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Foreword

AQUACULTURE IN SUBARCTIC AREAS

A Symposium on Aquaculture in Subarctic Areas was held at the University of Umeå, Sweden from June 4—7, 1985.

The aim of the meeting was to unfold present knowledge regarding possibilities and problems related to the development of aquaculture activities at high northern latitudes. The meeting was financed by The Swedish Council for Forestry and Agricultural Research and The Nordic Council.

At the meeting a wide range of topics was covered; general reviews of aquaculture in cold environments, potential species as candidates for subarctic aquaculture, the influence of temperature and photoperiod on growth and developmental rates in aquatic organisms, and aspects of extensive and intensive aquaculture techniques.

A considerable potential for aquaculture in subarctic areas was recognized at the meeting. It was decided to recommend scientists to undertake increased research efforts along three principal lines in order to facilitate future development:

(1) Research on the basic biology of potentially interesting species such as Arctic char and halibut, especially with regard to brood stock management, juvenile nutritional needs and environmental control of developmental rates.
(2) Research on the basic properties of molecular genetics and physiological adaptations in fish, especially regarding seasonal adaptations and growth performance at low temperatures.
(3) Research and development with regard to the combined use of high and low technology or extensive systems in areas with seasonally rich food supplies.

The University of Tromsø agreed to organize a second meeting on Aquaculture in subarctic areas along these lines in 1988.

Although there were originally no plans for publication of the contributions to the meeting, the participants expressed a great interest in the matter.

Because the topic of this Symposium falls within the scope of the Report of the Institute of Freshwater Research at Drottningholm, it was decided that this journal be used to print the Proceedings of the Symposium. This issue thus covers ten of the papers presented at the Symposium as well as the abstracts of all other papers and posters presented. We hope that these contributions will prove of value for the future of aquaculture in subarctic areas.

Lars-Ove Eriksson   *Lennart Nyman*

Convener   Editor-in-Chief

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Prospects and Limitations for Aquaculture in Scandinavia

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ABSTRACT

This paper analyses the prerequisites for aquaculture in Scandinavia including Finland. Important natural factors as sites, quantity and quality of water, temperature and salinity conditions have a great impact on the development. By comparing different regions it is possible to postulate the potential species in aquaculture. Biological and technical optimization are discussed. Market analyses are important before aquaculture operations are established. The structure of the current aquacultural activities and the potential for future development are considered. Legal constraints and environmental impact by aquaculture are of great importance when prospects for aquaculture are analysed. A check-list for planning of aquaculture is presented.

I. INTRODUCTION

Aquaculture is by definition the cultivation of aquatic organisms such as fish, molluscs, crustaceans and algae in order to increase the production or yield to a level above that naturally found in the environment. To achieve this goal you can apply different methods as extensive or intensive farming, integrated farming, fisheries enhancement or ranching. If you produce fish directly for consumption intensive farming is most common in Scandinavia. The cultivation is carried out in ponds, troughs, concrete basins or silos on land or in net cages in lakes or in coastal areas. The organisms are fed in contrast to extensive farming where no feed is given and they have to utilize the naturally produced food in *e.g.* the ponds. Mussel cultivation is also a form of extensive farming.

Fisheries enhancement is by definition extensive farming of seas or lakes by stocking juveniles followed by harvesting through fishing. A more specialized form of fisheries enhancement is lake-, sea- and ocean ranching, where the fishery is conducted at the point of release of the juveniles as they return to spawn. Fisheries enhancement is very often called fisheries management in freshwater.

The current aquaculture production of the world is in the order of 10 million metric tons or about 13 % of the total yield from sea areas and lakes. In Europe the production is close to 1.3 million tons which corresponds to a little more than 10 % of the total yield. It is roughly

700,000 tons of finfish produced and 600,000 tons of molluscs. Very few species contribute to the bulk of this production: carps (400,000 tons), trout (190,000 tons), salmon (50,000 tons), mussels (480,000 tons) and oysters (110,000 tons).

In Scandinavia the output from aquaculture is only about 60,000 tons (excluding aquaculture for fishery management as sea ranching). This is only about 1 % of the total aquatic yield from fisheries and aquaculture. It is then a natural question if the environmental prerequisites are not adequate for aquaculture in Scandinavia, or if other factors have constrained the development? The natural conditions precedent for aquaculture are in fact much better than most people expect: the cold climate is in many cases an advantage for some aquaculture and the quantity as well as the quality of water are in general satisfactory compared to most industrialized countries.

The fisheries enhancement is of utmost importance in Sweden, Finland and Norway. The artificial rearing of salmon smolts for restocking rivers flowing into the Baltic is the most important fisheries enhancement project in Europe. Originally, the rivers around the Baltic produced 10 million smolts annually (Fig. 1). The building of hydropower stations in the 1940—60's made natural spawning impossible. According to the Swedish Waterlaw the companies had to build hatcheries to compensate for this loss. In 1984, about 2 million smolts were stocked in the rivers. Finland is also producing smolts nowadays to compensate for the former loss of natural spawning

Fig. 1. The Scandinavian rivers that flow into the Baltic originally produced 10 million smolts. (From ACKEFORS 1980).

grounds. In 1984 the Finnish hatcheries produced 2 million salmon smolts.

In Finland there is also a stocking of fish in freshwater aimed at supporting a commercial fishery. More than 20 species of reared juveniles were stocked in rivers and lakes to enhance the native stocks. Nearly 39 million specimens were released in 1983 of which 32 millions were coregonids belonging to six different species. In Sweden fisheries enhancement is also very important. The stocking is mainly aimed for sport fisheries and to a minor extent for the commercial fisheries.

In this paper I place the main emphasis on natural requirements, and from these draw some conclusions about potential species in Scandinavia. The importance of research is expressed and the need for biological and technical planning optimization is discussed. Market analysis is important before planning large scale aquaculture operations.

The legal constraints and the environmental impacts are considered.

II. WATER RESOURCES

The available water quantity per person is considered to be four times more per person in Sweden compared to the conditions on the European continent (ANON., 1982 a). Due to the influence by the ice during the last glacial period the number of lakes and rivers are much higher in Scandinavia than on the continent (Fig. 2). During the present climatic conditions the amount of water is large and thus the prime factor for aquaculture is good. Not less than 9 % of the areas in Finland and in Sweden consist of freshwater lakes. However, in some areas the lakes have been regulated and
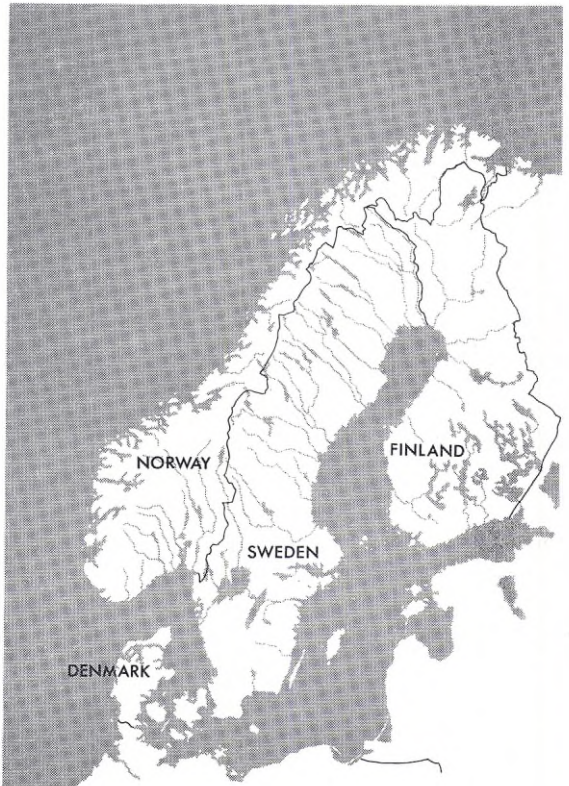
Fig. 2. Scandinavia is surrounded by marine and brackish water. No less than 9 % of the areas in Finland and in Sweden are covered by freshwater.

the available lake areas have been changed. Due to constructions of water reservoirs aimed for hydropower plants the water area is fluctuating during the year, which is a drawback for aquaculture operations. In other areas the water levels of the lakes have been lowered in order to gain more land for agriculture.

The available coastal zones are very extensive and a lot of the areas consist of sheltered sites as fiords and archipelagos. In Norway the length of the total coastline is about the same distance as the equator around. In Sweden the coastline is estimated to be 7,600 km of which 1/4 in marine waters and the rest in brackish waters. The sheltered areas are thus very extensive in Scandinavia and the potential water resources for aquaculture are comprehensive.

III. THE EFFECT OF ACIDIOUS WATER CONDITIONS

However, the most serious problem for aquaculture is the changing quality of water. The influence of polluted water from agriculture, forestry, industry and aquaculture itself as well as air pollution may drastically change the prerequisites for aquaculture in most countries. The load of pesticides, phenols, ammonia, chlorine, metals, nutrients and other compounds in the water have a great impact on the water quality. One of the most drastic and rapid changes during the last two decades have been caused by the acid rain with gradually sinking pH-values in lakes and rivers. The alkalinity of the ground is variable in various parts of Scandinavia. In Sweden, some parts are more threatened by acid rain due to low buffering capacity of the ground. This is valid for areas with an alkalinity of 0.1 m mol/l or less. Thousands of lakes now have a pH of 5.5 or less during the whole year. In slightly acidious lakes with pH around 6 the populations of crustaceans and molluscs may be wiped out. pH of 5.5 and less will have a great impact on reproduction, physiology and behaviour of most salmon species.

During such low pH conditions metals will be drained from the soil (Fig. 3). At moderate pH values aluminium will form aluminium hydroxide ($Al^3 + 3 H_2O = Al(OH)_3 + 3 H^+$). At pH 5 the
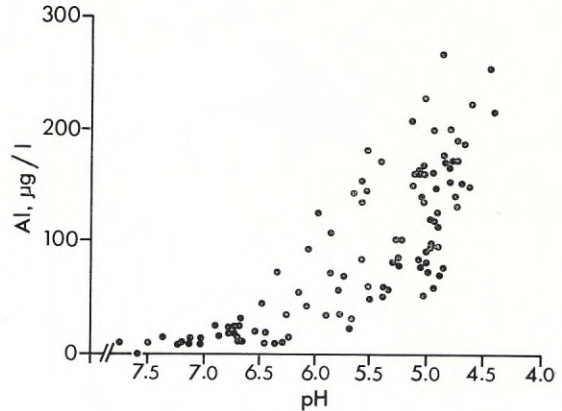
Fig. 3. The concentration of aluminium increases in freshwater under more acid conditions. At pH less than 6.5 the increase of the aluminium concentration is conspicuous. (From HENRIKSSON 1985).

metal hydroxide will react with more hydrogen ions and free aluminium ions are formed: $Al(OH)_3 + 3 H^+ = Al^{3+} + 3 H_2O$. The aluminium hydroxide may precipitate on the gills of the fishes and the aluminium ion is poisonous to the organisms themselves. A lot of heavy metals will also be released from the soil. The uptake of these metals in the organisms is governed by other substances and compounds in the water. The organisms can endure such metals in solution much better if the water is harder due to the content of hydrogen carbonate ions or various components in marine and brackish water. ALABASTER and LLOYD (1984) have given the maximum annual 95 per cent concentration of "soluble" zinc for coarse fish species (A) and salmonids (B) in various water conditions (Table 1). In general they can stand concentrations better in hard water than in soft water.

Table 1. *The toxic levels of metal concentrations vary with the concentration of ions in the water. The maximum annual 95 percentile concentration of "soluble" zinc for coarse-fish species (A) and salmonids (B) in waters with different degree of hardness is given in the table according to* ALABASTER *and* LLOYD (1984).

The amount of mg CaCO₃ per litre water	A mg zinc per litre	B mg zinc per litre
10	0.3	0.03
50	0.7	0.2
100	1.0	0.3
500	2.0	0.5

BIOACKUMULATION OF VARIOUS SUBSTANCES
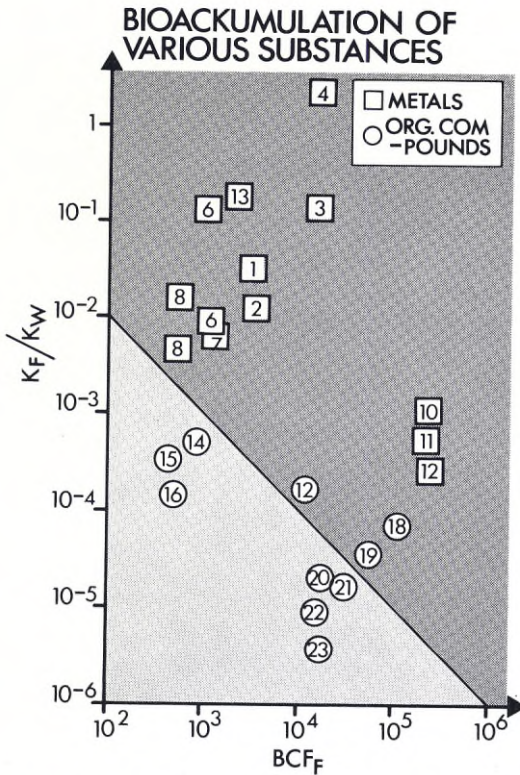
Fig. 4. Bioaccumulation of heavy metals (squares) and organic nonionized compounds as PCB, DDT, endrine and dieldrine (circles). BCF_F is the biocentration factor, which is equivalent to the ratio of the concentration of the test substance in the fish at $t=0$ and the concentration of the test substance in the water at $t=0$. K_F is the rate of uptake via the feed and K_W is the rate of uptake via the water. The figure indicates that organic compounds are mainly taken up through the water while it is the reverse for metals.

The same authors give such values even for other metals in solution:

Copper	0.001—0.005	mg/l
Iron	0.02 —1.0	mg/l
Cadmium	0.011—0.2	mg/l

Another serious problem in connection with water quality is the bioaccumulation of foreign substances in the cultivated organisms. In principle there are two ways of uptake, (1) through the feed or (2) through the water via the gills and the intestine. According to a summary of available literature made at NIVA in Norway the foreign substances could be divided into two categories:

(1) substances accumulated through the feed were metals and (2) substances accumulated through absorption by the gills were non-ionized organic compounds (ANON. 1982 b). In Fig. 4 the relation between the ratio K_F/K_W and BCF_F is plotted.

From the figure it is evident that organic substances as PCB, DDT, endrine and dieldrin are mostly taken up through the water and the metals through the feed. The conclusion is that fish might be raised in waters polluted by metals if the feed is made of a fishmeal of good quality.

IV. TEMPERATURE CONDITIONS

Scandinavia covers a wide area from about 55°N to about 71°N latitude. Hence, the climate conditions vary extensively. The mean temperatures for July and January are given in Figs. 5 and 6 (ABRAHAMSEN *et al.* 1977).

Temperature has a great impact on the physiology of the animals *e.g.* the energy metabolism and maturity. The temperature range in various areas restrict the number of species that can be cultivated. The farmer has to consider the lower and upper tolerance limit as well as the optimal temperature range and the length of the vegetation period. The temperature will also have an impact on dissolved oxygen and the sensitivity of pollution.

The length of the growth period and especially the period of optimal temperature conditions are the most important environmental conditions to be considered by the farmer. Periods of good growth and high conversion efficiency vary in various parts of the Scandinavian countries depending on regional and local temperatures in the water. The salmonids, which are the most popular farming objects, have optimal temperatures in the range of 10 to 18°C. It varies between the different species. Without using heated water the cultivation of salmonids is mostly profitable in Scandinavia. However, there might be adverse conditions in some areas with low winter temperatures or high summer temperatures. In winter we may get supercooled water in the Kattegat and Skagerrak areas (Fig. 7). The freezing point (T) is in the order of −0.5—1.5°C where the salinity range is from 10 ⁰/₀₀ to 30 ⁰/₀₀. (The formula is T= −0.054×S.

MEAN TEMPERATURE IN
JULY, °C
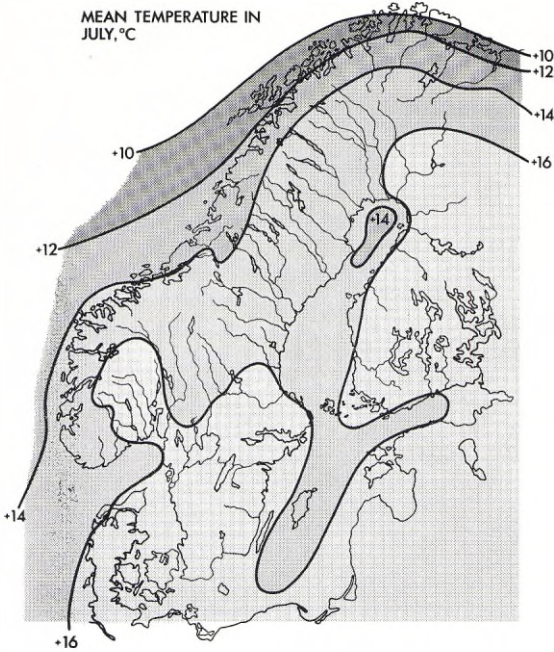
Fig. 5. The mean temperatures for July after ABRA-
HAMSEN *et al.* 1977.

MEAN TEMPERATURE IN
JANUARY, °C
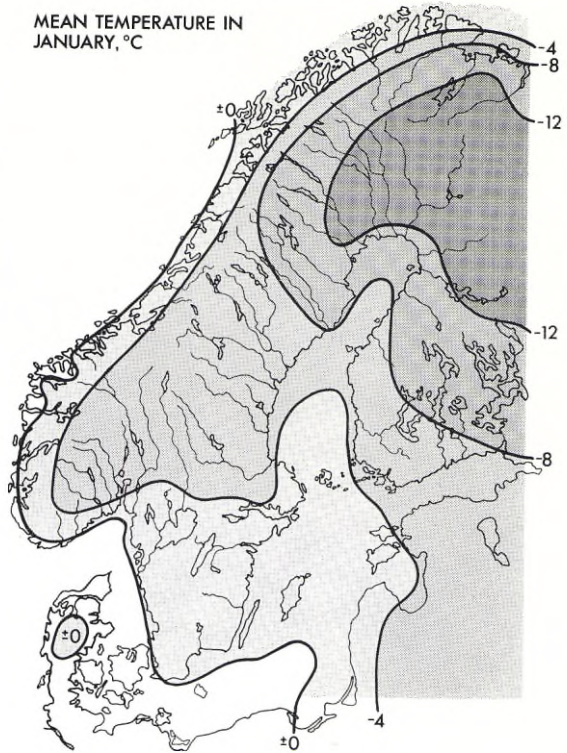
Fig. 6. The mean temperatures for January after
ABRAHAMSEN *et al.* 1977.

S=salinity in per mille). A temperature of −0.5°
is lethal to salmonids.

Along the Norwegian west coast there might
be the same problem in some areas. However, in
general most parts of the coast are influenced
by the warm Gulf Stream. In the Baltic area,
with low salinity conditions, the freezing point of
the water is around 0°C. Successful wintering of
salmon, rainbow trout and Arctic char in net
cages has been performed in the Baltic area as
well as in fresh water. The salmonids are depen-
dent of swallowing air at the surface under cer-
tain circumstances. This means that current de-
vices have to be installed to get an icefree surface
in the net cage (ERIKSSON 1983). Too warm
temperature conditions (above 20—21°C) in the
coastal areas of southern Baltic, the Baltic Sea,
Kattegat and Skagerrak may be harmful to sal-
mon. The species is easily attacked by diseases at
high temperatures or the temperature may be
lethal. As the salmonids in general prefer cold

water, the summer temperatures may hit such
species as Arctic char and brown trout in fresh
water in southern Scandinavia. Rainbow trout is
more resistant to high temperatures, especially if
the water is well oxygenated.

As a conclusion it is thus obvious that most
areas of Scandinavia are suitable for raising sal-
monids. However, cold temperatures restrict the
cultivation due to super-cooled water or too
short growth period in some areas in winter as
well as too warm temperatures in southern Scandi-
navia in summer.

V. ARTIFICIAL TEMPERATURE CONDITIONS

The drawbacks of cold climate can be reduced
very much by heating the water. Heat pumps,
waste heat water from the industry and nuclear
power stations and energy conservative reuse water

Fig. 7. The salinity conditions in the areas around Scandinavia. In winter you get supercooled water mainly in the hatched areas (the Sound, the Belt Sea, the Kattegat and the Skagerrak). Further to the west and north the water is influenced by the warm Gulf Stream.

systems may be the solutions to the cold climate. In ACKEFORS *et al.* (1982) a method is described how to reduce the rearing time by one year when farming rainbow trout up to 3.5 kg (Fig. 8). By using a temperature of 8°C it is possible to get mature spawners in December—January. The hatching takes place already at the end of February. During the first autumn the juveniles weigh about 200 g instead of 10—20 g when reared under natural water conditions.

There might also be a gain if the growth period is extended. In northern Scandinavia the cultivation of rainbow trout is not profitable because of the limited time when temperature is higher than 4°C. By using waste heat water from the industry and heat exchange in the rearing units, it is possible to get a longer period with adequate growth.

Different recirculating systems are now tested in Sweden. They are energy conservative. However, they are also complicated with either water treatment in biofilters and/or in chemical ion exchange. At present it is hard to say if the profitability is good enough. Such systems may give a good profit if highly priced species as eel and turbot are reared. In Sweden there are now a few companies, which cultivate eel in such systems.

Under artificial temperature conditions it is

Fig. 8. By using heated water it is possible to reduce the rearing time by one year when producing a 3 kg rainbow trout. Modified after TORE STERNER in ACKEFORS *et al.* (1982).

thus possible to speed up the growth rate of cold water species as salmonids and flatfish. Such technique will also make it possible to raise warm water species as eel and the prawn *Macrobrachium* sp.

VI. SALINITY CONDITIONS

The salinity conditions in Scandinavia vary from nearly freshwater in the Baltic to full marine water in the coastal zone of the North Sea and the Norwegian Sea (Fig. 7). Very few fish species tolerate the brackish water in the Baltic. From the farmer's point of view there are only salmonids like salmon and rainbow trout and turbot, which at present have a potential interest and are possible to rear in the area. The Kattegat and Skagerrak areas, which have brackish water of higher salinities are acceptable for most species. However, as mentioned above, the super-cooled water in winter may be an obstacle for rearing fishes in those areas. The sea areas are also suitable for cultivating blue mussels and oysters. In the future

attractive marine crustaceans like lobsters may also be profitable to raise. Going from the Kattegat through the Skagerrak into the North Sea and the Norwegian Sea the number of aquaculture candidates increases, although most of them can tolerate the salinities in the Kattegat. The most cultivated fish species are of course salmon and rainbow trout. However, the number of aquaculture candidates in Norway comprise also cod, halibut, turbot, lobster, scallop etc.

