% adjusted to the fork length of the fish. Also, given a choice by self-feeders, the charr actively chose the optimal food particle size, just over 2% of the fish length (Linnér & Brännäs, 1994). Full-scale feeding trials confirmed these laboratory trials where Arctic charr were fed with different pellet sizes gave an optimal growth at a pellet size of 2.3% of their body length (Linnér & Brännäs, 1994).

The need for adjusting feeding management to the behaviour of Arctic charr was demonstrated in several studies using rainbow trout as a comparison. Whilst a group of rainbow trout becomes very aroused when fed and catches most of the pellets in the water column, Arctic charr appear to be more careful and catches most pellet from the bottom of the tank (Brännäs & Alanärä, 1992). Arctic charr fed daily with frequent smaller meals had an increased growth with less variance compared than if they were given few larger meals, but the effect was opposite on rainbow trout (Linnér & Brännäs, 2001). These species-specific differences were probably an effect of the charr's lesser ability to catch pellets in the water, whilst frequent feeding is stressful for the trout.

Farming experiences

Start-feeding and grow-out tests

In full-scale hatchery trials, the timing of start-feeding in Arctic charr alevins were found to be of great importance for the growth and survival as they start to ingest feed when about 1/3 of the yolk sac still remains (Alanärä, 1993). During the start-feeding period, on the other hand, growth and survival is not negatively influenced by high rearing densities because groups of 1,000 individuals performed equally as well as groups with 24,000 individuals held in 200 l tanks (Alanärä, 1990a).

Several intense farming trials with Arctic charr have been carried out in Sweden between 1982 and 1990, mostly in net-pen farms, but a few also in landbased, surface-water or ground-water fed farms. In most grow-out trials, the fish (still unselected strains) grew in accordance with what could be expected from the growth model of Jobling (1983), although fish grew better than expected at low temperatures (Brännäs & Wiklund, 1992) and had a low growth performance at farms with temperatures exceeding 15°C for prolonged periods during summer (Alanärä, 1990b). The typical production cycle for Arctic charr farming was initially (i.e. in the late 1980s) 3–4 years, with fish reaching a market size of 500 g and with considerable problems related to variation in growth, high incidence of early maturation and losses from infections (mainly fungi) in connection with the spawning period. In spite of high retail prices (around 5 EUR/kg; Table 1), few farms could produce Arctic char with a profit before the year 2000. Now, however, most Arctic charr farms are profitable. First, our selective breeding programme has improved the genetic material that they use. Second, the increase in experience and the improved management at these farms has improved, in part, due to our development of a data-based production planning tool where initial weight, temperature and feed ratio are used to estimate of costs and time for slaughter (Alanärä & Staffan, 2008). A quality guidance system has been developed which gives advice for handling and feeding the fish before and after slaughter with respect to food safety and flesh quality (Eriksson & Elvingsson, 2007). The duration of the production cycle required to attain a market size of 600–900 g has been reduced from 3–4 to 1.5–2 years (Table 1). At present, the variation in growth has decreased, feed conversion ratios have improved to levels comparable with Atlantic salmon and rainbow trout (close to 1/1), and problems with early maturation and related fungal infections have diminished. Production costs have been reduced by at least 40% compared to the years before 2000 (Table 1).

Towards a subarctic aquaculture industry in Sweden?

Sweden has only a little aquaculture production, in spite of a wealth of water resources. The development has been hampered to a large extent by environmental concerns which were strongly advocated by various environmental groups, and lead to very strict regulation of the industry especially around the coast (Ackefors, 2000). In the case of Arctic charr, however, the majority of farms are in large, semi-oligotrophic freshwater lakes in the northern half of the country (Assn. Fish Farmers of Northern Sweden, Mr. Josef Nygren, pers. comm.).

Regulated rivers, production restoration and the 'Robin Hood' principle

The majority of the largest Swedish rivers originating from the Scandinavian mountain chain have been developed for hydroelectric power. These rivers, with an average length of 350–450 km from their headwaters to the coast consist of a more or less complete series of impoundments and large dams, and their upper reaches normally have a considerable seasonal variation in water level (6–40 m). Seasonal and annual regulation when water is stored or released from the reservoirs causes dramatic ice and water movements along the shore-line, and the resulting transport and deposition of organic matter means that these reservoirs will almost certainly be depleted of nutrients and carbon within 15–30 years (Stockner et al., 2000). In addition, spawning grounds of Arctic charr and other fish species are often destroyed or dry up in winter. As a result, these originally low productivity waters (P-levels 5–7 μg/l, production 50–70 g C m^2 per year) in many cases inhabited by Arctic charr, brown trout (*Salmo trutta*) and various whitefish populations have become extremely unproductive (P-levels 1–3 μg/l, production 30–50 g C m^2 per year).