In freshwater a number of salmonids like brook trout, lake trout, Arctic char, grayling are raised mainly for the purpose of fishery management. But the only species of interest reared for the commercial market are salmon, rainbow trout, Arctic char, whitefish, carp, eel and the two crustaceans, European crayfish (*Astacus astacus*) and signal crayfish (*Pacifastacus leniusculus*). Some of those species, like Arctic char and eel, may be raised in brackish water. The various species cultivated for commercial purposes in Scandinavia are summarized in Table 2 and the aquaculture candidates in Table 3.

Table 2. *The aquaculture species cultivated for commercial purposes in Scandinavia.*

(1) Salmon (*Salmo salar*)
(2) Rainbow trout (*Salmo gairdneri*)
(3) Brown trout (*Salmo trutta*)
(4) Lake trout (*Salvelinus namaycush*)
(5) Eel (*Anguilla anguilla*)
(6) Carp (*Cyprinus carpio*)
(7) Blue mussel (*Mytilus edulis*)
(8) Oyster (*Ostrea edulis*)
(9) Noble crayfish (*Astacus astacus*) (extensive cultivation)
(10) Signal crayfish (*Pacifastacus leniusculus*) (extensive cultivation)

Table 3. *The potential species of aquaculture in Scandinavia.*

(1) Arctic char (*Salvelinus alpinus*)
(2) Cod (*Gadus morrhua*)
(3) Turbot (*Scophthalmus maximus*)
(4) Halibut (*Hippoglossus hippoglossus*)
(5) Sole (*Solea solea*)
(6) Wolffish (*Anarhichas lupus*)
(7) Lobster (*Homarus vulgaris*)
(8) Noble crayfish (*Astacus astacus*) (intensive cultivation)
(9) Signal crayfish (*Pacifasctacus leniusculus*) (intensive cultivation)
(10) Scallop (*Chlamys opercularis, Pecten maximus*)

POTENTIAL SITES FOR AQUACULTURE

1. FJORDS
2. FINNISH BAY TYPE
3. ARCHIPELAGO
4. LAGOONS

Fig. 9. Potential sites for aquaculture are fiords, archipelagos or other sheltered areas. The figure shows such areas of different types (Fjords, Finnish Bay Type, Archipelago and Lagoons). After Abrahamsen *et al.* 1977.

VII. SUITABLE SITES

As a general rule the sites must be in sheltered areas as archipelagos, sounds etc, where the wave actions are small and the ice conditions are not too severe. The latter conditions may be especially in focus during late winter when drift ice may occur. In Fig. 9 the sheltered areas are marked. They are potential sites. However, the water quality, hydrographical conditions as well as bottom conditions may also be considered before an operation is established. Deep areas with a discontinuity layer (thermocline or halocline) are not suitable sites for net cages or other aquaculture operations.

Bottom conditions are essential to know before the operation is established. Soft bottoms, which are typical for most areas without bottom cur-

rents or a very little slope, are not suitable. They will accumulate organic material and food wastes. Hence, the oxygen concentration will decrease, when the organic substances are decomposed. Suitable sites are hard bottoms with currents and a suitable slope of the bottom. In such cases the organic matter will be dispersed over a wide area (Håkanson *et al.* 1984).

For fish farmers and other companies the infrastructure is of utmost importance. The access to bridges, roads and electricity is necessary in farming areas. In general, this is not a problem in Scandinavian countries. Remote and attractive areas from the production point of view may be excluded because adequate infrastructure is not available.

VIII. BIOLOGICAL AND TECHNICAL OPTIMIZATION

The biological knowledge (ecology, ethology, physiology) of the reared organisms is the basis of all farming. Most farmers get a practical knowledge based on many trials and errors. A good understanding of fish diseases and their patterns is essential as well as awareness of nutritional optimization. Such knowledge may also be acquired through practical experiences. However, a shortcut would be training courses or general information through journals and lectures. Short courses are now available in all Scandinavian countries. There is also a more comprehensive education available, which extends over a period of 1—2 years.

To get a biologically optimized production we have to put more emphasis on research and development in aquaculture. This is obvious in most branches of biological knowledge like genetics, nutrition and pathology. As aquaculture is a new branch of industry in Scandinavia, the scientific work is still in its infancy. The development is, however, quite rapid in some areas. This means among other things new strains of certain species with higher growth rates and better feed utilization. In this competition for higher efficiency research is an inevitable factor. In the same way it is necessary to widen the knowledge of reproduction of new species, which are demanded at the market.

From the technical point of view many break-throughs have been made during the last years. However, still there is a great need for development in all types of containers for culturing organisms (KLAPSIS and BURLEY 1984). Still we know very little about the hydrodynamics of various shapes of tanks and ponds. Such simple things as inlets and outlets have not yet been standardized according to an optimized model for various sizes.

Within the areas of energy conservation, pumping, aeration and other technical devices we still need a lot of science for optimizing the various processes within a farming system.

The lack of stocking material restricts the present development of aquaculture in Scandinavia. This is especially true when regarding juveniles of a good quality based on adequate genetical principals. A good growth rate should be combined with *e.g.* resistance to diseases and other characteristics. The Finnish way of solving this problem by dividing the country into four areas without any water connections (rivers, creeks, lakes) between them may be a good solution to this matter. In each area there is a central breeding station with connections to small hatcheries in the same area. The genetic material of one strain is always distributed among more than one hatchery.

IX. MARKET ANALYSIS

In the developing countries of the tropical zone even low priced fish protein may be produced. In Scandinavia this is not possible. Only high priced species as salmonids, flatfishes, eel, lobsters and crayfishes may be profitable to raise. The only exception may be blue mussel, which is produced in extensive farming without supplementary feeding and raised with rather cheap methods. The incitement for Scandinavian aquaculture is a good market within and outside its own area. The successful Norwegian export of fresh salmon to many European countries, the USA and Japan have already demonstrated that there is a great potential market abroad. It is with the present production costs possible to send fresh salmon by air freight to remote areas in other continents.

The advantage over fishing is obvious. The farmers' sales organization can guarantee a good quality during most parts of the year and it is possible to deliver the right quantity at the right time.

At present, the potential market for high priced fish and shellfish species as salmonids, eel, flatfish, crayfish and blue mussel seems to be large. However, a thorough market analysis must be the basis for all aquaculture developmental programs. This can be made by comparing international, regional and national demands, market trends, statistical analyses, consumer surveys and direct market experiments according to SHANG (1981). His examples about the demand for eel and kuruma shrimp in Japan are conspicuous. Postulating the potential market is possible by using facts like consumption, whole sale price index, consumer price index, income and price elasticity as well as mean national income.

The next step would be to develop marketing infrastructure in case this is not a reality. This refers to service of wholesale, retail, transportation, storage, ice plant, processing and packing. From this point of view the Scandinavian countries have already developed infrastructures for selling wild fish. However, for selling the cultivated fish the marketing infrastructure has only been partly adapted to the new situation except in some countries.

The possibilities to do this are very good. The Scandinavian countries have already developed the distribution of everyday commodities in a rational and effective way. This means that the farming products should easily reach the consumers if the transportation of fresh fish could use the same transportation system. However, there might be problems due to acts and regulations for the transportation of fresh fish which has to be separated from the other commodities in Sweden.

In order to build up a fish farming industry in Scandinavia it is necessary to make investments in various fields. The production units must be combined with adequate service units such as health care, the combat of diseases, slaughter houses, transportation units, marketing organizations etc. At present, such service is limited in *e.g.* Sweden, where the production of farmed products is rather small. In other countries, like Norway, with larger production there is a well developed service.

Local units can in some areas be competitive without such service but in the long run there has to be specialized people in various functions.

The input costs and returns from each operation must be carefully considered before any operation is started. The cost of production may vary very much for operations in the same region depending on natural prerequisites, husbandry techniques and skilfulness to rear aquatic organisms. A comprehensive calculation of various costs and potential income must comprise several factors like investment in equipment, working expenses, labour costs, capital costs, taxes, profit and analysis of liquidity.

X. LEGAL CONSTRAINTS AND ENVIRONMENTAL IMPACT BY AQUACULTURE

The legislative systems for aquaculture vary in the different countries of Scandinavia (ANON. 1982 c). In Sweden the application has to be sent to both the County Administration and the Regional Fishery Office. The basis for decision is the Environmental Protection Act for the former agency and the Fisheries Act for the latter. The applications are also referred to many other authorities. The Environmental Protection Act regulates the farming with regard to the impact of aquaculture on the environment (ANON. 1983). The load of nutrients and organic material in the receiving water are regarded in relation to the water volume and the residence time of the water. If the risk of eutrophication is great or the amount of oxygen for decomposing the organic material is too high there will be no permission to cultivate. The examination according to the Fisheries Act is mainly concerned with the risk of spreading fish diseases and introducing more vigorous fish species. In some cases permission even from a Water Court is needed.

XI. CHECK-LIST FOR AQUACULTURE DEVELOPMENT

In general, the environment in Scandinavia is very suitable for farming of fish and other aquatic organisms. However, for each farming unit the

A. NATURAL REQUIREMENTS

Quantity of water → NO → Reuse water systems Cultivation of Crustaceans
↓ YES
Quality of water → NO → Water treatment or no farming
↓ YES
Optimal temperature conditions → NO → Heat water systems or no farming
↓ YES
Required salinity concentration → NO → Alternative farming objects
↓ YES
Suitable sites → NO → Technical arrangements or move to another site

B. BIOLOGICAL AND TECHNICAL OPTIMIZATION

Adequate knowledge in biology → NO → Training courses
↓ YES
Biologically optimized production → NO → Biological research is needed
↓ YES
Technically optimized production → NO → Development of science and engineering is needed
↓ YES
Hatchery capacity → NO → Investment in hatcheries

C. MARKETING

Market analysis → NO → Wrong development is possible
↓ YES
Market infrastructure → NO → Slow development
↓ YES
Good profitability → NO → No investment

D. LEGAL REGULATION AND ENVIRONMENTAL IMPACT BY AQUACULTURE

Permission to cultivate → NO → Application
↓ YES
A slight impact on the environment → NO → Water treatment New Technology
↓ YES

AQUACULTURE PRODUCTION OF FISH IN SCANDINAVIA

Fig. 10. The aquaculture production of salmon and rainbow trout in Scandinavia 1950—84.

XII. THE CURRENT PRODUCTION AND DEVELOPMENT

The modern development of aquaculture in Scandinavia has varied very much in the different countries (ACKEFORS 1986). Denmark was the first country to get a high production of farmed rainbow trout in freshwater ponds (Fig. 10). The farmers have specialized in production of small, pansized fish. The yield in 1985 was 22,500 metric tons per year. In addition to that the newly established sea cage farming produced 1,600 tons of bigger size.

Finland has also specialized in rainbow trout, but the main production consists of larger fishes. The production takes place both in freshwater ponds and in brackish water net cages and was 9,410 tons in 1985. In addition to that 70 tons of salmon were produced.

Norway has become the largest producer in the world of farmed salmon in marine areas. The net cage production consisted of 45,700 metric tons of salmon and 4,300 tons of rainbow trout in 1986 (Table 4). The prognosis for 1987—90 indicates a further rapid increase. Norway is supposed to produce at least 90,000 tons in 1990.

Sweden has had a slow development. The production of rainbow trout was 3,500 metric tons in 1985. In addition to that 80 tons of salmon and 10 tons of Arctic char were produced. The blue mussel yield is about the same.

local conditions are decisive if the site is suitable or not. To get an overview of the various factors regulating the farming it might be a good idea to make a check-list (see below). For this purpose, they may be divided into the following groups:

(A) Natural requirements

(B) Biological and technical optimization

(C) Marketing

(D) Legal regulation and environmental impact by aquaculture
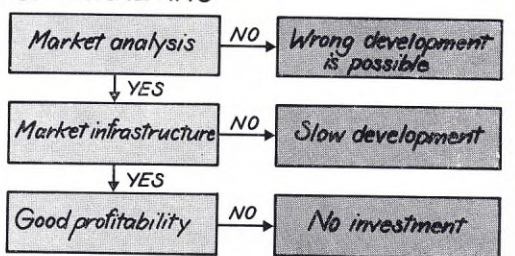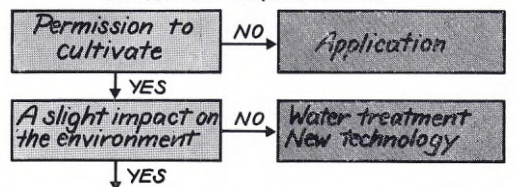
For each individual operation it is thus possible to get a first insight if the potential site and the planned operation are suitable or not.

Table 4. *The aquaculture production of salmon and rainbow trout 1971—86 in Norway in sea cages.*

Year	Salmon	Trout
1971	100	500
1972	150	800
1973	300	1,300
1974	600	1,700
1975	1,000	1,800
1976	1,400	2,000
1977	2,500	1,800
1978	3,500	2,100
1979	4,200	2,700
1980	4,200	3,400
1981	8,400	4,500
1982	10,300	4,700
1983	17,000	5,100
1984	22,300	3,600
1985	28,000	5,000
1986	45,700	4,300

It is quite obvious that Denmark, Finland and Norway have already developed their own aquaculture production in different directions and found their own niches on the market.

The future development of aquaculture in Scandinavia is dependent on many factors as mentioned above: The basic concept of commercial aquaculture comprehends a complex structure, in which the weakest links in the chain are determining for the development. This is indicated by ACKEFORS and ROSÉN (1979) and ACKEFORS (1983). Within the various fields of biology, technology and economy which promote aquaculture development there are of course some factors which have a greater bearing than others. The policy of the government towards the aquaculture is very important. The national trade policy with regard to custom regulations for import and export of fish products is essential.

The future development of aquaculture will also depend on the attitude to science and engineering and how much money that will be allocated to these areas. The organization of services like hatcheries and health care is of utmost importance. At present, the developmental rate is very different within Scandinavia. To a great extent this is caused by the difference of resources allocated to aquaculture in the various countries.

XIII. ACKNOWLEDGMENTS

XIV. REFERENCES

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Early Sexual Maturation of Male Sea Trout and Salmon – an Evolutionary Model and Some Practical Implications

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ABSTRACT

The precocious sexual maturation of male salmonids is involved in two types of reproductive strategy. p-males are resident in fresh water throughout their lives, and pm-males migrate to the sea after the early maturation. Either of these strategies often coexist with non-precocious, migratory males, called m-males. The p-m combination seems to be the normal state for sea trout and the pm-m combination for salmon in SW Scandinavia. The conditions for coexistence and the proportion of precocious males are discussed using models based on frequency dependent reproductive success. The main predictions are: (1) The p-m combination can exist under biologically reasonable conditions, (2) The possibility of coexistence for the pm-m combination is less obvious and strongly dependent on the difference in post-smolt survival for the two types, (3) The proportion of precocious males will tend to be larger in the pm-m combination ("salmon") than in the p-m system ("trout"). The field data available are in agreement with prediction (3). Speculations concerning mechanisms and practical implications are put forward.

I. INTRODUCTION

Why do some males in anadromous salmonid populations become sexually mature on the parr [1] stage? What determines the proportion of these? What can we do to reduce this proportion in sea ranching?

One way to achieve a better understanding of the factors affecting the reproduction pattern of salmonids is to make use of the fact that most stocks used in sea ranching have a life history which is the result of natural rather than artificial selection. The fish that we see today are thus those carrying the genes from ancestors and parents that happened to choose the most efficient way of reproducing under the conditions prevailing. In this paper we will discuss the evolutionary background to precocious maturation and try to explain why and how the proportion of these males is varying in natural populations of sea trout and salmon. Before we do, however, we will give examples of two types of male reproductive strategy, both involving precocious maturation.

II. THE "TROUT" SYSTEM

In River Norumsån, a small stream in SW Sweden, precocious males and immature individuals of the sea trout *Salmo trutta* (TL 100—160 mm) were branded by alcyan blue injected into the base of the caudal fin during spawning time in October. In the following spring, descending smolt were captured in a trap, operating from mid-April to early June. Fin clipping (adiposal fin) revealed no mark losses during this period. The result was the following:

Year		Precocious males	Immature trout
1983/84	Marked	126	345
	Recaptured	2.4 %	17 %
1984/85	Marked	124	373
	Recaptured	0.0 %	15 %

Obviously, the precocious males in this population do not contribute to the smolt production to any larger extent, if at all. Judging from their general appearance, the few precocious males recaptured in spring 1984 were strayers rather than smolt.

An additional evidence of a reduced smolting among precocious males is the fact that we usually find a population segment in sea trout streams of individuals older than smolt age, mainly males. In Norumsån, scale samples for

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[1] Parr is the juvenile stage prior to smolting/migration.

age determination were taken from smolt in 1982—84. 1.4 % (n=408) of these showed a smolt age of 3, and no older, and a main smolt age of 2 (1982: 36 %, n=135; 1983: 74 %, n=173; 1984: 95 %, n=100). Age determination from scales sampled in October showed that a substantial proportion of the population was of age 2+ and older (Fig. 1) and therefore mainly resident in the stream. A similar "tail" of older males is usually found in sea trout populations in other streams in the region (Fig. 1), indicating that the resident behaviour of precocious males is not confined to Norumsån.

If the hypothesis that precocious males do not smolt is accepted, we would expect that the sex ratio of sea trout smolt would be skewed in favour of females and reflecting the proportion of precocious males in the population. Assuming the same survival for immature males and females from spawning time to smolt migration, the proportion of precocious males among all males, p, would be related to proportion of males among smolt, f, in the following way: $p=(1-2f)/(1-f)$. The proportion of precocious males predicted in this way from smolt sex ratio may be compared with observations. This comparison turns out in the following way:

	f % males among smolt observed	p % prec. males among males observed	p % prec. males among males predicted
1-summer old	52 (n=50)	0	0
2-summers old	35 (n=220)	44 (n=460, 1983)	46
		37 (n=440, 1984)	

The proportion of males among smolt, f, is estimated using pooled values from the trap 1982—84. The proportion of precocious males, p, is based on electrofishing/scale sampling during the spawning periods 1983 and 1984 in a 500 m section of Norumsån. As we can see there is a fair agreement between prediction and observation, suggesting that the skewed sex ratio of sea trout smolt is a direct result of early sexual maturation of males.

We conclude that some males, denoted m-males, smolt and migrate without prior sexual maturation, and that others, called p-males, mature precociously and remain resident in fresh water throughout their lives. The system with m-males vs. p-males is called the "trout system". We do not infer, however, that all sea trout populations fit this scheme, or that it is confined to this species.

Fig. 1. Length frequency of sea trout parr in four streams in Bohuslän, SW Sweden. Note the occurence of trout older than main smolt age (older than 1+). TL=total length.

III. THE "SALMON" SYSTEM

In many populations of the Atlantic salmon *Salmo salar* the male reproductive system is different from that suggested above. ÖSTERDAHL (1969), LEYZEROVICH and MEL'NIKOVA (1979), DALLEY *et al.* (1983) and MYERS (1984) reported a pro-
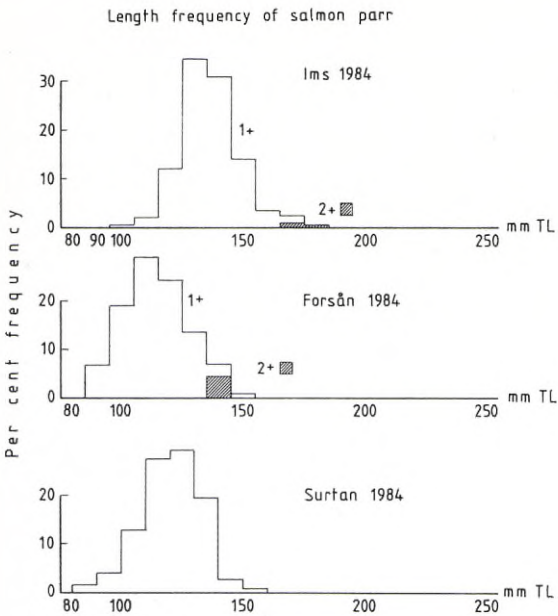
Length frequency of salmon parr

Fig. 2. Length frequency of salmon parr in streams in SW Scandinavia. Data from Surtan, a tributary to River Viskan, SW Sweden, were provided by A. Joh-lander at the Fishery Board of Sweden. TL=total length.

portion of spent males among smolt, although smolting may be delayed (MITANS 1972, GIBSON 1983, MYERS 1984). Further, there are often few males older than smolt age among parr (DALLEY *et al.* 1983, MYERS 1984), indicating that early sexual maturation will result either in smolting or death.

From River Imsa, a small salmon stream in SW Norway, BROR JONSSON, DVF, Trondheim, Norway (pers. comm.) reported the following result from salmon smolt caught in a trap:

	%o males among smolt	%o spent males among males
1983	41	55
1984	36	33

The main smolt age in this population is 2 (*op. cit.*). In October 1984 we checked the age structure and proportion of precocious males using electrofishing/scale sampling. We found very few individuals older than 1+, and that 82 %o of the males (1+) were mature. Two other streams in SW Sweden were checked, in which main smolt

age is 2, and the population structure was similar (Fig. 2).

We conclude that some males, as in the case of sea trout, called m-males, smolt and migrate without prior sexual maturation, and that others, called pm-males, adopt a mixed strategy on the individual level with sexual maturation followed by smolting. We call the system of m-males vs. pm-males the "salmon" system, as this combination seems to be found in salmon populations, at least in SW Scandinavia.

IV. WHY EARLY SEXUAL MATURATION?

The traditional "explanation" has been to consider the existence of precocious males as a "biological insurance" (*e.g.* JONES 1959) for the population. This view is largely abandoned since it is based on group selection.

One of the first explicit theories was that of SVÄRDSON and ANHEDEN (1963). They noted the skewed sex ratio of sea trout smolt and related this to early sexual maturation of a fraction of the males and suggested a simple two-allelic genetic system balanced by overdominance of the heterozygote (balandced dimorphism). As sexual maturation seems to be under environmental influence, at least partly (LUNDQVIST 1983), the genetic system is probably more complex.

A second theory was proposed by ÖSTERDAHL (1969). If homing is perfect, he argued, there is a large probability that a returning big male is the father of the precocious males in the area. If so, it would increase his fitness to cooperate rather than to compete with these. This mechanism (kin selection) would result in coexistence. The problem with this theory is that big males seems to be aggressive even against small males (JONES and KING 1950, BOHLIN 1975).

A third theory is based on frequency dependent reproductive success (MAYNARD SMITH 1982, GROSS 1984, 1985). This philosophy may be expressed as: "My reproductive success is not only depending of my own behaviour or characters, but also on how my competitors respond to my behaviour". It is easy to imagine that a single big male competing only with small, precocious

males would perform quite well and thus that it might pay to switch from early to late reproduction if the gain is large enough. If so, the proportion of late reproducers would increase. If, however, all males are big, the competitive advantage of being big is outruled (no one bigger than anybody else). For a male in such a population it might pay to switch to a "sneaking" strategy: "Don't fight with the big ones, use your small size, hide behind a stone and make a quick rush when the female is depositing the eggs". It would then pay to be large among small competitors and small among large ones, a mechanism that might lead to a stable coexistence between the two "types". GROSS (1984, 1985) argued in favour of this theory and showed that small coho males (jacks) by sneaking reach a reproductive success (fitness) approximately equal to that of big males (hooknose coho). Middle-sized males had lower fitness than either small or big ones, which would lead to a "disruptive" selection in favour of small and big males in this species.

V. A MODEL BASED ON FREQUENCY DEPENDENT REPRODUCTIVE SUCCESS

One way to analyse the conditions for coexistence of two "types" is to use the net reproductive rate R, which is the multiplication rate per generation and which can be expressed as (number of offspring) x (their survival to reproductive age). If $R=1$, the population size is constant, and if $R > 1$ it is increasing. If R_0 is the net reproductive rate for a single "mutant" male in a steady state population of "normal" males, the A type will invade the B population if $R_0(A) > R(B) = 1$. Conversely, a single B will invade an A population if $R_0(B) > R(A) = 1$, if the A population is in equilibrium. A mixture of A and B will be the result if $R_0(A) > R(A)$ and $R_0(B) > R(B)$. To use these relations we adopt the following population model.

In the "trout" system (p-males vs. m-males), we assume that p-males become mature after a juvenile survival S, and that the spawning is repeated annually with a constant annual survival

S_p. In each season, a p-male in a pure population of other p-males fertilizes n eggs on the average, and a p-males in an (otherwise) pure population of m-males fertilizes N eggs. Thus

$$R(p) = n \, S \, s_p = 1 \qquad (1)$$

where $s_p = (1 + S_p + S_p^2 + S_p^3 + \ldots) = 1/(1 - S_p)$
and
$$R_0(p) = N \, S \, s_p \qquad (2)$$

The m-males have the same juvenile survival as the p-males (up to the age at which p-males start to mature). From this age through smolting/migration and to the first spawning the survival is S_m, whereafter the spawning is repeated annually with a constant annual survival S'_m. In each season, an average m-male will fertilize m eggs if he is a member of a pure m-male population, and M eggs if he is alone in a population of p-males. This yields that

$$R(m) = m \, S \, s_m = 1 \qquad (3)$$

where $s_m = S_m/(1 + S'_m + S'^2_m + S'^3_m + \ldots) = \dfrac{S_m}{1 - S'_m}$

and
$$R_0(m) = M \, S \, s_m \qquad (4)$$

For coexistence we know that $R_0(p) > R(m) = 1$ and $R_0(m) > R(p) = 1$, yielding the simple conditions

$$N > n$$
and
$$M > m$$
or
$$\frac{M}{n} > \frac{m}{n} > \frac{m}{N}$$

provided that the survival rates are independent of the densities. A stable coexistence between p-males and m-males is thus possible under the condition that a single big male will fertilize a larger number of eggs when competing only with small males than does an average male when competing with other big ones, and that a single small sneaker is more efficient than each of a large number of small ones competing with each other. We conclude that it would be surprising if these conditions are not valid, and thus that frequency dependent reproductive success may be a reason why "pure" populations of m- or p-males are not known to us.

For the "salmon" system, in which the pm-males adopt a mixed strategy on the individual level with precocious maturation followed by

smolting and subsequent spawning as a big male, and in which the m-males skip the precocious maturation, the situation is more complicated. Based on observations from SW Scandinavia, we assume that the smolting age is the same for pm-males and m-males, and that pm-males become sexually mature in the autumn before main smolt age. We assume further, that big males of either kind are equivalent in fertility, and consequently that the reproductive cost for precocious matura- tion is increased mortality rather than reduced growth. The juvenile survival up to the age at which pm-males become mature, S, is assumed the same for both types. From this age through smolting and to the first spawning after sea residence, the survival for pm-males is S_{pm} and for m-males S_m. They may then spawn annually with the annual survivals S'_{pm} and S'_m, respec- tively. In a pure population of pm-males, a male fertilizes n eggs as a precocious male and m_1 eggs as a big male, so that in this case

$$R(pm) = S(n + s_{pm}m_1) = 1 \qquad (7)$$

where $s_{pm} = S_{pm}/(1 + S'_{pm} + S'^2_{pm} + S'^3_{pm} + \ldots) = S_{pm}/(1 - S'_{pm})$

A single pm invader in a pure population of m-males fertilizes N eggs as a precocious male and m_2 as a big male, so that the net reproductive rate is

$$R_0(pm) = S(N + s_{pm}m_2) \qquad (8)$$

In a pure population of m-males, such a male fertilizes on the average m_2 eggs, so that

$$R(m) = m_2 S s_m = 1 \qquad (9)$$

A single m-invader in a pure pm-population fertilizes m_1 eggs, yielding

$$R_0(m) = m_1 S s_m \qquad (10)$$

For coexistence, we know that $R_0(m) > R(pm) = 1$ and $R_0(pm) > R(m) = 1$, or $R_0(m) > R(m)$ and $R_0(pm) > R(pm)$. An m-male would thus invade a pm-population if $m_1 > m_2$ (from eq. 9 and 10). The success of an m-male in this case is not as clear as in the "trout" system, as an m-male in the "salmon" system has to compete not only with sneakers (as in the "trout" system), but also with the big pm-males. Thus if there are many big pm-males (s_{pm} large) and efficient sneakers (n large), m_1 will be small and m-males may fail to invade.

Combining eq. (7), (8), (9) and (10), we can express the coexistence conditions as

$$\frac{N}{m_2} > s_m - s_{pm} > \frac{n}{m_1}$$

Not surprisingly we find that the possibility for m-males (using one of two modes of reproduction) to compete with pm-males (utilizing both modes) is closely related to the cost of using both modes, in this case expressed as the reduction of survival $s_m - s_{pm}$. If this difference is small enough, pm will win. Further, as a single small sneaker among big males probably will have good opportunity of fertilizing many eggs, N will be large. Gener- ally, thus, it appears that pure m-male popula- tions would be more unlikely than pure pm- populations, reflecting the fact that a single m- male has no "niche" of its own — he has to compete with big pm-males — whereas a single pm-male more easily can get foothold by sneaking.

VI. EQUILIBRIUM PROPORTIONS OF PRECOCIOUS MALES IN THE "TROUT" AND "SALMON" SYSTEMS

Assuming that the male types are maintained by a reproductive success which is negatively cor- related to the frequency, how would the equi- librium proportion p* of males choosing the preco- cious strategy vary with the type of reproductive system ("trout" and "salmon") and with survivals? Our strategy is the following:

We define q as the proportion of eggs fertilized by small males, *viz.* q = (number of eggs fertilized by small males)/(number of eggs fertilized by all males), and F as the proportion of small males in the population, *viz.* F = (number of small males)/ (number of all males). p is the proportion of a male cohort choosing precocious maturation, so that p and F are related by the survival rates. Then we

(1) construct equilibrium lines for q as a function of p for the two systems "salmon" and "trout", along which the populations by definition are in equilibrium,

(2) assume that q in a population is a specific function of F,

(3) try to figure out the shape of this function from some speculative arguments concerning salmonid reproduction behaviour,

(4) transform this function q of F into a function q of p using numerical examples of survivals. Finally we

(5) find the equilibrium p values p^* as the intersections between the transformed q function and the equilibrium lines obtained under (1).

The tendencies are then discussed and compared with available data.

The equilibrium line for the "trout" system is simple, as, by definition $q=p$ in equilibrium, which also is easily shown by setting $R(p)=R(m)=1$ and using the fact that $q=(p\,n\,s_p)/(p\,n\,s_p+(1-p)\,m\,s_m)$. In Fig. 3 this equilibrium line is the diagonal from origo. For the "salmon" system, the situation is more complex, as q in this case is referred to small pm-males, not all pm-males. As $R(pm)=R(m)=1$ and $q=p\,n/(p\,n+p\,m\,s_{pm}+(1-p)\,m\,s_m)$, the equilibrium line for "salmon" turns out as $q=p(1-s_{pm}/s_m)$. In Fig. 4 a and b, two examples are drawn using different values of the ratio s_{pm}/s_m.

We now need to know how q is affected by the frequency F of small males. As we lack both data and methods of estimating this, we have to use the following speculative argumentation.

(1) Males compete for females by aggressive behaviour. The best female strategy would then be to await the winner, as she thereby will increase the possibility that her sons will share the winning character. If no big males appear within a certain time, we assume that she will accept a small male as a mate rather than to skip spawning.

(2) The aggressive behaviour of big males combined with the "awaiting" female strategy will result in a large proportion of eggs fertilized by big males even if the proportion of these is low (F large).

(3) During a spawning, the big male and the female are in close lateral contact, and the ventral side of the female is close to the substrate. The sneaking activity from small males will therefore be limited largely to the opposite side of the female. Therefore we assume that the sneakers compete mainly for about one half of the eggs in each spawning.

Fig. 3. The "trout" system: graphic solution to the equilibrium frequency p^* of males choosing precocious maturation, shown by asterisks. p is the proportion of males choosing precocious maturation, q is the proportion of eggs fertilized by precocious males. The stippled curve $q=f(F)$ is the assumed function of q in relation to F, the proportion of precocious males among all spawning males. The solid curves are derived from this using different survival rates, s_p for precocious males and s_m for migratory males. See text for further explanation.

(4) A single small sneaker has the opportunity to choose the best place and female for sneaking.

If this tentative scenario is realistic, q as a function of F would have the general shape as the stippled lines in Figs. 3 and 4, with a plateau somewhere between $F=0.5$ and 1 at a q value possibly in the magnitude of 0.5 (assumption 3), and with a sharp rise as F approaches 1 (assumption 2). Accepting this q function, as a starting point, we now procede to transform it into a function of p. For the "trout" we use the relation $F=$(number of small males)/(number of males)$=p\,s_p/(p\,s_p+(1-p)s_m)$. Solving for p yields $p=F/(a-F\,a+F)$, where $a=s_p/s_m$. In Fig. 3 this relation is used to transform the stippled curve into the solid curves using values of a ranging from 2 to 16. The equilibrium p^* is represented by the intersection between the equilibrium line (the diagonal) and the solid curves. These intersections are shown by asterisks. The "salmon" system is analysed using
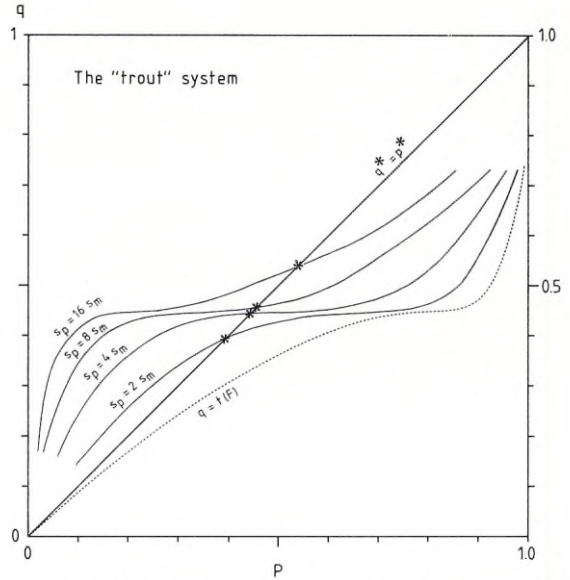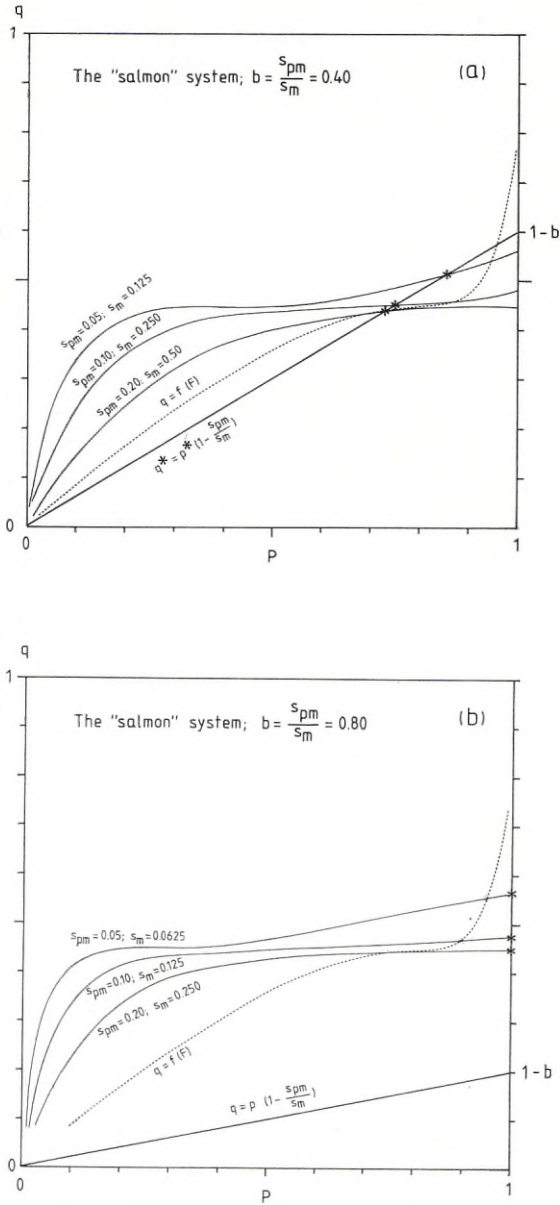
Fig. 4. The "salmon" system: graphic solution to the equilibrium frequency p* of males choosing precocious maturation, shown by asterisks. p, q and q=f(F) the same as in Fig. 3. Solid curves are derived from the stippled curve q=f(F) using different values of survival rates, s_m for m-males and s_{pm} for pm-males. (a) s_{pm}/s_m=0.40. Equilibrium p values indicated at the intersections between the equilibrium line and the solid curves. (b) s_{pm}/s_m=0.8. In this case the equilibrium line is below the solid curves, resulting in p*=1. See text for further explanation.

the same technique, in which $F = p/(p + p\,s_{pm} + (1-p)s_m)$. In Fig. 4 a and b the transformation is completed using various values of s_{pm} and s_m, and the result is shown by the solid lines. As for the "trout" system, the intersection between the equilibrium line and the solid curves is the p*. The emerging features are then the following.

(1) For the "trout" system, intermediate p* values are expected. The largest values are associated with low sea survival and/or large survival of precocious males. Stocks with a prolonged sea residence and subjected to heavy fishing might be an example of stocks in which the largest proportion of precocious males might be found.

(2) For the "salmon" system, p* is closely related to the ratio s_{pm}/s_m. If this ratio is in the magnitude of one half or more, the p* value will be near 1. A proportional change in s_{pm} and s_m will affect the system to a lesser extent, although the largest p* is expected for populations in which both s_{pm} and s_m are small, *e.g.* stocks with heavy fishing.

(3) If "salmon" and "trout" have similar basic q functions (q of F), we expect lower frequencies of precocious males in "trout" populations than in "salmon" populations.

For "salmon", the ratio s_{pm}/s_m is obviously crucial. We have few data on this, although we from the Imsa data, by comparing the proportion of precocious males with the proportion of spent males among smolt, can calculate s_{pm}/s_m as about 0.7 (1983) and 0.4 (1984), provided that the survival of immature males and females is the same. A similar calculation by MYERS (1984) indicates a magnitude of 0.6. Further, the sex ratio of salmon smolt is usually about one third males, so that about half of the males are "missing". This means that s_{pm}/s_m would be at least 0.5 and probably larger, as all males may not become precociously mature. Thus there are a number of indications that s_{pm}/s_m may be in the magnitude of 0.5, and our prediction from Fig. 4 would be p* values approaching 100 % for salmon.

Estimated proportions of precocious males in sea trout and salmon in SW Scandinavia are

generally of the magnitude predicted by the model.   We have the following results:

Sea trout	River Norumsån 1983	44 % (n=460)
	River Norumsån 1984	37 % (n=440)
	River Arödsån	25 % (n=246)
	River Imsa	42 % (n= 34)
Atlantic salmon	River Imsa	82 % (n=505)
	River Forsån	100 % (n=130)

For sea trout, the proportion of males among smolt appears to fluctuate around one third (SVÄRDSON and ANHEDEN 1963, JENSEN 1968, PEMBERTON 1976), which would correspond to a p value of about 50 %. For Atlantic salmon, MITANS (1972) reported 75—86 % precocious males, MYERS (1984) 80 % in Codroy River, Newfoundland, DALLEY *et al.* (1983) high but varying values in 12 streams in Newfoundland (median 75 %, range 12—100 %), and JONES (1959) 75 % in British rivers. As expected from the model, the proportion of precocious males is generally lower in sea trout populations than in populations of Atlantic salmon.

Is increased fishing associated with an increase in the proportion of precocious males, as predicted? The communications dealing with this are few. BARACH (1960) states that the male proportion of parr in Black Sea sea trout increased "along with a marked decline in the population as the result of intensive fishery during those years". GIBSON (1978) found a decrease in the male proportion of salmon smolt in a Canadian stream and an increase in the proportion of precocious males during a 9 year period, and related this to a reduced egg deposition, "probably caused by either natural factors or increased exploitation at sea". Although incidental, the tendency in these cases is in the predicted direction.

VII. DISCUSSION

Our model remains speculative until we can measure the fitness for the different male forms under realistic conditions. It seems reasonable, however, that the fitness for small and big males

is frequency dependent: a rare "mutant" of either type has an advantage, and one problem is to show whether this leads to a frequency where the fitness for the forms is equal. There may be genetic constraints, operating *e.g.* by overdominace, which prevents the system from reaching this equilibrium frequency (MAYNARD SMITH 1982, p. 40).

Another problem with practical relevance is the mechanisms involved: what makes one male mature sexually on the parr stage while another remains juvenile? An answer to this question would be useful in fish farming, as it might lead to methods of reducing the proportion of early spawners. In principle, a balanced system can be maintained with or without genetic inheritance involved. There might well be direct inheritance, though its phenotypic expression seems to be under environmental influence (*e.g.* LUNDQVIST 1983). A rigid genetic system for age or size at first maturity seems unlikely, since a phenotypic plasticity in response to environmental factors (including *e.g.* the behaviour of other males) probably would gain the individual and since the cost for retaining a physiological preparedness may be small. If there is no direct inheritance involved, the following mechanism is possible: All males are potential early spawners. Phenotypic differences induced by the environment make some males mature earlier than others. The behaviour of these maturating males may then affect the choice of strategy for those that still have not made up their minds, *e.g.* by feromones etc. Natural selection will then favour those assessing the "right" proportion of competitors as a cue whether or not continue to early sexual maturation. Experimentation in this field would be interesting.

A practical implication of our results is that

p-males in the "trout" strategy would result in a direct loss of about 50 % of the males in sea-ranching due to early maturation. We have indications that the salt water tolerance of both wild and hatchery reared precocious males of sea trout is reduced as compared with immature trout, suggesting an inhibited smolting even for the artificial ones. We are presently making marking experiments which may give us an answer.

In contrast to wild populations, precocious maturation of Atlantic salmon in hatcheries may not drastically reduce survival, although growth and nutrient reserves are affected negatively. It is therefore possible that the best trout in sea ranching would be one with the "salmon" reproductive pattern if, indeed, such a trout were found.

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The Control of Spawning in the Rainbow Trout (*Salmo gardneri* RICHARDSON) Using Photoperiod Techniques

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ABSTRACT

The effects of altered seasonal and constant light regimes on the times of spawning, *i.e.* production of mature eggs, of rainbow trout (*Salmo gairdneri* RICHARDSON) are described and discussions made of the mechanisms involved in the photoperiodic response and the uses of daylength control to provide out-of-season supplies of eggs for commercial farms. Seasonally-changing light regimes compressed or extended into shorter or longer periods than a year, respectively advanced or delayed the times of spawning. Results from regimes involving exposure of fish to daylengths of constant duration confirm the dependence of the photoperiodic response on the duration of the light period and not with its seasonal rate of change. It is proposed that at least two light cues are required to entrain the natural cycle of reproduction; the first, a long day cue which entrains the earlier stages of ovarian recrudescence and growth and the second, a short day cue which is concerned with the synchronization of later events. Fish maintained for periods up to 4 years under constant short days spawned with an annual periodicity, 3—4 months out-of-phase with the natural cycle, whereas those under continuous light or constant long days spawned successively at 5—7 month intervals. It is suggested that the reproductive cycle is controlled by an endogenous annual or circannual rhythm and that it is the entrainment of this rhythm by seasonally-different light cues which accurately coordinates reproductive development with the natural pattern of daylength change.

I. INTRODUCTION

In the farming of fish there are considerable commercial advantages to be gained from an 'all-year-round' or 'out-of-season' production of eggs (Fig. 1). Modest alterations in spawning time of salmonids can be achieved by injecting pituitary extracts, gonadotropins or synthetic releasing hormones (FITZPATRICK *et al.* 1984; CRIM and GLEBE 1984). In general these methods have only been used to advance the final stages of maturation and ovulation and attempts to modify spawning time by influencing the earlier stages of ovarian development have been largely unsuccessful (FUNK *et al.* 1973; FITZPATRICK *et al.* 1984; CRIM and GLEBE 1984) probably because of the number of different hormones involved in the control of reproduction and the complexity of their interplay. Daily or weekly injections of large numbers of broodstock over extended periods of time would also make significant additional demands on the time of fish farm staffs. Much more effective and convenient for use on farms are environmental manipulations of spawning time. Salmonids are particularly suitable because their reproductive cycles are entrained by the seasonal changes in daylength and methods for the photoperiod control of spawning time are relatively easy and inexpensive to install on farms. A further advantage of using these methods is that the daylength cues operate at the highest levels of the neuroendocrine pathway which controls reproduction. This means that provided the appropriate photoperiod cue(s) are received then ovarian development proceeds under the direction of natural endocrine mechanisms. The timing of spawning in relation to the seasonally-changing photoperiod is precise and unchanging for each stock of rainbow trout and hence there has been considerable commercial interest in using photoperiod techniques to produce out-of-season eggs. Some of these methods are considered in the present paper which also discusses the nature of the photoperiodic response.