In order to restore these waters, rather successful experiments were performed to improve their productivity and increase the growth and condition of fish populations by adding fertilizers, mainly fossil phosphorus (Stockner et al., 2000). Another possible way to restore the productivity would be to farm fish in the nutritionally depleted reservoirs (Assn. Fish Farmers of Northern Sweden, Mr. Josef Nygren, pers. comm.). We have estimated that the well-balanced emissions from fish farms producing 50,000–70,000 tons distributed in the impounded reservoirs could restore pre-regulation nutrient and carbon levels in each of the five biggest regulated rivers in Northern Sweden (Larsson et al., 2009). As an additional advantage, fish farms could promote business and job opportunities in rural areas of north-western Sweden where unemployment is high. In several cases, impoundments with fish farms have also developed into popular sport fishing areas, probably as a result of increased feeding opportunities for wild fish near the farms.

A more large scale environmental perspective is to move nutrients from the eutrophic Baltic Sea to the nutrient-depleted river impoundments in the northern Sweden. This can be achieved by catching surplus pelagic fish in the Baltic Sea, processing the harvest to feed ingredients, cleansing it from dioxin and other anthropogenic substances by an inexpensive method (developed by the Danish fish meat and oil companies) and use it to feed cultured Arctic charr (Fig. 6). For example, the harvest of rich populations of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the Baltic Sea could remove more than 1,000 tons of phosphorous and 7,000 tons of nitrogen (Kiessling, 2009). Development of a feed based on sustainable ingredient for Arctic charr, such as single cell organisms, mussels, plant oils, etc., without reducing the quality of the fish for human consumption is another important field of research (Pettersson et al., 2009; Kiessling, 2009).

Present limitations

A reliable supply of viable eggs is of major importance for the further development of Arctic charr framing. The farmer must know that starting materials are available to plan production and also that they are available in sufficient quantities, so that investments in production facilities can be profitable. At present, there is a shortage due to the poor survival of fertilized eggs. For example, in Sweden typically only 30–70% of eggs survive and hatch as fry—this is the problem that is considered the most pressing (Pickova & Brännäs, 2006). One of the most probable factors contributing to poor egg survival is the temperature regime under which parent fish (i.e. the brood stock) are held especially the final 6 months prior to spawning (Jobling et al., 1998). The effects on subsequent egg quality of elevated water temperatures even during short time intervals are poorly known in charr. Furthermore, there must be a considerable development of the market to fulfil the ambitions of having an important subarctic fish farming industry in Sweden, Iceland and Norway.

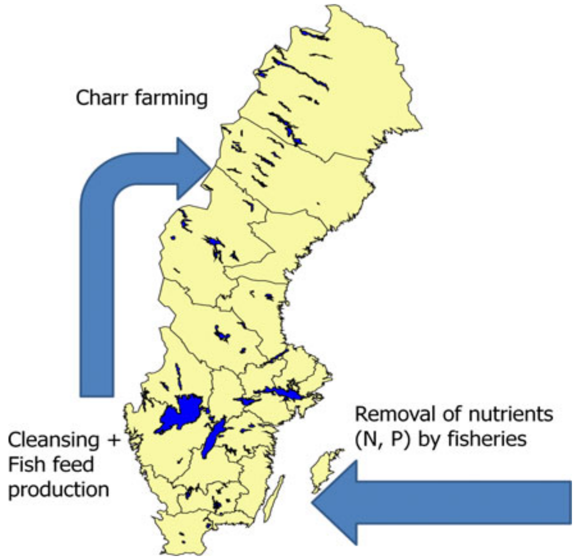

Fig. 6 A schematic description of the 'Robin Hood principle'; recirculation of nutrients from the Baltic Sea to nutritionally depleted regulated rivers (from Kiessling, 2009)

Conclusion

Our experience with Arctic charr may serve as an example of the work, efforts and time that it may take to introduce a new species of fish for sub-arctic aquaculture, although the biological characteristics of this species appeared initially favourable. Many detailed studies to understand various aspects of natural behaviour and environmental requirements of Arctic charr were necessary, but this has provided farmers with tools to provide welfare and productivity in the production of this sub-arctic, coldwater species. Changing economically important traits is still a slow process. Nevertheless, our selective breeding programme carried out through seven generations during 23 long years now provides farmers with a high-quality source. The strain we selected for is now used by the majority of Arctic charr farmers in Sweden and the increased demand has lead to the formation of a fish breeding company 'Aquaculture Centre North Inc.' (ACN), jointly owned by the farmers, the government through the Holding company of the Swedish University of Agricultural Sciences, and local authorities. ACN will provide the growing Arctic charr farming industry with the best possible genetic stocking material currently possible based on our selective breeding programme, and carry on the programme.

The location of Arctic charr farms has been of both social and ecological value, providing job opportunities in sparsely populated areas with high unemployment, as well as some ecosystem services with the nutrients added from fish farms in regulated lakes at high altitude. Arctic charr farming in Sweden have become a very profitable undertaking at present production levels and available markets.

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