II. SEASONAL LIGHT CYCLES

All organisms whose reproduction is stimulated by light, and salmonid fish are no exception, are cued by the seasonal changes in daylength (de VLAMING 1972). Even in sub-tropical regions, where there is

Fig. 1. Advantages of controlled spawning or all-year-round egg and fry production in farmed rainbow trout.

little seasonal change in daylength, the spawning time of many fish species is influenced by the daily cycles of dawn and dusk (SUNDARARAJ and VASAL 1976). In temperate and also polar regions where the annual change in daylength becomes progressively more pronounced with higher latitudes, different species and also stocks of the same species in different localities spawn at different times of the year by responding either to different lengths of day or differentially to the same daylength (SCOTT and SUMPTER 1983, ELLIOT et al. 1984). Thus, the sea bass, the trout and also other salmonids ovulate under a short or decreasing photoperiod (GIRIN and DEVAUCHELLE 1978, MACQUARRIE et al. 1978, 1979, WHITEHEAD et al. 1978, BROMAGE et al. 1984, ELLIOTT et al. 1984) whereas in general flatfish spawn under long or increasing daylengths (HTUN-HAN 1977). Even though the spawning of each of these fish occurs under a specific daylength, the initial growth and development of the ovary and the subsequent incorporation of yolk by the ripening oocytes will have occurred at earlier times in the reproductive cycle under quite different daylengths. In the rainbow trout for example histological changes are apparent in the ovary a year or so before the mature eggs are ovulated (ELLIOTT et al. 1984, SUMPTER et al. 1984) and it has been suggested that a series of cues are involved in the triggering and modulation of the different stages of ovarian growth and recrudescence (BROMAGE et al. 1982 b, 1984). Consequently, all stages of ovarian development must be considered when using photoperiod techniques to modify the spawning times of salmonid fish.

The dependence of salmonid fish on the annual changes of daylength for the entrainment of spawning, *i.e.* the production of mature eggs and spermiation, has been demonstrated in a number of studies (HOOVER 1937, HAZARD and EDDY 1951, CORSON 1955, ALLISON 1951, WHITEHEAD et al. 1978, BROMAGE et al. 1982 a). Furthermore, work in this laboratory has shown that the time of spawning, can be advanced or delayed by respectively compressing or extending the annually-changing daylength into shorter or longer periods of time than one year (Fig. 2). Thus, seasonal light cycles compressed into 6 months with the longest and shortest days in April and late June respectively, advance spawning by 3—4 months when compared with fish under a natural light cycle. Seasonally-changing light cycles compressed into 9 months produce only a 1—2 month advancement in the time of spawning whereas 18-month cycles, with the longest and shortest days in September and March respectively, delay development by up to 3 months. In all the experiments reported in this paper, temperature and feed levels were maintained at constant levels of 9—10°C and 0.5 % of body weight. day^{-1} of a proprietary trout pellet respectively. Most of the data described relate to female fish and the timing of mature egg production (*i.e.* spawning) in broodstock at 2, 3 or 4 years of age. All fish irrespective of age show similar responses to photoperiod although in the majority of fish stocks spermiation begins 2—3 weeks in advance of the time at which the first female of the stock spawns (BROMAGE 1978, unpubl.). All other experimental conditions and methods are as described in BROMAGE et al. (1982 a, b, 1984).

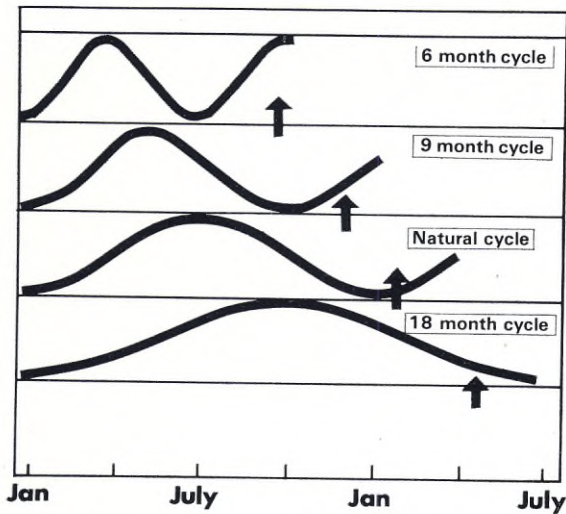Modified seasonal light cycles have also been

Fig. 2. Effects of compressed and extended seasonal light regimes on the time of spawning of farmed rainbow trout. Under the natural cycle, the daylengths of the winter and summer solstices were 7 and 17 hours respectively. Under each regime the time of first spawning of a stock is shown by the arrow. The vertical line on the horizontal axis represents the first day of the month as marked.

used to alter spawning times in the brook trout (HOOVER 1937, HAZARD and EDDY 1951, CORSON 1955, CARLSON and HALE 1973) the coho salmon (MACQUARRIE *et al.* 1978), the pink salmon (MACQUARRIE *et al.* 1979), and the Atlantic salmon (LUNDQVIST 1980). Under each photoperiod manipulation the sequence of endocrine changes, although modified in timing, parallels those which occur during natural maturation (WHITEHEAD *et al.* 1978; BROMAGE *et al.* 1982 a, b). Daylength cycles, in which the seasonally-changing annual light regime is 6 months out-of-phase with the natural photoperiod, show similar advancements in the timing of spawning and in the sequence of endocrine changes which initiate and control this process (ELLIOTT *et al.* 1984). Alterations in spawning time of 4 months or more can, however, only be achieved by progressively changing the light cycle over a period of two or more reproductive cycles. Exposure of fish, particularly females, to a seasonal photoperiod regime which is markedly different to the one in which they have previously been maintained may cause a phase-shift to the next appropriate light cycle (BROMAGE

and WHITEHEAD 1978, unpubl.). Similar phase-shifts have been reported for other organisms (GOSS 1969, L.-O. ERIKSSON, pers. comm. 1985). Not withstanding this limitation, it is evident that rainbow trout and possibly all salmonids may be spawned at any time of the year providing that the appropriate light stimuli have been received (ELLIOTT *et al.* 1984).

III. CONSTANT LIGHT CYCLES

Although the spawning alterations achieved by manipulation of seasonal light cycles are able to produce eggs at any time of the year, the necessary weekly adjustments of time clocks makes the application of these techniques to commercial farms somewhat complex. Clearly, it would be easier to use constant or "square-wave" light regimes. Initially, we attempted to replace portions of the seasonally-changing light cycle with regimes involving constant daylengths. In the experiment described in Fig. 3, fish of a late October/early November-spawning strain of trout were maintained on a seasonal light cycle compressed into a 6 month period; this gave a 3—4 month advancement in spawning. Subsequently, the fish were exposed to the first half of a further 6 month compressed photoperiod but at the longest day, the daylength was abruptly reduced to a constant short day (8L: 16D) *i.e.* 8 hours light and 16 hours dark each day. Spawning was advanced in a similar way to that produced by the compressed seasonal cycle suggesting that the decreasing phase of the annual light cycle can be replaced by a square-wave or constant daylength. The ability of the fish to spawn three times in a 15 month period is also of considerable commercial significance.

Other experiments with constant light regimes have also been conducted (Fig. 4; BROMAGE *et al.* 1982 b). They show clearly that, as far as the induction of reproductive development is concerned, the response of salmonid fish to light is determined by the amount of light received each day and/or where it appears in the 24 hour light-dark cycle and not by the rate of change of a seasonally-changing light cycle (BROMAGE *et al.* 1982 b). These results also demonstrate that ex-
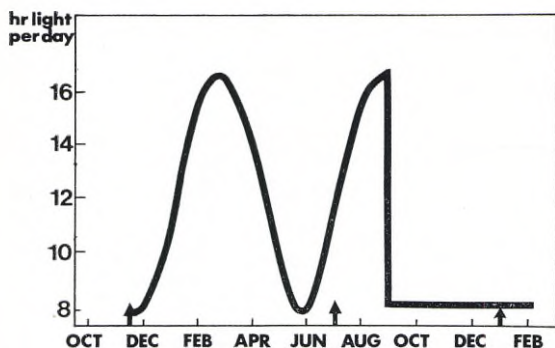
Fig. 3. Effects on the spawning time of the rainbow trout of a seasonal light regime compressed into 6 months and a cycle in which the increasing pattern was seasonal but, at the longest day, daylength was reduced to a constant 8 hours light/day^{-1}. Spawning is indicated by the arrows in each case.

posure of fish to constant long days, of either 16 or 18 hours duration, early in the year advances spawning by 1—2 months. Continuous light (24L: 0D) has also been shown to produce similar effects in the trout (BROMAGE *et al.* 1984) and the masu salmon (TAKASHIMA and YAMADA 1984). Clearly as far as the initiation of gonadal development is concerned salmonids are "long-day" animals confirming earlier proposals by WHITEHEAD and BROMAGE (1980), BROMAGE *et al.* (1982 b) and SUMPTER *et al.* (1984). In contrast exposure of fish to constant short days of either 6 or 8 hours
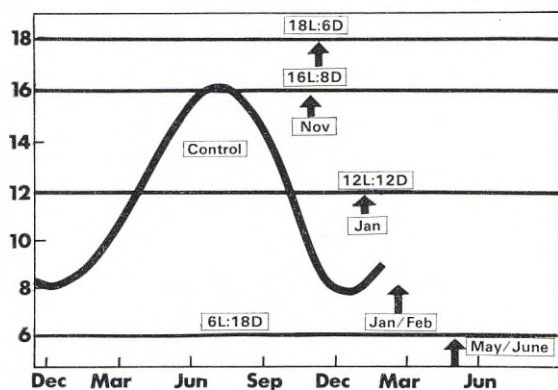
Fig. 4. Effects of a constant 18L: 6D (long day), 16L: 8D (long day), 6L: 18D (short day) and 12L: 12D on the timing of spawning (vertical arrows and labelled) of the rainbow trout. The control is a simulated natural seasonal cycle and under this regime spawning occurred in Jan/Feb.

duration during the early stages of development delays maturation (Figs. 4 and 8). This confirms results reported by HENDERSON (1963) for the brook trout and TAKASHIMA and YAMADA, (1984) for the masu salmon. An intermediate light regime of 12L: 12D throughout the year modestly advanced spawning when compared to fish under a natural cycle (Fig. 4). Collectively, these data indicate that there is a strong endogenous component in the timing of reproduction in the rainbow trout.

It might be mentioned that the spawning times of individual fish within stocks of rainbow trout exposed to constant year-long light regimes is less synchronised than those produced by seasonal cycles. From the commercial viewpoint this may be a considerable disadvantage because of the requirement for batches of eggs of reasonable size and the additional stress of repeatedly handling broodstock if the overall spawning period of the stock is extended.

IV. SEASONALLY-CHANGING LIGHT CUES

Although trout are able to spawn in response to light regimes in which the daylength is maintained at constant levels throughout the year, it would be surprising if these regimes were providing equivalent cues to those normally offered by seasonally-changing light cycles. A single light cue whether provided by a specific length of daylight in either a seasonal or constant light regime would provide only limited information about calendar time. Photoperiodic mechanisms involving just one cue would, for instance, be unable to distinguish between Spring and Autumn when daylengths of equivalent length reoccur. Two or more cues operating in sequence would provide the necessary information regarding the direction of change of daylength and thus ensure that ovarian development occurs at the appropriate time each year.

Initially, investigations were made of the possibility of two daylength cues in the annual cycle. This hypothesis was considered because we found that the most stimulatory regime, as far as the advancement of spawning was concerned, was
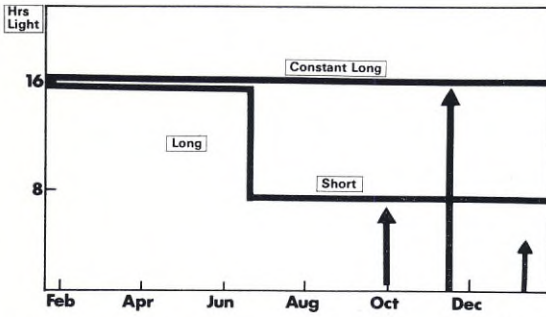
Fig. 5. Effects of a constant 16L:8D and a 16L:8D until June 21 followed by a direct change to 8L:16D ('long-to-short switch') on the time of spawning of the rainbow trout. The controls under ambient light spawned in Jan/Feb (arrow on right of figure).

Fig. 6. Effects of a variety of long-to-short (a, b, c & d) and short to long (f & g) photoperiods on the time of spawning (vertical arrows) in the rainbow trout. The figure also includes the effects on spawning time of a constant long (e), short (h), 18-months seasonal (i) and control (j) light regimes. (Reproduced from Aquaculture Vol. 43, with the kind permission of Elsevier Science Publishers B.V.: Amsterdam.)

one in which fish were exposed to long days early in the cycle followed by a direct change to short days (Fig. 5). Spawning in this "long-to-short switch" occurred 3—4 months earlier than corresponding controls maintained on ambient daylength and 1—2 months in advance of fish subjected to constant long days. "Long-to-short" regimes have also been reported to induce maximal advancements in spawning time in other studies of salmonids (HENDERSON 1963, SHIRAISHI and FUKUDA 1966; WHITEHEAD and BROMAGE 1980, TAKASHIMA and YAMADA 1984).

A requirement for long and then short days is also supported by a series of other experiments (Fig. 6). These data demonstrate that long days early in the year advance spawning whereas exposure to short days over this portion of the cycle delays maturation. Furthermore, as little as 6 weeks of long days in an otherwise constant short day regime (Fig. 6, d) are able to bring about spawning at the same time as control fish. TAKASHIMA and YAMADA (1984) reported similar results with the masu salmon and suggested that 1 month of long days during the early portion of the cycle was all that was necessary for normal maturation. The differential effects of long and short days at different times of the year are summarized in Fig. 7. Although this model is primarily based on data from the rainbow trout it is probable that all salmonids respond in a similar manner.

The constant long and then short day regimes have also been used on a number of commercial

Fig. 7. Diagrammatic representation of the differential effects of exposure to long and short days, at different times of the year, on the spawning time of the rainbow trout.
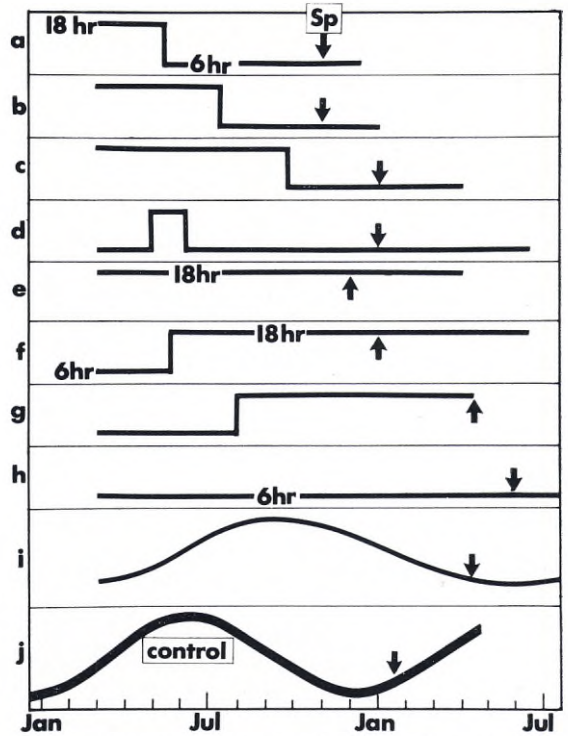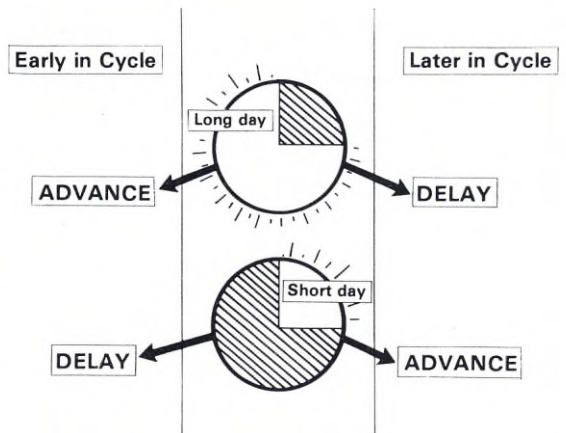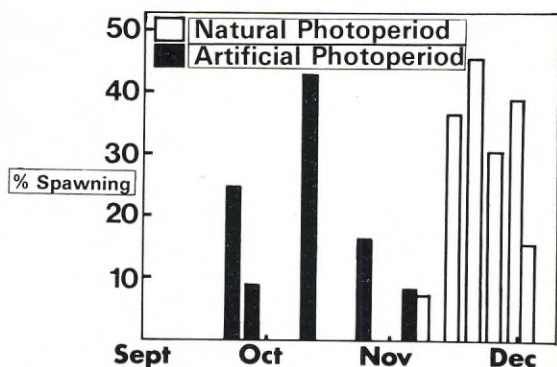
Fig. 8. Effect of 17L:17D from April until June 23 followed by a direct change to 7L:17D on the time and spread of spawning in a commercial stock of rainbow trout (filled histograms). The spawning of controls which were maintained under ambient daylength are represented by the open histograms.

trout farms. One such example is shown in Fig. 8. The aim was to advance spawning by 6—8 weeks; this was achieved by subjecting fish to long days (17L:7D) from April until the summer solstice (June 22) at which time there was an abrupt change to constant short daylengths (7L:17D). The eggs produced in the photoperiodically-advanced group were significantly smaller in size when compared to the eggs of the control fish but had similar rates of survival up to the fry stage. Similar differences in egg size, but with no adverse effects on the viability of the eggs and fry, have been reported by BROMAGE (1982) and BROMAGE *et al.* (1984) after other photoperiodic manipulations. Generally photoperiodically-advanced fish have slightly lower total fecundities (*i.e.* number of eggs fish^{-1}) as might be expected from their earlier spawning times and lower spawning weights (SPRINGATE and BROMAGE 1984). However, the relative fecundities, *i.e.* number of eggs unit weight^{-1} of fish, increase thus confirming the inverse relationship or "trade-off" between egg size and egg number as proposed by SPRINGATE and BROMAGE (1984).

Constant photoperiods have also been used to delay the spawning of commercial stocks. Two methods have been employed: the first involving short days for at least the first 7 months of the natural seasonal light cycle and the second, long days from the summer solstice onwards (Figs. 4 and 6). Constant short days (either throughout the year or until the end of July) delay spawning by 1—4 months (Figs. 4 and 6, h). Similar delays are also achieved by exposing fish to constant long days during the later half of the cycle, after initial treatment with either short days (Fig. 6) or a naturally-increasing photoperiod. In general our results correspond well with the findings of ALLISON (1951) working with the brook trout, COMBS *et al.* (1959) with the sockeye salmon, SHIRAISHI and FUKUDA (1966) with the chum salmon, the amago salmon, the brook trout and the rainbow trout, ERIKSSON and LUNDQVIST (1980) with the Atlantic salmon and also other studies on the rainbow trout from this laboratory (WHITEHEAD and BROMAGE 1980; BROMAGE *et al.* 1984). The 3 month delay in spawning which followed exposure of trout to an 18 month seasonal cycle (Figs. 2 and 6, i) may also be due to the influences of short days early in the year and/or of long days after the summer solstice.

In all our commercial trials we have found that the responses to constant short days throughout the year or long days later in the cycle are not consistently shown by all members of a broodstock. Furthermore the spread of spawning is extended in time in much the same manner as fish exposed to constant light regimes. Possibly, this is due to the failure of these regimes to offer the sequence of photoperiod cues which are necessary for normal or accelerated development. Under such conditions possibly the cycle "free runs" with a periodicity which approximates to a year (see section on photoperiodic mechanism below).

Returning to the requirement for a mid-cycle switch from long to short daylengths. Earlier it was mentioned that an abrupt change from long to short days is as effective in advancing spawning as either a progressively-decreasing seasonal photoperiod or a stepwise reduction from long to short days over a period of 3—4 weeks (BROMAGE *et al.* 1984). However, there may be species differences here for ERIKSSON and LUNDQVIST (1980) have reported that a stepwise reduction of 1 hour's light day^{-1} over a ten day period advanced the ripening of Atlantic salmon parr more rapidly than a direct change to short days. In contrast the masu salmon appears to respond to sudden changes in daylength in much the same way as the rainbow trout (TAKASHIMA and YAMADA 1984).
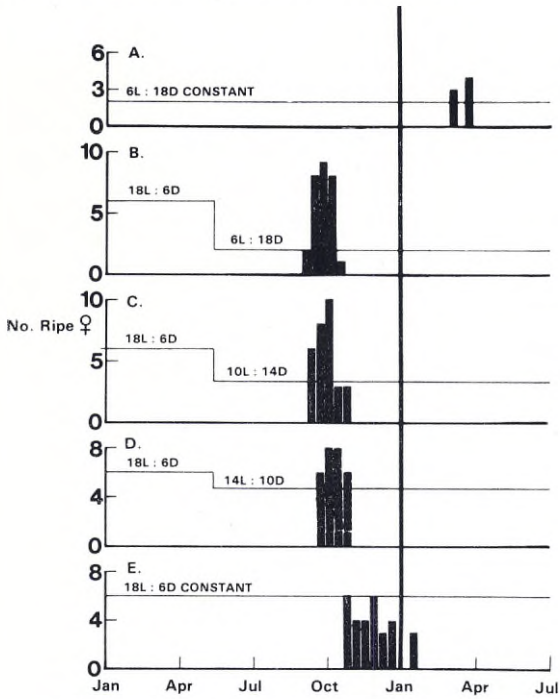
Fig. 9. Effects on the spawning of rainbow trout of a constant short day (6L:18D), a constant long day (18L:6D) and 3 different long day to short day switches ie. (18L:6D to 14L:10D, 18L:6D to 10L:14D and 18L:6D to 6L:18D). All switches were made on May 1st.

Recently, we have also observed that the magnitude of the reduction in daylength involved in a "long-to-short switch" has only a marginal effect on ovarian development and that the spawning response to light cycles in which the daylength was reduced from 18L:6D to 14L:10D or 18L:6D to 10L:14D was similar to that produced by a 18L:6D to 6L:18D switch (Fig. 9, DUSTON and BROMAGE 1983, unpubl.). Under all three "long-to-short switches" spawning occurred up to 7 weeks earlier than fish exposed to constant long days (18L:6D). It would thus appear that it is the direction of the change in photoperiod which provides the all-important cue for normal reproductive development and not the absolute size of this reduction. Such a mechanism would be a considerable adaptive significance to many species of salmonids whose spawning ranges often extend over many degrees of latitude. The close synchrony and advancement of spawning of the groups under

the long-to-short switches, when compared with those under constant long days (Fig. 9) also confirms the importance of a short day cue in the control of development of the later stages of oocyte maturation.

V. PHOTOPERIODIC MECHANISMS

Although it is clear that reproduction in the rainbow trout is entrained by the seasonal alterations in daylength, it is also evident that reproductive development can occur under conditions of constant light of widely different lengths (Fig. 4). It has been suggested that without appropriate photoperiodic entrainment the reproductive cycle "free-runs" with a periodicity which approximates to a year *i.e.* a circannual rhythm. However, general acceptance of a cycle as circannual is dependent on the rhythm satisfying a number of criteria: firstly, the rhythm should approximate to, but be significantly different from, one year; secondly, it should be observed and manifest over at least two cycles; thirdly the rhythm should be capable of entrainment to normal or altered seasonal light cycles; and lastly, it should show temperature compensation (GWINNER 1971, 1981). Not surprisingly, relatively few examples are able to fully meet these exacting criteria and of these the majority relate to insects, birds or mammals (GWINNER 1971). Few studies pertain to fish which is difficult to understand in view of their strongly-defined seasonality. Only the investigation of SUNDARARAJ *et al.* (1973) on the ovarian weights of catfish maintained under continuous light or darkness for periods of 33 months provides clear evidence of a circannual rhythm. Other studies are less convincing, primarily because the cycles have not been followed for sufficiently long periods of time. Thus, ERIKSSON and LUNDQVIST (1982) described 10 month cycles of growth and smoltification in a 14 month study of Atlantic salmon maintained under constant temperature and a 12L:12D light regime. Under the same 12L:12D photoperiod and also constant water temperatures and feed levels, we have shown that the spawning of rainbow trout occurred after 49 rather than 52 weeks (Fig. 4); this confirms an earlier study by WHITEHEAD *et al.* (1978). Exposure of trout to different lengths of constant long

or short days also produced spawning times whose period-lengths were similar to, but significantly different from, one year *i.e.* the length of the natural reproductive cycle which is normally entrained by the seasonally-changing ambient light cycle (Figs. 4 and 6).

Although the period lengths of these cycles in trout are well within the range of 215—460 days which is generally accepted to be the widest limits of variability of circannual rhythms (GWINNER 1981), unfortunately, none of them may be fully considered as circannual because, the experiments were discontinued after the completion of the first spawning cycle. The asynchronous spawning times produced by these constant light regimes are, however, suggestive of a free-running rhythm. Irregularities in the frequency of spawning of different members of a broodstock under constant light regimes have also been described by HENDER-SON (1963). Possibly, under constant long days, the early stages of ovarian development are entrained by the long photoperiods but, later in the cycle, in the absence of further cues (*e.g.* short days) control of the remaining stages of oocyte development free-runs as a result of an endogenous rhythm. In contrast, under constant short days, possibly the earlier stages of the ovarian cycle free-run and subsequently the later sections of development become entrained by the short day cue. The presence of an endogenous circannual rhythm which exhibits seasonal variations in sensitivity to light cues of varying length would explain in part the results achieved by the exposure of fish to constant light regimes of markedly different lengths. It would also explain the inability of any of the different light regimes to fully arrest reproductive development.

Since the above studies were completed further experiments have been conducted in which fish have been maintained for periods up to 4 years under continuous light or constant long or short days and constant temperature and feed levels. Firstly, if we consider the results under continuous and long photoperiods. In several experiments we have shown that exposure of rainbow trout to constant long days or continuous light produces a 1—2 month advance in spawning, a period length which is significantly different from the normal 12 months. However, continued exposure of the fish to the same constant photoperiods produced further spawnings at 5—6 month intervals (BROMAGE *et al.* 1984; DUSTON and BROMAGE 1983, unpubl.). Similar repeat cycles under constant long days have also been reported by SCOTT *et al.* (1984). At present we have followed the same group of fish over 4 successive reproductive cycles and have found that the spawning times of the different members of the group became progressively less synchronised with each successive cycle (BROMAGE *et al.* 1984; DUSTON and BROMAGE 1983, unpubl.). Although this rhythm would superficially appear to be "free running", its period-length probably prevents it from being described as circannual.

Whereas long days in the first instance advance maturation by 2 months, exposure of fish to constant short days from February onwards in a December-spawning strain produces a 1—4 month delay in the time of the next spawning (Figs. 4, 6, h and 9). However, if maintained under the same short photoperiod, these fish then assume an annual periodicity up to 4 months out-of-phase with the natural cycle (DUSTON and BROMAGE 1983, unpubl.; BROMAGE *et al.* 1984). The same fish have now been observed over a 3—4 year period and although a full evaluation of the hormonal and spawning cycles has, as yet, not been completed, it would appear that the period lengths of the rhythms are significantly different from 365 days "*i.e.* the rhythms are free-running with a circannual periodicity. As this rhythm is capable of entrainment, it is concluded that the differential effects of long and short days on spawning time, during the early and later portions of the cycle (Fig. 7), are due, respectively, to phase-advancements and delays of this endogenous circannual rhythm and not to a direct effect of photoperiod on maturation."

VI. ACKNOWLEDGMENTS

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The Baltic Salmon: Ecological and Economic Evaluation of a Natural Resource

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ABSTRACT

Ecologists and economists try to incorporate contributions from the environment to the human society into the evaluating process. Ecologists seem to favour measures based on physical parameters such as energy, while many economists favour the cost/benefit approach. These approaches are described and exemplified by the exploitation of the Baltic salmon from the offshore fishery, sport fishery and fish farming. Conventional economic calculations, energy- and cost/benefit analyses and traditional environmental impact assessments applied to different rearing and fishing strategies can all contribute usefully to a sound resource management of the Baltic salmon.

I. INTRODUCTION

The Baltic salmon is a highly valued natural resource. To maintain this resource for human utilization in the long run, it is necessary to preserve the genetic diversity of the wild population. Human perturbations of salmon habitats and exploitation of the salmon have led to a critical situation for both reared and naturally reproducing populations.

About 20 of the original 70 Baltic salmon rivers remain today (KARLSTRÖM 1984). The natural production was about 7.25 million smolts at the beginning of the century, 1.9 million in 1970 (CHRISTENSEN and LARSSON 1979) and has decreased to between 900,000 and 600,000 smolts per year (ANON. 1985 a, b).

During the last 30 years, artificially reared smolts have been released into the Baltic to compensate for the loss of natural river production of salmon mainly attributed to hydro-electric power plant construction (JOHANSSON 1981). Today about 70—80 % of salmon smolt entering the Baltic are artificially reared (ANON. 1985 a).

The mortality of salmon during the first year after release is about 85 % (LARSSON 1984). Fifty-five percent of the remaining salmon are caught entering their second winter at sea and 65 % entering their third (JOHANSSON pers. comm.).

The situation for the natural population is critical, especially from a genetic perspective. The densities of parr have decreased considerably in rivers with natural production of salmon (in some rivers up to 90 % since the 1960's). It is likely that certain strains of salmon have already gone extinct (KARLSTRÖM 1984).

The number of females available for artificial breeding purposes has also decreased. In some rivers it is below the number required to maintain the hatchery reared stocks (FOLKE 1986) and has been below the limit for inbreeding (JOHANSSON pers. comm.).

The main reasons for the low numbers of both wild and reared spawners seem to be the intense activity of the offshore fishery and an increased coastal fishery in areas adjacent to rivers with artificial rearing (HANNERZ 1984). Diseases (mainly ulcerative dermal necrosis and a yolk sac fry disease) also negatively affect the wild and reared populations (JOHANSSON 1981). The quality of the smolts released is also important (JOHANSSON pers. comm.).

Furthermore, the offshore fishery using selective gear, catches the fastest growing individuals and as a result the average size of the salmon has decreased. It is also possible that genetic deterioration has reduced the homing ability (STABELL 1984).

There is an obvious need for upgrading the management of Baltic salmon stocks. Rather than implying a technological solution for the problem a combined ecological/economic analysis is suggested to re-evaluate the various fishing and rearing strategies currently in use, including the
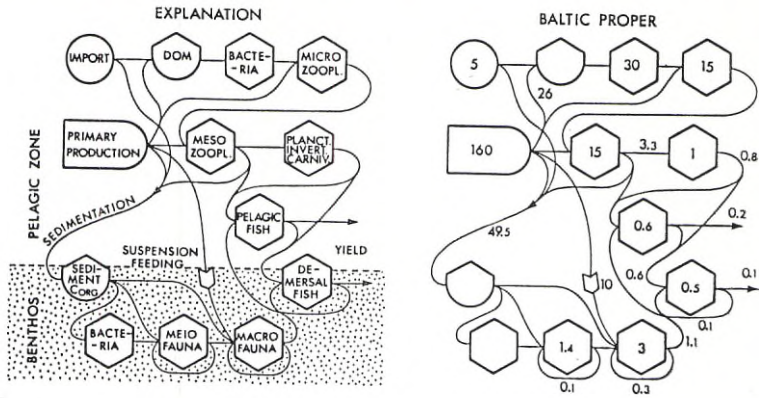
Fig. 1. Energy flow diagram for the Baltic Proper. Flows enter symbols at left, exit at right. Figures (gC m^{-2}yr^{-1}, 1gC=40—45 kJ) inside symbols are annual production, those outside, annual flows (ELMGREN 1984).

evaluation of natural salmon production and natural salmon habitats.

In the present study two approaches of environmental evaluation, the energy- and the cost/benefit analysis are described and discussed in relation to the exploitation of the Baltic salmon.

II. THE ENERGY APPROACH

Some ecologists and physicists (*e.g.* ODUM 1971, SLESSER 1978) suggest that one useful way to reveal the contributions from natural ecosystems to the human society is to study the flows of energy· The object of the analysis is to obtain a better understanding of environmental processes using energy as a common denominator. Energy analysis gives a quantitative description of the relative importance of different compartments and interactions in the system. This is illustrated in Fig. 1.

Ecological processes in the system measured by energy flows are subject to thermodynamic constraints. Thus, inconsistencies in our understanding of system functions might be revealed by studying these flows. Furthermore, this type of analysis makes it possible to compare systems and reveal differences between them. A major problem with energy flow studies, as with any ecosystem study, is to set the boundaries of the system, another is describing the mechanisms controlling the system.

Ecosystem theories based on energy transformation and energy quality are still in their infancy, although theories based on energy transformation

and energy quality concepts are in continual development (COSTANZA 1980, ODUM 1983).

The energy approach uses the *laws of thermodynamics*. The first law implies that energy outputs from the system must equal inputs minus storages within the system. The second law implies that much of the energy transferred between system components will be dissipated.

Some energy ecologists use the term *embodied energy* for the total energy required for the production of environmental goods and services. Physicists use the term *exergy* to combine the first and second law of thermodynamics. K. E. ERIKSSON (1984) defines exergy as "the maximal amount of work which may be extracted from a system as it tends to equilibrium with the environment". Ecologists often use gross photosynthesis as a measure of total system work.

The energy in the form of sunlight contains a lot of exergy (about 96 %) but is very dilute. Photoautotrophic organisms (mainly plants) transform this solar exergy to chemically bound exergy. In an ecosystem the sun forces a flow of exergy, bound in material, through a food web where each connection corresponds to a population, which by consuming exergy from its part of the flow maintains and develops its structure. In every transformation of energy a part of the exergy is lost as heat (low exergy content). This is symbolised by the heat sink in Fig. 4 (the heat sinks in Fig. 1 are not drawn, although they exist). The same amount of energy entering the system will sooner or later leave the system as heat. Only a fraction of the energy can do work.

The flux of energy is necessary for the organization of matter into living systems, the maintenance of these systems and the cycles and transfers of nutrients and materials (JANSSON and ZUCCHETTO 1978).

According to COSTANZA (1984) the embodied energy approach allows an "energy accounting" with the energy derived from the sun as the primary input to the system. In this way all of the commodities of the system could be valued in terms of embodied energy. There are two different views on how to estimate embodied energy. In the *input-output based* approach the sum of the energy partioned in the system is equal to the energy entering the system. In the *non-partitioned* approach all the by-products within the system have the same embodied energy (ODUM 1983).

The input-output based approach seems to be more consistent with economic accounting (COSTANZA 1980, 1984) and he suggests that ideal market conditions in the economy (*i.e.* perfect competition) would equilibrate embodied energy and market value. Empirical studies of certain sectors of the economy that approximate perfect market conditions showed good correlations of embodied energy and market values (COSTANZA 1980). CLEVELAND *et al.* (1984) used the input-output approach to examine energy use in the United States in relation to United States' economic activity. They suggested how some economic problems can be understood more clearly by explicitly accounting for the physical constraints imposed on economic production. However, according to ODUM (1984) the input-output approach assigns only part of the necessary energy for a process to a pathway within the ecosystem. ODUM (1983) argued that although less energy remains within the system compared to the energy entering the system, the quality of that energy increases in the sense that it can amplify and accelerate other energy flows. In other words, he suggests that species higher in the food chain develop feedback mechanisms which affect species in lower trophic levels in such a way that they can operate more efficiently. According to GOLLEY (1984) ecosystems tend to move from a condition of low complexity, dissipating relatively large amounts of high order energy toward a condition of higher complexity, dissipating large amounts of lower order energy.

III. THE COST/BENEFIT APPROACH

With the cost/benefit approach, the economist tries to identify and quantify environmental effects and evaluate them in monetary terms. Individual preference theory, briefly described below, is accepted as the basis for defining and measuring the gains and losses in welfare associated with alternative environmental policies (FREEMAN 1979).

Cost/benefit analysis has its roots in *neo-classical welfare theory* developed by economists. In this theory the *tastes and preferences* of individuals are fundamental for the evaluation of commodities and services. It is assumed that the individual is rational and chooses the combination of commodities and services that, at a certain budget, render him the highest satisfaction. His wants and needs are reflected in demand curves. A demand curve for a certain commodity is derived from the relation between the price of the commodity and the quantity demanded. The demand curve shows how much of the commodity will be purchased (per unit of time) by the consumer in the market at each possible price (given that the level of money income of the consumers and the prices of other commodities are held constant) (MANSFIELD 1982).

If the market price of a commodity such as salmon is 100 SEK, Fig. 2 shows that there are individuals prepared to pay a higher price per kg salmon. These individuals gain a surplus called the *consumer surplus* illustrated by the shaded area in Fig. 2.

The consumer surplus is defined as the difference between how much people are *willing to pay* for the commodity in question and how much they actually pay (MANSFIELD 1982). The consumer surplus is a measure of welfare and is used to estimate welfare changes in monetary terms. This is exemplified in Fig. 3.

If the price of the commodity increases from p0 to p1 the consumers will suffer a welfare loss corresponding to the shaded area in Fig. 3.

SEK PER KG SALMON
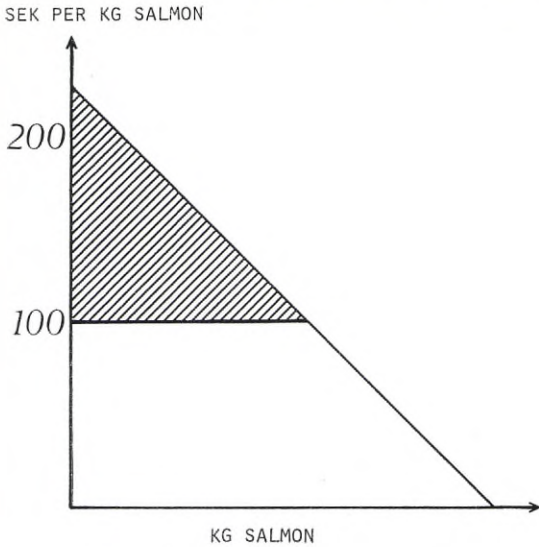
Fig. 2. Demand curve and consumers' surplus.

Environmental economists use the same approach as described above when estimating the value of "commodities" such as clean water or a river with salmon. These types of products *i.e.* environmental resources, normally have no market price and thus the whole area under the demand curve is equal to the consumer surplus.

PRICE PER QUANTITY
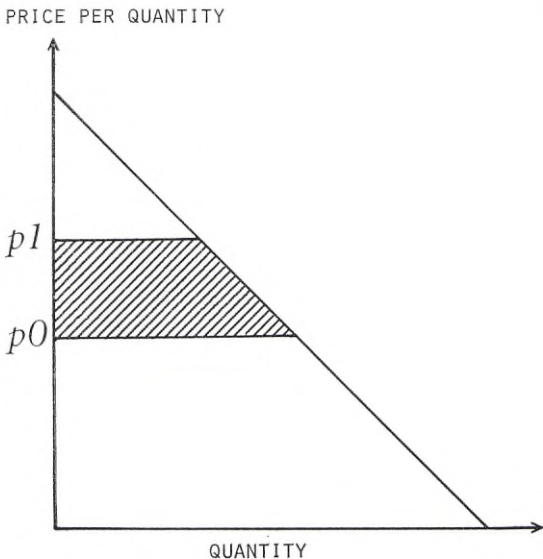
Fig. 3. Demand curve illustrating a welfare change, in this case a decrease in consumers' surplus.

The difficulty in the monetary valuation process of an environmental resource lies in estimating the demand curve since there are normally no markets for environmental "commodities". Environmental economists try deriving these demand curves, *i.e.* revealing peoples' willingness to pay, by studying market data for commodities associated with the environmental resource in question or by posing questions to people, directly or through surveys, about their willingness to pay for using or preserving the resource.

IV. ENERGY ANALYSES APPLIED TO OFFSHORE FISHERY AND FISH FARMING

JANSSON and ZUCCHETTO (1978) studied the energy, economic, and ecological relationships for the Island of Gotland. In this study, the Gotland fisheries were evaluated in energy terms (Table 1).

JANSSON and ZUCCHETTO (1978) calculated the primary production in the Baltic required to support a given catch of fish, by expressing the catch in energy units and by using thermodynamic and trophic food chain concepts (Fig. 4).

In Fig. 4, each species of fish caught is connected through a food chain to phytoplankton. For each species a part of the energy ingested is converted to heat and the remaining into additional growth. This food chain is of course a simplification

Table 1. *The salmon catch in the Gotland fisheries 1920, 1944 and 1973 in weight, energy value and protein value* (GJ=10^9J) (JANSSON and ZUCCHETTO 1978).

Measurement	Year		
	1920	1944	1973
weight (10,000 kg)	34	87	259
energy value [1] (GJ)	306	783	2331
protein value [2] (GJ)	110	282	840

[1] the energy value of salmon, internal organs excluded=8.99 kJ g^{-1} (ABRAHAMSSON 1976) (1 kcal= 4.187 kJ, 1 kWh=3.600 kJ).

[2] protein value assumed to be 17.16 kJ g^{-1}, weight of protein per weight of salmon=0.189 g g^{-1}.
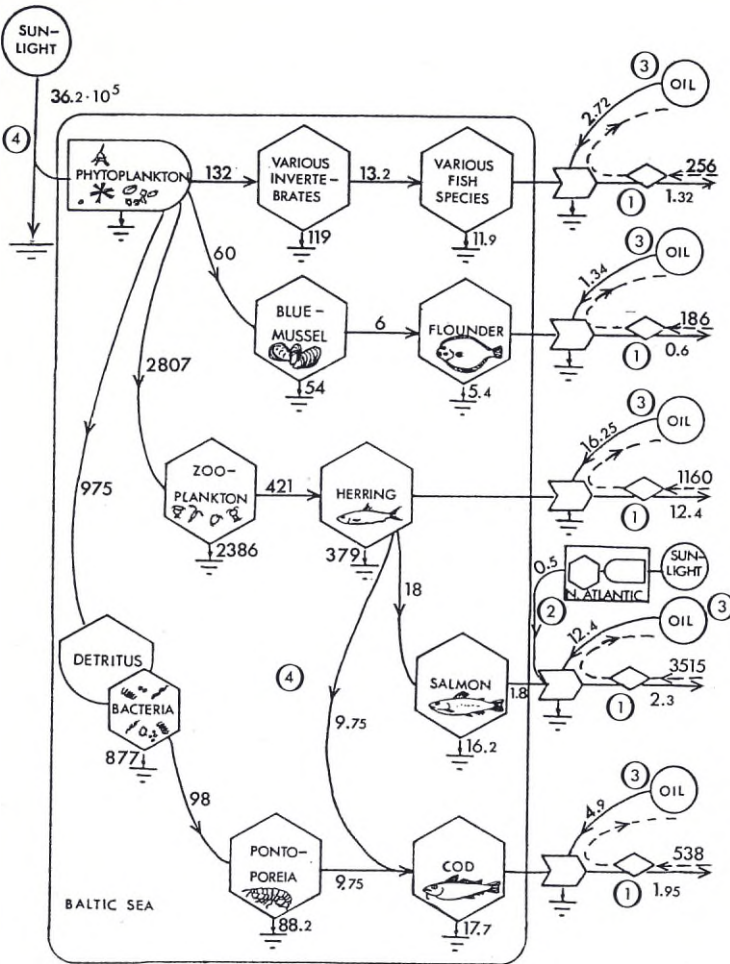
Fig. 4. Food chain of the Baltic coupled to the Gotland fisheries in 1973, by the expenditure of oil. Energy flows ($\longrightarrow$) in TJ (10^{12}), money flows (- - - - $\rightarrow$) in 10,000 SEK. Circled numbers refer to notes (Jansson and Zucchetto, 1978).

① The energy value of the fish was calculated from the weight of the catch and energy values per weight (Abrahamson, 1976) see Table 1. Economic flows associated with the catch were obtained from fishery statistics for 1973.

② The catch of salmon in the North Atlantic was approximately 22.2 % of the total salmon catch.

③ The amount of diesel fuel used for salmon fishing was 349.2 m³·35.6 GJ=12.4 GJ and for trawling 630 m³·35.6 GJ=22.43 GJ. The percentage by species for trawling was cod=16.9 % herring=70.3 %, flounder=2.9 %, other species=9.9 %. 20.4 m³ diesel and 66 m³ were used in the coastal fisheries=2.8 GJ and the percentage allocation by species was cod=40 %, herring=17.5 %, flounder=23.9 %, other species (salmon excluded)=18.6 %. Energy cost was allocated by these percentages. Thus, the oil flows represent direct fuel costs.

④ Trophic efficiencies are assumed to be 10 % in the simplified linear foodchain except for zooplankton assumed to have a 15 % efficiency. The total net primary production (NPP) required amounted to 3,974 GJ and the gross primary production (GPP) was estimated to be 5,961 GJ. Ackefors and Lindahl (1975) measured GPP in the Baltic to about 6,279 kJ m⁻²yr⁻¹. Thus, the area of the Baltic required for this production was estimated to 5,961 GJ/6,279 kJ m⁻²yr⁻¹=9.49·10⁸ m². The average solar insolation was 10,666 kJ m⁻²day⁻¹ resulting in a total solar radiation supporting the Gotland's fisheries of 10,666·365·9.49·10⁸=36.2·10¹⁴kJ·yr⁻¹.

"since the reality is a food web in which each of the straight line food chains transfer food energy between them" (Jansson and Zucchetto 1978). The energetic basis for the Baltic ecosystem is also provided by benthic macrophytes and microalgae, and by allochthonous organic matter entering the Baltic through rivers and as a direct municipal and industrial waste input (Elmgren 1984). This would result in an even higher amount of solar energy needed to produce the salmon.

Table 2. *Energy calculations of fish farming in net pens and of the Gotland salmon fishery in 1979, in GJ (10^9J).*

Input—output	Fish farming		Gotland fishery	
Energy expenses[1]				
investments	47	(2 %)	—	
labour	—		—	
fuels[2]	6		16610	(74 %)
smolt input	638[3]	(31 %)	1600[4]	(7 %)
fish food	1374	(67 %)	—	
miscellaneous	(< 1)		4150[5]	(19 %)
	2065		22360	
Energy yield				
fish meat[6]	110		1000	
fish waste[7]	18		170	
	128		1170	
Yield/Expenses	0.062		0.052	

[1] energy required for production and energy content.
[2] only energy content.
[3] energy required for production of 25,400 smolts with a weight of 75 g/smolt and 10,900 smolts with a weight of 500 g/smolt, energy content in smolts excluded.
[4] energy required in artificial rearing of smolts necessary to produce catch. Production of 1,000 smolts = 4.72 GJ. Fiftyfour percent of reared smolts released by Sweden and 270 kg salmon per 1,000 smolts released caught by Swedish fishermen.
[5] corresponding to 25 % of the expenses in fuels.
[6] 4,320 kJ/kg.
[7] 720 kJ/kg.

A comparison of the energy content in the salmon catch of 1973 and the amount of fuel used for fishing salmon in the same year revealed that the fuel energy required was about 5 times greater than the energy content in the salmon catch. However, the financial return was large resulting in an economic value of salmon of $1.53 \cdot 10^{-3}$ SEK $\cdot$ kJ^{-1}.

ADLING (1981) calculated energy content and energy expenditures in the Gotland offshore fishery for salmon in 1979 and compared this with a similar calculation for fish farming in net pens (Table 2).

The calculation of the Gotland fishery corresponds to the catch of 170 tonnes of salmon in 1979. The calculation for fish farming corresponds to four rainbow trout (*Salmo gairdneri*) farms in Sweden. The farms were situated in both fresh-, brackish- and saltwater. The average length of the rearing period was 5.5 months.

A comparison of these two analyses showed some 20 % less energy required in fish farming in net pens than in the Gotland salmon fishery, when related to the yield of salmon. Fish food was the dominating energy expenditure in fish farming while fuels dominated in the offshore fishery. It is interesting to notice that investments in fish farming in net pens were only about 2 % of the energy expenditures. Unfortunately, ADLING (1981) did not calculate the investments in boats and equipment in the Gotland salmon fishery. In economic terms, these investments correspond to about 70 % of the total expenses in salmon fishing (HANNERZ 1984, Table 33). Adling's calculations concern mainly auxilary energies such as fossil fuels. The solar energy that drives natural systems is not estimated, although discussed in his article. The work of natural systems is crucial both for the production of fish in the sea and for maintaining a suitable environment for net pen rearing.

V. COST/BENEFIT ANALYSES AND SPORTS FISHERIES

Cost/benefit analyses have often been used to estimate the monetary contribution to welfare derived from salmon rivers or lakes. Several studies have calculated this contribution by estimating the recreational value in terms of willingness to pay.

In Lake Taneycomo in the United States, the sports fisheries for rainbow trout (*Salmo gairdneri*) were threatened by discharge of oxygen deficient water from an upstream reservoir. WEITHMAN and HAAS (1982) estimated the value of the fishery to anglers using the travel-cost method (for explanation see CLAWSON and KNETSCH 1966 or FREEMAN 1982). In their study the welfare gain, *i.e.* the consumer surplus, was calculated to 2.9 million dollars per year (Fig. 5).

According to WEITHMAN and HAAS (1982) the consumer surplus measure represents the value of the rainbow trout fisheries to anglers fishing at Lake Taneycomo, but does not include the benefits to the region. They estimated the value of recreational fisheries to regional development by the income multiplier method (see WEITHMAN and HAAS, 1982 for explanation) and found that the
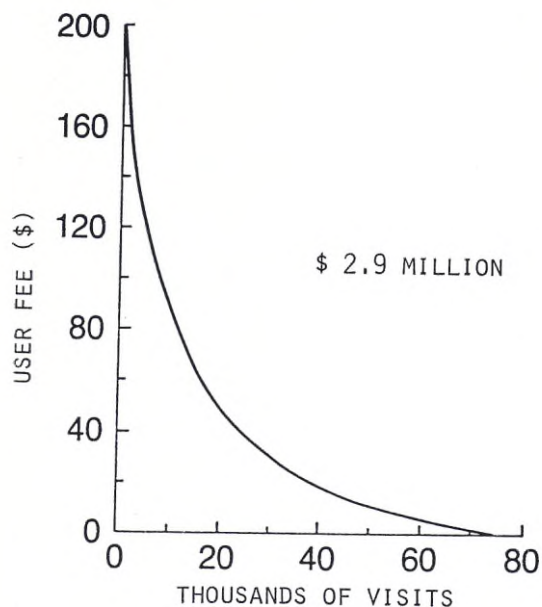
Fig. 5. Demand curve for trout fishing at Lake Taney-como. The area under the curve represents benefits to anglers in excess of their expenses *i.e.* consumers' surplus (WEITHMAN and HAAS 1982).

sportfishermen contributed 7 % of the economic activity in Taney County.

The welfare benefit/cost ratio derived from sports fisheries was about 22:1 when comparing the income multiplier value to the costs of stocking rainbow trout. The corresponding ratio using the consumer surplus measure was 7:1.

MEYER (1974 in GREENLEY *et al.* 1982) surveyed the recreation and preservation values related to salmon in the Fraser River in British Columbia, Canada. He asked the residents of the river system to estimate the values of different environmental and recreational services provided by the Fraser River. The total annual preservation value was estimated at 100.6 million CAD (223 CAD/year and household) and the total annual recreational value was estimated at 185.6 million CAD giving a total annual preservation and recreation value of the Fraser River of 286.2 million CAD/year.

STRAND (1981) estimated the value of the sport fisheries in the salmon river Gaula in Norway. The consumer surplus *i.e.* the welfare gain for the average angler was estimated at about 1.150 NOK (1974). The total value of the sport fishery was

estimated at 7.5 million NOK/year. The recreational value per kg salmon caught by a sports fisherman, was 8 times higher than the fisherman's price.

In another study from Norway the travel-cost method was used for estimating the recreational fishing value in a salmon river, resulting in a willingness to pay for access to the river of 100—200 NOK/day and person (WAAGE 1981).

In the south of Norway many sportfishing areas have been destroyed by lake and stream acidification. All fish have died in an area of 13,000 km², and all fish are likely to disappear in an area of at least 20,000 km². In 1979 about 750,000 persons older than 15 years were active sportfishermen in southern Norway. If all opportunities for sport fishing were to disappear, the annual loss of welfare has been estimated to about 700 million NOK (WAAGE 1981).

In some studies the total expenditures of anglers have been used as an expression of the value of sports fisheries.

PAULSSON and STENSON (1983) surveyed the value of sport fishing in the River Dalälven in Sweden. According to their calculations the recreational value, expressed as the total expenditures of anglers, was 845 SEK/kg salmon. Sportfishermen valued the salmon 16 times higher compared to the fisherman's price for salmon.

The corresponding value was 6.3 times greater in a study of sport fishing in the River Teno running through Norway and Finland (NIEMELÄ *et al.* 1982).

VI. DISCUSSION

Today, a major portion of natural production of salmon is compensated for by hatchery production, releasing salmon into the Baltic for artificial stocking. Some of the hatchery production is used in commercial sea ranching and fish farming. The Baltic salmon are exploited by the offshore fisheries that capture 75—80 % of the total salmon catch. Coastal fisheries capture 20—25 % and 2 % are caught in the river fisheries (FOLKE 1986).

The couplings between the Baltic salmon, its environment and the human economy are sum-
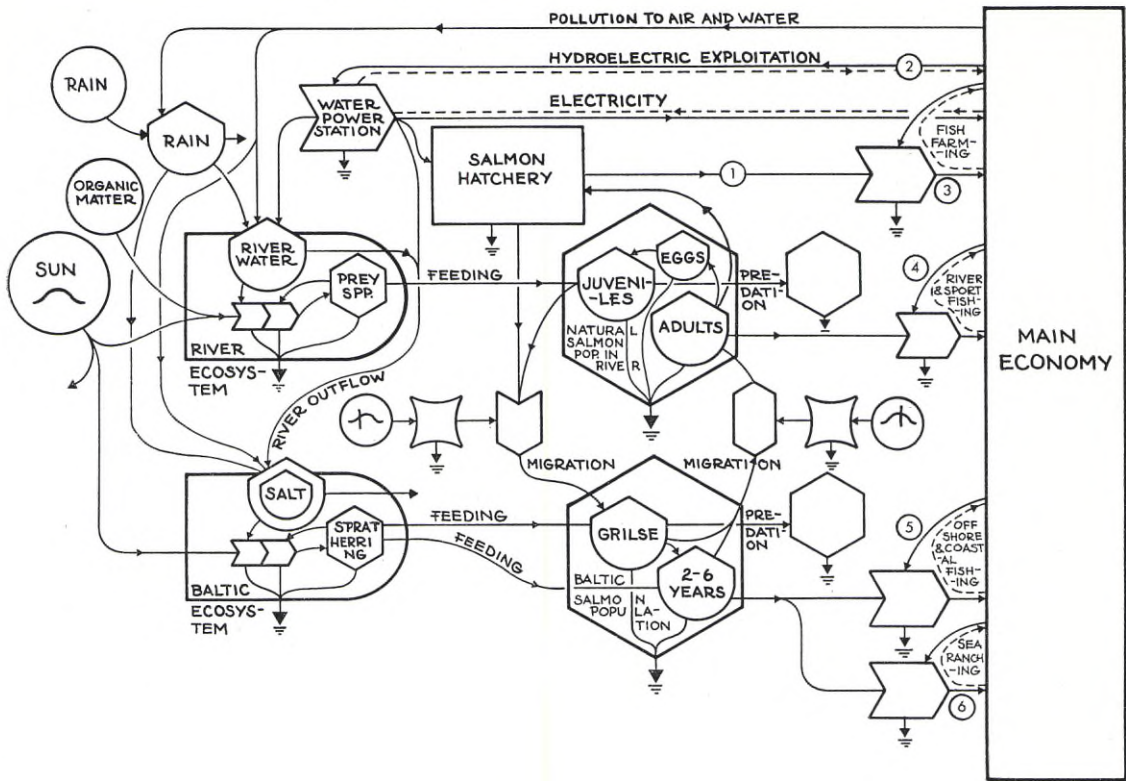
Fig. 6. Model of the Baltic salmon and its environment coupled to the activities of man.

marized in a conceptual model given in Fig. 6. The model shows the life cycle of the Baltic salmon, the natural ecosystems and the flows between systems. Human interference and the couplings with the economy are illustrated by *1;* artificial stocking and rearing of salmon in hatcheries substituting the river life of the salmon, mainly destroyed by the constructions of hydroelectric power stations *2;* pollution to air and water as a result of human activities *3;* fish farming *4;* sports and commercial fisheries in the rivers *5;* commercial fisheries in the sea and on the coast and finally *6;* sea ranching for human consumption.

In recent years commercial sea ranching has been suggested as an alternative to the offshore fisheries. In sea ranching the salmon are caught returning to the coast from where they were released as smolts. Switching from offshore to coastal fishing, this method would increase the survival of both naturally reproducing and artificially stocked populations. The result would

probably be more salmon returning to spawn in both rivers and hatcheries.

This might develop sports fisheries of great economic importance to the regions concerned. For example, sport fisheries in Scotland accounted for 97 % of the monetary turnover of the total Scottish salmon fisheries but only 15 % of the total salmon catch (SHAW 1983 cited in HANNERZ 1984). In Sweden sports fisheries are badly developed.

The reduced mortality in sea ranching with delayed release (smolts released in autumn instead of early summer to avoid the high postsmolt mortality mainly caused by predation) increases the economic return. LARSSON *et al.* (1979) estimated that a 5 % reduction in mortality is equivalent to about 8 million SEK. JOHANSSON (1981) estimated a 10 % reduction up to the adult stage to be equivalent to 20 million SEK. Furthermore, fishing expenses, in both energy and in monetary terms, could be greatly reduced by obviating the journeys to offshore fishing grounds.

Today about 600 kg salmon are caught out of 1000 smolts released. Sea ranching with delayed release would theoretically increase both recapture rates and mean weight of salmon to about 3500 kg/1000 smolts released, if the offshore fisheries for growing salmon could be switched to a coastal fishery for spawning migrating salmon (ERIKSSON and ERIKSSON 1985). The economics of sea ranching has been discussed by L. O. ERIKSSON (1984).

However, the offshore fisheries are economically important to the salmon fishermen and most of them do not believe in commercial sea ranching. They think it might be difficult to fish with boats in coastal waters in competition for space and fish with tourists and land owners. Another problem is the increased amount of algal blooms in coastal waters.

The probabilities for a greater survival of both the natural population and the salmon reared for artificial stocking in the Baltic will likely be enhanced by the increasing amount and quality of reared salmon produced outside the Baltic Sea area, that will cause a decrease in the profits in the Baltic offshore fisheries. About 50,000 tonnes of Atlantic salmon will be reared in Norway in 1987 (B. MYRSETH pers. comm.) to be compared to the total Baltic salmon catch of 2,000—2,500 tonnes in the 1980's and the corresponding Swedish catch of 550—650 tonnes (ANON. 1985 a). In Sweden, 25 tonnes of Baltic salmon are reared in fish farms. Rainbow (*Salmo gairdneri*) dominates in Swedish fish farms and in 1982 about 2,400 tonnes were produced (CEDRINS 1984).

The quality of salmon is very important to the consumer. According to sales, today's consumer most values the reared Norwegian Atlantic salmon. Salmon caught in the fishery have about the same value as large reared rainbow, and Pacific species are regarded as low quality salmon (CEDRINS pers. comm.).

Calculations of different production forms and exploitation patterns would be useful to get an overall economic picture of the Baltic salmon as a natural resource· Also, the contributions of natural ecosystems in producing and maintaining the wild and artificially reared salmon population ought to be evaluated. Two methods for this evaluation have been discussed. In my opinion the cost/benefit approach is interesting when the aim is to evaluate peoples' preferences, such as the preferences for sportfishing. However, the method does not illuminate the production values of natural ecosystems. The energy approach might be one way to include such aspects. Energy flow analysis this far appears to be one of the best ways to describe and analyse natural ecosystems. It can provide a basic description of the connections within the system, but it does not necessarily reveal the functional aspects. A very important aspect that is hard to evaluate in energy terms is the quality concept. It is not obvious that the energy quantity in a group of organisms corresponds to qualitative functions of these organisms. ODUM (1983) has discussed the quality aspects, but his theories have not been verified. Furthermore, energy is not always the limiting factor for system production. Material flows (such as nutrients), genetic or biological constraints may limit the production. FIELD *et al.* (1985) question the applications of thermodynamic laws on ecological systems. They state that "it is certainly useful to talk about mass and energy flows in such systems, and even in some cases to associate "forces" as causing these flows" but continue that "the existence of forces and flows does not guarantee the properties normally associated with thermodynamic equilibrium or thermodynamic behaviour".

Environmental production and environmental aspects are often disregarded in economic calculations. In my opinion, the possibilities for a sound resource management are reduced if the contributions of natural production are not considered and explicitly expressed in the evaluation. Energy flows in combination with material flows and other biological information would increase the understanding of natural ecosystem production. This understanding in combination with conventional economic analyses perhaps complemented by cost/benefit analyses could all contribute usefully to a sound resource management of the Baltic salmon. The present study will be followed by further ecological and economic analyses concerning the evaluation of the Baltic salmon and its relationships with natural and man made environments.

VII. ACKNOWLEDGMENTS

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Salmon Ranching Experiments in The River Imsa: Effects of Day And Night Release and of Sea-Water Adaptation on Recapture-Rates of Adults

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ABSTRACT

The aims of this paper were to test differences in the recapture-rates of adult Atlantic salmon (*Salmo salar* L.) released as smolts during the day or at night, and to test if sea-water (~ 32 $^0/_{00}$ salt) or brackish-water (~ 10 $^0/_{00}$ salt) adaptation of the smolts increased adult returns. There were no significant differences in the recapture-rate of adults released as smolts during day or night, or between smolts retained for 0 (control) or 2 weeks in sea-water. The recapture-rate decreased significantly for the smolt groups retained for 4 weeks in sea-water before being released. This tendency was further increased for smolts kept for 8 weeks in sea-water. There was no significant difference in adult recapture between the groups kept for 4 weeks in brackish water during smoltification and released with the freshwater controls. The recapture decreased significantly when the brackish-water groups were retained for an additional 4 weeks in sea-water. The number of precocious males returning to the River Imsa the same autumn increased when the smolts were retained in sea-water for more than 4 weeks before release.

I. INTRODUCTION

Several factors associated with the production and release of hatchery smolts account for variability in survival and return of adults. Among these factors are physiological and behavioural preparation for hypo-osmotic regulation and migration (SAUNDERS 1983), and release at a place where and a time when predation is at a minimum. A recent study from the River Eira, Norway, suggested that survival of the smolts might be improved if they were kept a few weeks in brackish water before release (JENSEN 1979). One reason for this may be that sea-water adapted smolts leave the fjord faster than smolts which are not sea-water adapted. Predation is probably smaller in the open sea than in the estuary.

Wild smolts usually migrate during dark hours (THORPE and MORGAN 1978), which is also the case in the River Imsa, Norway (HANSEN and JONSSON 1985), where the present study was performed. The nocturnal activity maxima of the smolt migration may be a predator avoidance behaviour (SOLOMON 1982). However, hatchery smolts released in the River Imsa started their seaward migration immediately after they were released. Those released during the day moved downstream in day-light, whereas those released during the night moved downstream in the dark (HANSEN and JONSSON 1985). Hatchery smolts are probably most vulnerable to predation shortly after release. Thus, smolts released during night might have higher survival than those released during day, as they may recover from the handling stress in darkness.

Aims of the present paper were therefore to test (1) if there were differences in adult recapture of salmon released as smolts during day and night, and (2) if sea-water adaptation of the smolts affected the survival and return of adults. To do this we released comparable smolt groups during day and night, and smolt groups which had been kept in sea-water for varying lengths of time before release.

II. METHODS

The smolts were released at the outlet of the River Imsa, near Stavanger, south-western Norway (HANSEN *et al.* 1984). A fish trap 100 m above the river outlet catches all ascending salmon. The smolts were reared in the Ims hatchery, in River Imsa water until smolting. The smolts were

anaesthetized with chlorobutanol, total length measured (0.1 cm), and tagged individually with numbered Carlin tags (CARLIN 1955). After tagging the smolts were allowed to recover for at least 2 weeks before release. When testing differences between day and night releases, smolts from 6 Norwegian stocks (termed after their river of origin) were used. One group of each stock was released at noon (12.00, summertime), the other groups were released at midnight (24.00). When testing the importance of sea-water adaptation for the survival and return of adults, 6 stocks were used in 1981, and 3 stocks in 1982. During the sea-water adaptation, the fish were put directly into brackish water (ca. 10 ⁰/₀₀ salt) and then gradually during one week adapted to sea-water (ca. 32 ⁰/₀₀). The recaptures were partly reported by fishermen, and partly made in the fish-trap in the River Imsa. In the results, we have pooled the recaptures from the sea fishery and the trap.

III. RESULTS

There was no significant difference in recapture-rates of adults of smolts released during the day or at night (Table 1, χ^2-test of the frequencies, $Z^*=6.00$, 6 d.f., $P > 0.3$), nor between smolts retained 0 and 2 weeks in sea-water before release (Table 2, $Z^*=5.04$, 5 d.f., $P > 0.4$). In the latter case, however, for 4 of 5 stocks the recapture-

Table 1. *Recapture of Atlantic salmon (Salmo salar) released as smolts at 12.00 (day) and 24.00 (night) May 7, 1981, at the outlet of the River Imsa, Norway. Mean smolt length (L) and total range of variability of the stocks are given in cm.*

| Stock | Release | | | | Recapture | |
	Time	No	L	Range	No	⁰/₀
Imsa	Day	977	16.6	13—33	102	10.4
	Night	954	16.3	13—19	93	9.7
Sandvik	Day	974	16.6	13—35	51	5.2
	Night	976	16.7	13—31	59	6.0
Figgjo	Day	968	16.9	13—26	83	8.6
	Night	962	17.7	13—36	100	10.4
Alta	Day	972	19.0	13—34	47	4.8
	Night	970	17.8	13—37	57	5.9
Eira	Day	980	20.5	13—34	50	5.1
	Night	978	21.0	14—35	40	4.1
Suldal	Day	977	17.2	13—33	43	4.4
	Night	977	19.1	13—36	53	5.4

Table 2. *Recapture of Atlantic salmon (Salmo salar) with sea-ages 0+ and ≥ 1+ years, released as smolts (2+) in 1981 at the outlet of the River Imsa. The smolts were retained in sea-water (ca. 32 ⁰/₀₀ salt) from 0 to 8 weeks. Mean smolt length (L) and total range of variability of the 6 stocks are given in cm.*

| Stock | Release | | | | | Recapture | | | |
| | Retained | Date | No | L | Range | 0+ | | ≥ 1+ | |
						No	⁰/₀	No	⁰/₀
Imsa	0 week	May 7,	1931	16.5	13—33	2	0.1	195	10.1
	2 weeks	May 29,	977	17.8	13—34	3	0.3	113	11.6
	4 weeks	June 9,	1942	17.9	13—36	2	0.1	115	5.9
	8 weeks	July 7,	969	18.5	13—37	12	1.2	10	1.0
Sandvik	0 week	May 7,	1950	16.7	13—35	4	0.2	110	5.6
	2 weeks	May 29,	948	18.4	13—35	3	0.3	53	5.6
	4 weeks	June 9,	974	17.7	13—34	2	0.2	34	3.5
Figgjo	0 week	May 7,	1930	17.3	13—36	1	0.1	183	9.5
	2 weeks	May 29,	979	19.6	13—36	2	0.2	101	10.3
	4 weeks	June 9,	976	19.4	13—36	15	1.5	74	7.6
Alta	0 week	May 7,	1942	18.4	13—37	6	0.3	104	5.4
	2 weeks	May 29,	952	19.3	13—35	2	0.2	64	6.7
	4 weeks	June 9,	974	20.5	13—35	3	0.3	66	6.8
Eira	0 week	May 7,	1958	20.8	13—35	6	0.3	90	4.6
	2 weeks	May 29,	330	23.4	16—33	0	0	20	6.1
Suldal	0 week	May 7,	1954	18.2	13—36	9	0.5	96	4.9
	4 weeks	June 9,	978	21.7	13—36	18	1.8	28	2.9

Table 3. *Recapture of Atlantic salmon (Salmo salar) with sea-ages 0+ and ≥ 1+ years, released as smolts (2+) in 1982 at the outlet of the River Imsa. The smolts were kept for 4 weeks in brackish-water (ca. 10 ⁰/₀₀ salt) during smoltification and retained for 0 to 7 weeks in sea-water (ca. 32 ⁰/₀₀ salt) before release. The control smolts were kept in freshwater only. Mean smolt lengths (L) and total range of variability of the 3 stocks are given in cm.*

| Stock | Release | | | | | | Recapture | | | |
| | Retained | Date | No | L | Range | 0+ | | ≥ 1+ | |
						No	%	No	%
Imsa	Control	May 19,	1930	24.7	14—32	3	0.2	98	5.1
	0 week	May 19,	1943	25.2	14—35	10	0.5	90	4.6
	4 weeks	June 22,	1891	25.5	14—39	13	0.7	69	3.6
	7 weeks	July 9,	900	28.3	15—34	33	3.7	15	1.7
Sandvik	Control	May 19,	949	22.5	13—32	5	0.5	88	9.3
	0 week	May 19,	965	19.7	13—33	9	0.9	77	8.0
	4 weeks	June 22,	979	23.4	13—34	9	0.9	53	5.4
Figga	Control	May 19,	1733	17.6	13—41	4	0.2	26	1.5
	0 week	May 19,	965	17.7	14—34	1	0.1	11	1.1
	4 weeks	June 22,	440	21.2	13—34	1	0.2	1	0.2
	7 weeks	July 9,	958	35.0	28—41	23	2.4	38	4.0

rates were higher than for the controls, and equal to the control for the fifth stock (Wilcoxon's signed-ranks test for 2 groups of paired observations, $P = 0.0625$). The recapture-rates decreased for smolts retained 4 weeks in sea-water before release ($Z^* = 63.47$, 5 d.f., $P < 0.001$). This tendency was further increased in smolts kept 8 weeks in sea-water ($Z^* = 80.72$, 1 d.f., $P < 0.001$).

There was no significant difference in recapture-rates between smolts kept 4 weeks in brackish water during smoltification and the controls kept in freshwater (Table 3, $Z^* = 2.09$, 3 d.f., $P > 0.5$). These smolt groups were released together. When brackish-water adapted smolts were retained for 4 weeks in sea-water, the recapture-rates decreased ($Z^* = 19.89$, 3 d.f., $P < 0.001$). For Imsa smolts kept for 4 weeks in brackish-water and retained for 7 weeks in sea-water before release, the recapture-rate of adults decreased, whereas the corresponding figures for the River Figga smolts increased. However, the Figga smolts were exceptionally large in size compared with the other smolt group. Among smolts kept 7 weeks in sea-water before release, the percentage of fish recaptured at sea-age 0+ increased significantly compared with the controls ($Z^* = 86.56$, 2 d.f., $P < 0.001$). A large part of these fish were sexually mature (precocious) males captured in the fish trap in the River Imsa.

IV. DISCUSSION

We expected that smolts released at night would have better survival to adults than smolts released at day (HANSEN and JONSSON 1985). Our argument is based on the assumption that smolts are most vulnerable to predation shortly after release. However, the adult recapture-rates of the smolts released at night did not differ from those released at day. The most important smolt predators in the estuary of the River Imsa are gulls (*Larus* spp.) and probably various gadoids such as cod (*Gadus morhua*), saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*). The reason why recapture-rates of day and night released smolts did not differ might be an effect of the large number of smolts released together. We have observed that the released smolts school when migrating downstream during day. This may give the fish effective protection against predators (RADAKOV 1973, SOLOMON 1982). This suggestion is supported by our observation that wild smolts associate with shoals of hatchery smolts and descend the River Imsa during day in contrast to the normal nocturnal migration pattern in the system (HANSEN and JONSSON 1985).

We expected higher survival of sea-water adapted smolts. Observations by JENSEN (1979) on Atlantic salmon indicated that sea-water

adaptation of smolts could improve the survival of released hatchery smolts. Our results differ from this. Survival did not differ significantly between smolts kept in brackish water for 4 weeks during the smoltification, for those retained for 2 weeks in sea-water, and for the corresponding freshwater controls. Thus, sea-water adaptation seemed to have little or no effect on smolt survival.

The survival decreased significantly for salmon retained in sea-water for 4 weeks or more during smoltification, despite that they increased in size during the retainment. This result seems to differ from that of ERIKSSON and ERIKSSON (1985) who found that by retaining and feeding smolts in net pens during summer and releasing them in the autumn, the survival to adults was improved considerably. But, whether this improvement in survival was the result of the time of release or of growth during summer is an open question.

The reason for the decreased survival of the retained smolts in our experiments may be that the smolt migration must occur within a short period during spring to give maximum survival. Previous studies in the River Imsa have shown that delayed downstream migration of smolts resulted in decreased survival to adults (HANSEN 1985). Based on successive smolt plantings in the River Indalsälven, Sweden, LARSSON (1977) showed that the optimal time for smolt release was in late May and early June. CROSS and PIGGINS (1982) reported a very low return of wild salmon from the 1980 smolt year-class compared to the returns of released hatchery smolts. They suggested that the main reason was a delay in the wild smolt migration. The high survival of the very large Figga smolts retained for 7 weeks in sea-water, suggests that the smolts are exposed for size dependent mortality factors, *e.g.* predation. However, we have no parallel experiment verifying this result.

For the groups delayed 7 and 8 weeks in sea-water before release, there was a small, but significant increase in return to the River Imsa trap of precocious males compared to all other groups. This increase in male precocity may be a result of our rearing conditions of the retained smolts. From the Baltic, LUNDQVIST and FRIDBERG (1982) observed 7 % male precocity when the smolts were retained in net pens in brackish water

during summer. However, the proportion of precocious males was 90 % when the smolts were retained in freshwater. The maturation of males is correlated with the growth-rate of the fish (THORPE 1986) and the salinity of the water (LUNDQVIST and FRIDBERG 1982).

This study indicates that the survival to adults of released hatchery smolts in the River Imsa is independent of whether the smolts were released during day or night. Furthermore, we could not detect any effect of sea-water adaptation on survival. However, if these smolts were released after being retained for one month or more in sea-water, their survival decreased.

V. ACKNOWLEDGMENTS

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Fish Cage Culture – in which Coastal Environment?

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ABSTRACT

This is a paper from a Swedish research project, "The coastal zone—scientific criteria for planners", which was initiated in 1980 and ended in 1984. The basic goal has been to establish simple yet general scientific methods and criteria for planning, management and control of Swedish coastal waters. That is, evidently, a vast multi-disciplinary task. In this paper the focus is on two specific environmental factors regulating the suitability/unsuitability of coastal areas for fish cages, namely the water exchange and the prevailing bottom dynamic conditions. These two factors should be known when location sites for fish cages are discussed, both from the perspective of the producer and the authorities responsible for the status of the environment. The main purpose of this paper is to demonstrate how the two key factors can be estimated and used in practice. The formulas/methods are only valid for the bioproductive season (May—October) and for small (1—100 km²) coastal areas in non-tidal waters.

I. BACKGROUND AND AIM

This work is part of a research project called "The coastal zone—scientific criteria for planners" (FRISÉN et al. 1980). The inter-disciplinary project has focused on better means of managing small (1—100 km²) Swedish coastal areas. The project was initiated in 1980 and the final field work was done in the autumn of 1983. In Swedish contexts, this has been a major research effort with a yearly budget of about 400,000 US dollars. Here, however, we will not discuss the organizational structure, themes of interest and set-up of the project, merely say that about 150 scientific papers have been published from the project and that the results have been summed up in Swedish in three main reports: (1) Practical coastal ecology (HÅKANSON and ROSENBERG 1985), (2) Water dynamics and bottom dynamics in coastal areas (HÅKANSON et al. 1984), and (3) Fish and bottom fauna in coastal areas—a comparison and biological evaluation (ROSENBERG 1985).

This paper focuses on two key environmental factors (the surface water retention time and the bottom dynamic conditions) regulating the suitability/unsuitability of coastal areas for fish cage culture. Of course, these two factors are not the only ones that have to be accounted for in these contexts; the paper will not, however, discuss, e.g., administrative problems, matters concerning distribution of fish to consumers or organiza-tional infra-structure, technical constructions of cages, fish diseases, water quality criteria, etc. (KARLGREN 1981, PEDERSEN 1982, ENELL and LÖF 1983).

The methods to determine the surface water retention time and the prevailing bottom dynamic conditions (erosion, transportation, accumulation) have been described in HÅKANSON et al. (1984), HÅKANSON (1986) and HÅKANSON et al. (1986) and will not be discussed here, where the linkage to fish farming is in focus.

The Swedish coast is long and diversified. It provides excellent but hitherto only little exploited possibilities for various forms of aquaculture. There is an increasing awareness of this interesting niche and a rapidly growing number of persons, from scientists to producers, have discovered the potentials of aquaculture along the Swedish coast (ACKEFORS et al. 1984).

II. ENVIRONMENTAL KEY FACTORS

To know the retention time is of the utmost importance in many practical issues (concentrations and ecological effects of pollutants from point sources, like fish cages, cannot be predicted without data on the water retention time) and in most ecological issues, since the water exchange sets the framework for the entire biotic life; the prerequisites for life are quite different in coastal

waters where the retention time varies from hours to days to weeks to months. With traditional methods, it is generally very laborious and costly to determine the water retention time in open coasts. The method used in this context is valid for small areas (1—100 km²) unaffected by tide, for the water above the thermo- and/or the halocline and for the productive season (April —October). It cannot be used close to river mouths. It gives one characteristic value (a median) and not a frequency distribution.

The formula for the surface water exchange is (HÅKANSON *et al.* 1984):

(1) $$T = 42.7 \cdot W \cdot E^{-0.71}$$

where

42.7 and -0.71 are empirical constants;

T = the requested retention time (in days) for the surface water;

W = the mean coastal width (km), the larger W, the longer the retention time;

E = the topographical openness (or exposure, in %); the higher E, the faster retention time and vice versa.

To determine the prevailing bottom dynamic conditions at a given natural site, in a strict scientific manner, would require numerous measurements of flow velocity just above the bottom for a long period as well as measurements of shear strength of the sediments. Because this is not generally possible in contexts of coastal planning, one must accept approximations and crude simplifications, such as provided by the subsequent method (HÅKANSON 1986), which like formula (1) is based on certain morphometric parameters which can be determined directly from a bathymetric map.

(2) $$BA + 1 = 101 - (BE + BT) = 11.7 \cdot E^{-0.82} \cdot xm^{0.92}$$

where

BA = the area of accumulation in percent of the water surface;

BE = the area of erosion in per cent of the water surface;

BT = the area of transportation in per cent of the water surface;

xm = the mean slope (%);

E = the topographical openness, or exposure, of the coast (%);

11.9, -0.82 and 0.92 = empirical constants.

This formula enables the determination of areas of accumulation (*i.e.*, bottom areas dominated by fine sediments) and areas of transportation and erosion (*i.e.* areas dominated by mixed and hard sediments). This is important since, by definition, processes of resuspension characterize the areas of transportation, whereas the areas of accumulation are characterized by continuous deposition of fine materials, low water energy and relatively stagnant waters enhancing the risks for formation of anoxic conditions; coasts with areas of accumulation act as pollutant/sediment traps, or "purification plants" for the open waters, since most pollutants appear with a strong affinity for fine materials; coasts without areas of accumulation function as transportation routes for pollutants.

III. NUTRIENTS

The species of primary interest for fish farming are salmonids, such as rainbow trout, salmon and sea trout. The environmental effects of special concern here are an increased dose of nutrients (nitrogen and phosphorus), organic materials, and the oxygen problems that may arise in connection with the degradation of organic materials. The O_2-concentration should preferably never be lower than 4—5 mg per liter for the fish to flourish.

The total P- and N-discharge from a fish cage is generally in the order of 12—22 kg P and 75—95 kg N per ton produced fish and season (ENELL and LÖF 1983, ENELL, pers. comm.). The lower values apply to small fish, which foremost are produced in limnic environments. The higher values are more relevant for marine areas, where most of the large rainbow trout (about 3 kg) are produced. The values are based on today's food types and are given per production quantity and not per maximum amount of fish in a cage at a given time. The discharge of nutrients can be divided into a particulate and a dissolved load.

Table 1. *Phosphorus and nitrogen data for a first assessment of environmental impact of nutrient discharges from a fish farm (from* ENELL, *pers. comm.).*

A.	PHOSPHORUS	
1.	Production	x kg
2.	Food coefficient	1.6
3.	Amount of food	$1.6 \cdot x$ kg
4.	Food spill	$0.6 \cdot x$ kg
5.	P in fodder (1.1 %)	$0.0176 \cdot x$ kg
6.	P in the fish (0.4 %)	$0.004 \cdot x$ kg
7.	P dissolved in the water (11 %)	$0.001936 \cdot x$ kg
8.	P in food spill	$0.0066 \cdot x$ kg
9.	P in faeces	$0.005016 \cdot x$ kg
10.	P bound to other particles (66 %)	$0.011616 \cdot x$ kg

B.	NITROGEN	
1.	Production	y kg
2.	Food coefficient	1.6
3.	Amount of food	$1.6 \cdot y$ kg
4.	Food spill	$0.6 \cdot y$ kg
5.	N in fodder (7.2 %)	$0.1152 \cdot y$ kg
6.	N in fish (2.9 %)	$0.029 \cdot y$ kg
7.	N dissolved in the water (62 %)	$0.071424 \cdot y$ kg
8.	N in food spill	$0.0432 \cdot y$ kg
9.	N in faeces	? kg
10.	N bound to other particles (13 %)	$0.014976 \cdot y$ kg

? = values not available

The particulate load, mainly constituted by food spill and faeces, is primarily deposited beneath the cages; the spread depends on the water currents/water exchange.

The given values are based on food coefficients, *i.e.* added dry fodder divided by fish growth in kilo, in the range of 1.6—2.2. In a well-run farm, with a minimum of spill and fodder of high quality, the food coefficient may be about 1.5; automatic feeding generally yields more spill than manual feeding.

The P-load from a fish cage on the surrounding waters is dominated by the particulate load (about 85 % part.-P); the N-load, in contrast, is dominated by the dissolved load (80—85 % of the total), (Table 1). Phosphorus is generally regarded as the most limiting nutrient in fresh water environments, whereas nitrogen plays that role in marine environments.

Table 1 gives important data which will be subsequently used to give a first outline to quantify the environmental impact of fish cages on coastal waters.

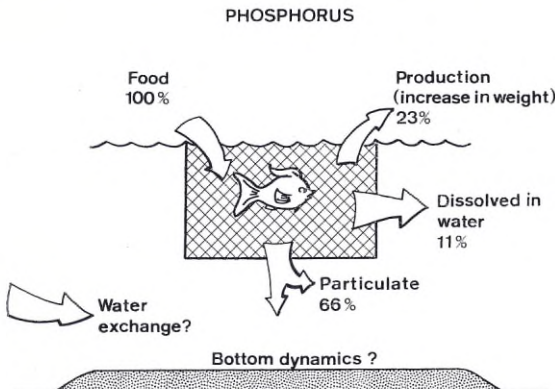The data from Table 1 can be used to illustrate

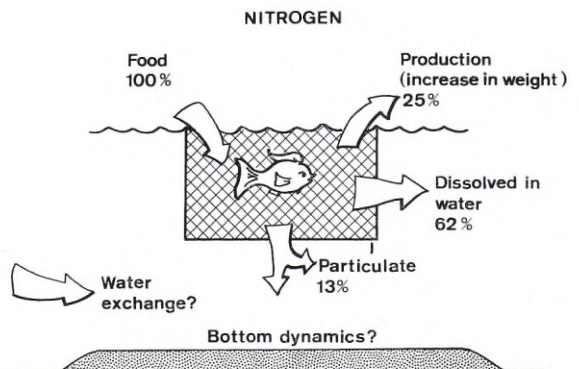Fig. 1. A budget for phosphorus (data from Table 1).

Fig. 2. A budget for nitrogen (data from Table 1).

the central concepts in a nutrient budget (see Fig. 1 for P and Fig. 2 for N). These two figures also illustrate our special focus on water exchange and bottom dynamic conditions. To get an overall view of the impact on the water system from fish cages, one must, evidently, also include other sources discharging nutrients to the coastal areas; as a general reference concerning, *e.g.*, the atmospheric deposition in Sweden, we may note that the values are about 0.1—0.2 kg phosphorus (per hectare water surface a year) and 5—15 kg for nitrogen.

IV. DIMENSIONING OF PROBLEMS

A first assessment or dimensioning of the environmental impact of nutrient discharges from fish cages must include considerations to the two question marks in Figs. 1 and 2. Subsequently, we will use formulas (1) and (2) to answer the following two questions: What is a probable increase in nutrient concentrations in the water mass from a given fish cage enterprise? Will the spill be spread/diluted or enclosed/concentrated? In addition it is evident that the conditions within and just below the cage will be more influenced by the spill than waters at a distance from the cage. In this paper the question concerning the geographical definition of impact areas will be circumvented since formulas (1) and (2) are based upon certain premises concerning the areal definition of the coast. So, we will not discuss site typical information concerning the actual cage site but rather local typical information concerning an entire coastal area defined by the limitation lines towards open water areas drawn at topographical bottlenecks to yield a minimum of topographical openness (E).

The general rationale behind the two questions is illustrated in Fig. 3. If the fish cage is placed at a site dominated by transportation processes, the possibilities for the O_2-demanding organic material to accumulate beneath the cage will be minimized—but the material from the cages will be spread to surrounding waters and sediments. If the cage is placed within an area dominated by fine sediments and accumulation processes, the spread will be smaller. Possible O_2-problems
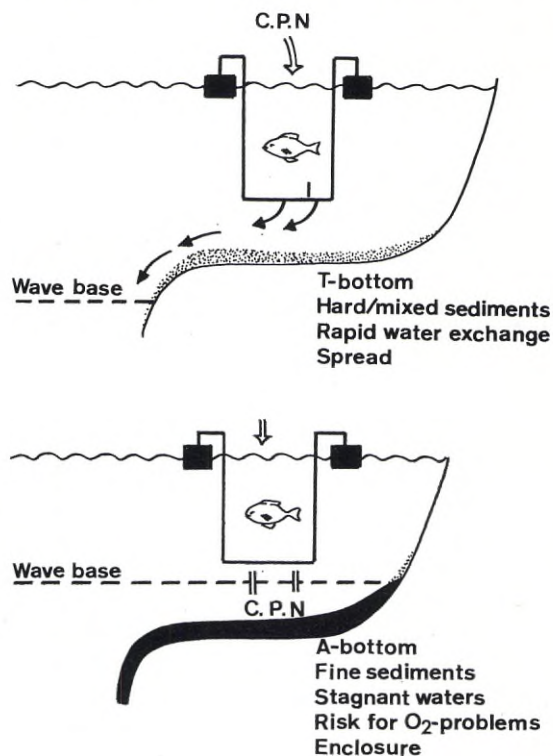
Fig. 3. Schematic illustration of the importance of knowing the bottom dynamic conditions (erosion, transportation and accumulation) and the water exchange around a fish farm.

will be accentuated if the water exchange is small. If O_2-problems do arise in the sediments below the cage, this may lead to formation of lethal H_2S-gas. Areas of erosion, *i.e.* bottoms dominated by sand and harder materials, are generally well exposed to winds, waves and currents and therefore, for practical reasons, less suited for fish farms.

V. DETERMINATION OF WATER RETENTION AND CONCENTRATIONS

Let us assume:

— a farm with a production of 50 tons per year (rainbow trout) without special purification equipment. This corresponds to, according to Table 1, a yearly P-discharge from food spill of 330 kg ($0.0066 \cdot 50 \cdot 1000$), 251 kg from faeces ($0.005016 \cdot 50 \cdot 1000$) and 97 kg dissolved directly

Table 2. *Example illustrating the calculation of phosphorus increase from a fish farm for two different localities.*

FORMULAS: $T = 42.7 \cdot W \cdot E^{-0.71}$
$R = V/T$
$C = (D + R \cdot Co)/R$

where

T = retention time of surface water (days);
W = mean coastal width (km);
E = exposure (%);
R = water flow in the section area (coast—open sea) in m³/day;
D = dose (of P) from the fish farm (mg/day);
Co = background level (assumed as 20 mg P/m³);
C = probable concentration in the given coastal area (mg P/m³).

Assume the following environmental characteristics for the two alternative areas A and B.

BASE DATA:	Area A	Area B
Water volume (V, mill. m³)	120	72
Area (A, km²)	12	15
Coastline length (l, km)	60	25
Mean coastal width (W, km)	0.20	0.60
Exposure (E, %)	1.3	17.6
Background conc. (mg P/m³)	20	20
P-dose to the water (kg/yr)	97	97
P-dose to the water (mill. mg/day)	0.3	0.3
Long-term release from sediments	?	?
CALCULATED DATA:		
Water retention time (T, days)	7.1	3.3
Water flow (R, mill. m³/day)	16.9	21.8
P-conc. (mg/m³)	20.02	20.01
Increase in P (mg/m³)	0.02	0.01

in the water (0.001936 · 50 · 1000). Note that in this example we have not calculated the amount of P that may leak from the sediments on a long-term basis, since the present state of knowledge seems too meagre for such calculations. The corresponding data for nitrogen (also based on Table 1) are: 2160 kg N from food spill, an unknown quantity (probably about 1500 kg) from fish faeces and 3570 kg N directly dissolved in the water. The total discharge of nutrients from a farm of 50 ton/year would correspond to discharges from a purification plant from a town of about 7500 inhabitants (assuming a 90 % reduction in the plant).

— that there are two alternatives to place the cage. The producer as well as the authorities would first like to know which alternative would cause the smallest increase in nutrient concentration in the given coastal area. To make such a calcula-

tion one must first assume/determine a background value; in this example we will use a background value of 20 mg P per m³. It should be noted that this value can vary widely for P and N between different coastal areas and in time.

To determine a possible increase in concentrations, according to formula (1), one must know the water volume of the coastal area (V) and the water retention time (T). The calculations also require data on the topographical openness (E) and the mean coastal width (W). The actual calculation is exemplified in Table 2 for P. The same type of determination could be carried out for any element/pollutant from point sources. In this example, it is also assumed that the fresh water input to the area from rivers in negligible.

Table 2 shows that the probable increases in the two alternatives are very small: 0.02 and 0.01 mg P/m³. This is an important first indication.

VI. DETERMINATION OF POTENTIAL BOTTOM DYNAMIC CONDITIONS

To determine the potential bottom dynamic conditions dominating in the given coastal area, the following additional information is required (from formula 2): The mean slope (xm) and the form factor (Vd). The calculation is exemplified in Table 3.

Area B is, according to the calculations, dominated by areas of erosion (64 %) and areas of transportation (36 %); area A, on the other hand, is dominated by areas of accumulation (59 %). Area B would be a alternative for dilution, area A an alternative for enclosure of the nutrients and the spill from the fish cages. The risks of getting O_2-problems would be smaller in area B.

These are important considerations when these two alternatives for location site are discussed. But it should be noted that, at present, there is no Vollenweider-diagram (VOLLENWEIDER 1968) available for coastal regions where N is the most limiting nutrient. Thus, further determinations on the possible effects of the fish farms on the eutrophication process are very hard to make.

The results indicate with objective data that

area B would be preferable to area A for the producer because it has a shorter water retention time and because the risks of O_2-problems would be lower since area B is not likely to have any areas of accumulation. The environmental authorities, on the other hand, could argue that area A would contain the spill in a more effective way. This would minimize the potential eutrophication in surrounding coastal regions.

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Table 3. *Example illustrating the calculation of potential bottom dynamic condition in two coastal areas.*

FORMULAS:	$BA = 11.7 \cdot E^{-0.82} \cdot xm^{0.92} - 1$		
	$BE = 23.1 \cdot E^{0.36} \cdot Vd^{-0.76}$		
	$BT = 100 - BA - BE$		
where	BA = area A-bottoms (in % of the water surface);		
	BT = area T-bottoms (in % of the water surface);		
	BE = area E-bottoms (in 5 of the water surface);		
	E = exposure (%);		
	xm = mean slope (%);		
	Vd = form factor (dim. less).		

BASE DATA:		Area A	Area B
Mean slope (xm)		7.5	1.3
Mean depth (Dm, m)		10	4.7
Max. depth (Dmax, m)		32	14
Form factor (Vd)		0.94	1.01
Exposure (E)		1.3	17.6
CALCULATED DATA:			
BA		59	0
BE		27	64
BT		14	36

Returns of Comparable Microtagged Atlantic Salmon (*Salmo salar* L.) of Kollafjörður Stock to Three Salmon Ranching Facilities

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ABSTRACT

Salmon ranching from release sites which are not physically tied to a salmon farm is gradually building up in Iceland. This paper deals with experimental releases at Lárós and Súgandafjörður ranching sites, using smolts from Kollafjörður Fish Farm, where control releases have been performed. The experiments have given information on total return rates, ratio of grilse *v.* salmon as well as stray between ranching sites.

Experimental releases from 1978 through 1982 have shown that returns to the Súgandafjörður site which is located in a colder region with respect to air and sea temperatures have been averaging 3 %, less than a third of those at the other ranching sites. Returns to the other sites during the same period average 9—10 %. Returns to the Lárós site have sometimes exceeded those at Kollafjörður where the smolts were reared, indicating that release sites where smolts are only adapted and fed for one month are a viable proposition in salmon ranching ventures. Up to 50 % of salmon returning to the Súgandafjörður ranching site stay two years in the sea. Comparable figures at the other ranching sites never exceed 20 %. Delayed smolt migration and cold sea temperatures at Súgandafjörður in the spring are probably the main causes, considering that late maturation is characteristic for salmon stocks in northern Iceland.

Compared to 5,048 salmon returning to Kollafjörður Fish Farm as the place of release, only 13 have returned to Lárós (0.2 %) and 5 to Súgandafjörður (0.1 %). Similarly 2,291 salmon have returned to Lárós, 13 strayed to Kollafjörður (0.6 %) and none to Súgandafjörður. Releases of Kollafjörður smolts at the Vogar ranching site have yielded particularly interesting stray figures where 91 % homed correctly, 3 % of returnees went to Kollafjörður as the place of rearing but almost 6 % went to Pólarlax ranching station located halfway between the two sites. That station uses ground water of similar origin as that used at Vogar for pre-release adaptation and salmon attraction.

I. INTRODUCTION

Salmon ranching experiments from a site where the smolts were also reared have been conducted at the Kollafjörður Experimental Fish Farm for over 15 years. It is very important for further development of salmon ranching in Iceland if it could be carried out at release sites distant from the fish farm where the smolts are reared. Suitable rearing sites are limited in number, and only in a few instances located close to the sea.

Ranching experiments from a release site were tried at Lárós in the 1960's apparently with limited success, using Carlin-tagged two-year smolts. In the early 1970's ranching was started at Súgandafjörður on a small scale using one- and two-year smolts. Most of the smolts were untagged and success was difficult to evaluate. Returns, however, varied a lot between years and were generally low. In 1978 the Nordic council granted some funds to conduct salmon ranching

experiments in Iceland. Initially experimental releases were done at several release sites around Iceland but were later confined to Kollafjörður and Súgandafjörður, the only sites with proper recapture facilities. Lárós ranching site was added to the program through support from the Icelandic Rural Development Fund, and turned out to be a valuable addition.

The primary objective of the experiments was to see if one could develop viable salmon ranching at release sites which were not attached to a smolt station. Secondary objectives were to compare return rates and length of stay in the sea as one moved from a relatively warm area (Kollafjörður, Lárós) into an area affected by cold polar currents (Súgandafjörður). It was also suspected that return rates would drop as one moved further from the site of original homing.

The smolt releases at Kollafjörður, Lárós and Súgandafjörður provide an excellent opportunity
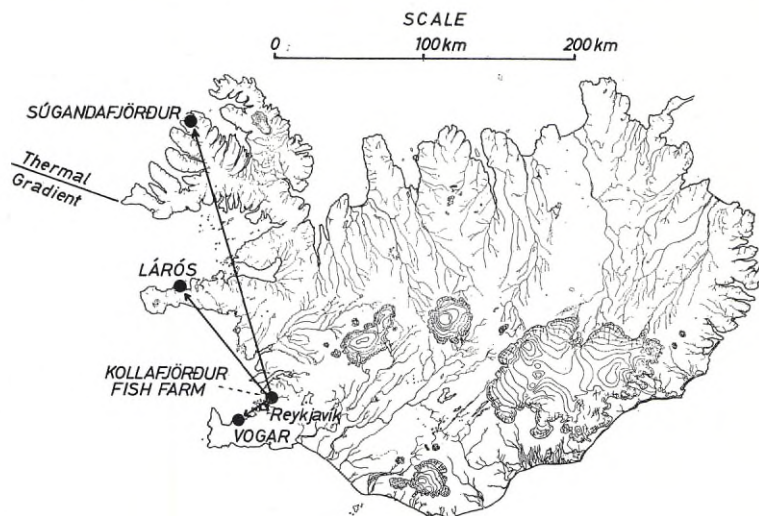
Fig. 1. Location of Kollafjörður Experimental Fish Farm and the salmon ranching sites at Vogar, Lárós and Súgandafjörður. Arrows indicate the transport of smolts of Kollafjörður strain to the release sites where they were adapted and fed for a month before release.

to study the return rates of identical smolts to different ranching sites and to observe any trends in return rates as one moves further away from the area, to which the salmon are acclimatized with respect to homing. It is also of great interest to study any changes that might occur in the grilse-salmon ratio as one moves further north into a colder sea. Salmon in northern Iceland tend to stay longer in the sea than those in the south. It has been suspected that this might be caused by a combination of environmental factors such as late smolt migration due to delayed warming of freshwater as well as colder and less productive oceanic areas. The Súgandafjörður site would be fairly characteristic for those areas. These studies have also provided excellent information on straying between the various ranching sites and to complete that picture data from the Pólarlax and Vogar ranching sites have also been included.

II. METHODS

The experiments

The experiments discussed here include three release places, Kollafjörður where the smolts were reared, Lárós and Súgandafjörður ranching sites, all shown in Fig. 1. Smolts from Kollafjörður Fish Farm have also been released from the Vogar ranching site operated by Iceland Investment

corporation. This has given valuable supporting information on return rates as well as straying. Kollafjörður, Lárós and Vogar release sites are located in an area influenced by warm oceanic surrents. Súgandafjörður on the other hand is adjacent to a colder sea. The distance from Kollafjörður Fish Farm to Vogar as the crow flies is only 40 km, ca 100 km to Lárós but over 200 km to Súgandafjörður. Distances along the shoreline are clearly much greater.

Smolts used

All smolts used in the experiments were reared at the Kollafjörður Experimental Fish Farm. They had been exposed to comparable rearing routine which is shown in Fig. 2. Hatching is normally at 8—9°C and startfeeding begins in early February. The parr are reared at 13°C and some may reach smolt size (30 g) in August at which time they are moved into outdoor ponds with ground water flow (4°C). The slowest growing parr are put into these ponds in early March.

During indoor rearing the 2×2 m tanks are half covered with polyethylene plastic and the fish exposed to subdued electric light at night (4—9 lux). Daytime lighting comes through overhead windows (Fig. 3) and varies from a minimum of 100 lux during winter to a maximum of 2000 lux during the summer. The fish in outdoor ponds are only exposed to natural photoperiod.
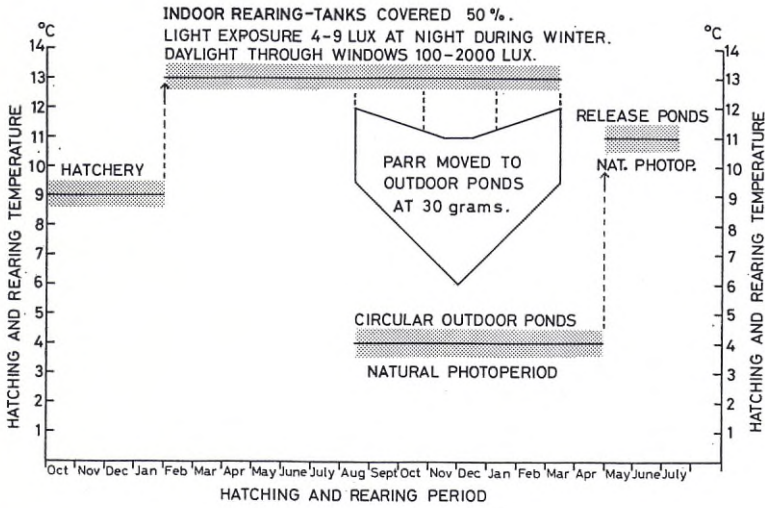
Fig. 2. Hatching and rearing program used at the Kollafjörður Experimental Fish Farm to produce smolts for the ranching experiments.

The rearing program shown in Fig. 2 has given fairly stable return rates to Kollafjörður Fish Farm in the last 6 years and any variations in return rates between tagged groups, which invariably occur, indicate that smolts put in outdoor ponds in March may perform just as well as those put in the ponds in September. It has repeatedly been shown that on-growing salmon parr need to be exposed to natural photoperiod for considerable time in order to smoltify properly in the spring (Saunders and Henderson 1970, Ísaksson 1976, Saunders *et al.* 1985). One must therefore assume that the parr in the present experiments are responding to natural photoperiod through overhead windows (Fig. 3) during the indoor rearing phase. Complete darkness at night does not seem to be necessary since the parr are exposed to dim electric lights just enough to keep them feeding.
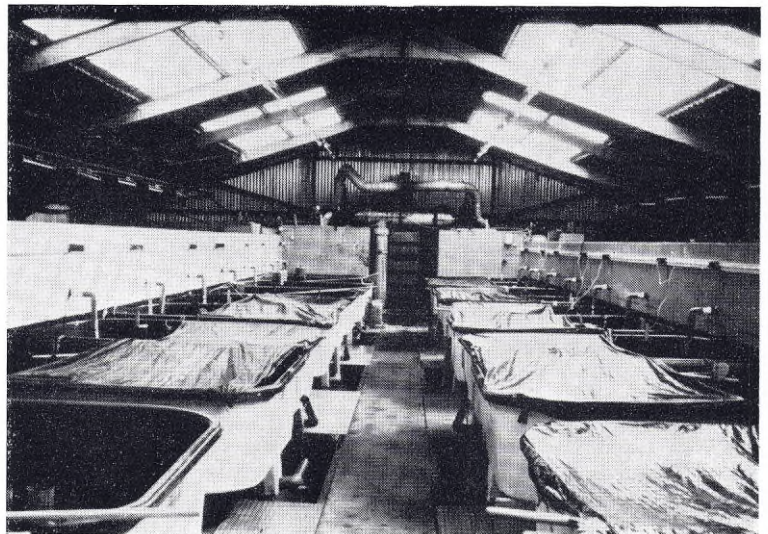
Fig. 3. The inside of the main rearing house at Kollafjörður Experimental Fish Farm, showing rearing tanks half covered with polyethylene sheeting and considerable light shining through overhead windows.

KOLLAFJÖRÐUR FISH FARM

LÁRÓS SALMON RANCHING SITE

SÚGANDAFJÖRÐUR SALMON RANCHING SITE

▤ =SEA-WATER   ▦ =FRESH-WATER

Fig. 4. Diagram of the three main salmon ranching sites discussed, showing location of release and recapture facilities.

The methods of release

Fig. 4 gives a diagrammatic representation of the release facilities at each site. At Kollafjörður, releases have conventionally been from freshwater release ponds. Smolts released from those may take up to a month to leave freshwater after the ponds are opened in early June. In 1979 a salinity adaptation release technique was added where the smo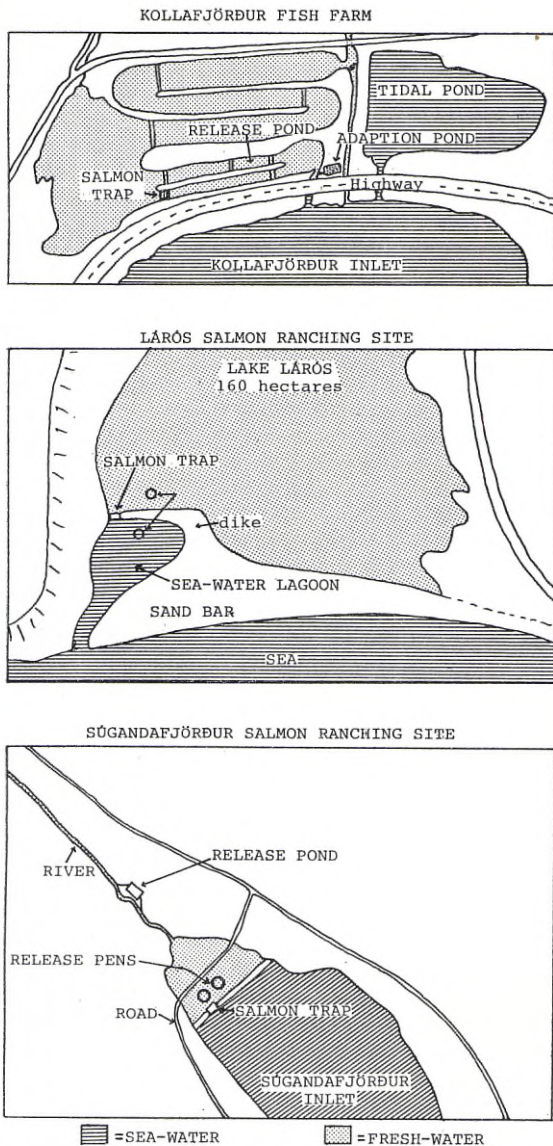lts are gradually acclimatized to saltwater during a months period. Full salinities are rarely achieved but are variable from 15 to 25 $^0/oo$. After acclimation, the smolts are normally released over a 24 hour period in mid-June, preferably in dull rainy weather.

At Lárós the smolts have been released from floating pens, some of which are located on a freshwater lake but others are on a seawater lagoon (Fig. 4). Salinities in the lagoon are very high, approaching 35 $^0/oo$. The smolts are in both cases released by cutting the netting but the lake reared fish are moved close to the outlet before release.

At Súgandafjörður the smolts were originally released from a release pond located on the river system. Since the river is mainly fed by melting snow it warms up late in the summer and smoltification is often delayed. In 1979 and 1980 additional releases from net pens on a freshwater pond were performed. The pond can warm up considerably during sunny days although water temperatures at this site are always much lower than at the other two sites. Since 1981 releases at Súgandafjörður have only been from net pens. Since no consistent differences were observed between the two release methods they have been pooled in the present experiment.

Smolts at Kollafjörður and Lárós were normally placed in release ponds during early May. Due to a colder climate at Súgandafjörður transport from Kollafjörður frequently took place anywhere from May 20th to June 5th depending on weather conditions. Releases at Kollafjörður and Lárós were usually performed in early June but at Súgandafjörður smoltification was slower and fish could only be released in early July.

Fish at all sites have been fed during the adaptation period with Ewos salmon feed. Feeding at Kollafjörður has normally been by hand only, but at Lárós and Súgandafjörður handfeeding has been supplemented with automatic feeders.

The tags used

All fish used in these experiments have been microtagged. Microtags are small pieces of wire with a binary code which are injected into the snout of salmon smolts. Only external indication

Table 1. *Numbers released and return rates to Kollafjörður, Lárós and Súgandafjörður in the freshwater release experiments.*

Year of release	Place of release	Number released	% Return as grilse	% Return as salmon	Total return rate %
1978	Kollafjörður	2000	4.1	1.1	5.2
	Súgandafjörður	2000	1.0	0.9	1.9
1979	Kollafjörður	2100	6.9	1.9	8.8
	Súgandafjörður	4000	1.7	1.3	3.0
	Kollafjörður	2000	6.7	0.7	7.4
1980	Lárós	3400	10.9	1.6	12.5
	Súgandafjörður	4000	2.9	0.4	3.3
	Kollafjörður	2000	7.2	0.4	7.6
1981	Lárós	2600	7.4	0.5	7.9
	Súgandafjörður	4000	1.5	0.9	2.3
	Kollafjörður	2000	11.2	2.6	13.8
1982	Lárós	3000	10.9	1.0	11.9
	Súgandafjörður	3000	2.2	1.2	3.4

of tagging is a cut adipose fin. All returning adults have to be killed and the snout removed for tag retrieval and identification.

Microtagged smolts are easy to transport both in tanks and in plastic bags which are commonly used for flight transport. All smolts to Lárós were transported in tanks with oxygen but Súgandafjörður transport was by air in oxygen inflated plastic bags.

Microtags have been used at the Kollafjörður Experimental Fish Farm since 1974. Experience has shown that survival for 40 g. smolts is at least double that for smolts tagged with Carlin tags (ÍSAKSSON and BERGMAN 1978). It is likely that this difference is greater for smaller smolts and experience at the Fish Farm indicates that survival of microtagged smolts may not be much different from that of untagged hatchery smolts.

III. RESULTS

The numbers released in the various experiments and the per cent return rates after one and two years in the sea are shown in Tables 1 and 2. The numbers tagged in each group are usually over 2,000 smolts which is quite satisfactory for statistical purposes. The results will be discussed under the following headings:

Total return rates.
Grilse salmon ratio.
Freshwater release *v.* salinity adaptation.
Straying between release sites.

Total return rates

The return rates to the various ranching sites are shown in Fig. 5. They are both shown as percentage of released smolts and as average returns in kgs per 1,000 smolts released. Only freshwater releases are included in those figures. Looking first at Kollafjörður one can see that percent return rates range from 5 % to approximately 14 %, averaging 8.5 % for the 5 years. This, however, is only representative for smolts released as control groups for Lárós and Súgandafjörður releases. Comparable returns in weight are 280 kg per 1,000 smolts released.

At Lárós the percent return rates range from 8 % to 12 %, averaging 10 %. This corresponds to approximately 300 kg of salmon per 1,000 released smolts. These results show clearly that smolts of Kollafjörður origin can have equally high return rates after being transplanted and fed for a month at a release site located over 100 km from the home site. This observation is very important for future development of salmon ranching in Iceland, since sites where a ranching

Table 2. *Number released and return rates to Kollafjörður and Lárós in release method experiments.*

Year of release	Place of release	Release method	Number released	% Return as grilse	% Return as salmon	Total return rate %
1979	Kollafjörður	Freshwater release	2100	7.0	1.9	8.9
		Salinity adaption	2100	6.2	1.4	7.6
1980	Kollafjörður	Freshwater release	2000	5.9	0.6	6.5
		Salinity adaption	2000	6.7	0.4	7.1
1980	Lárós	Freshwater release	3400	10.9	1.6	12.5
		Salinity adaption	3100	10.9	1.1	12.0
1981	Kollafjörður	Freshwater release	2000	7.2	0.4	7.6
		Salinity adaption	2100	6.7	0.5	7.2
1981	Lárós	Freshwater release	2600	7.4	0.5	7.9
		Salinity adaption	2800	5.0	0.7	5.7
1982	Kollafjörður	Freshwater release	2000	11.2	2.6	13.8
		Salinity adaption	2000	13.3	2.5	13.8
1982	Lárós	Freshwater release	3000	10.9	1.0	11.9
		Salinity adaption	3000	8.8	0.6	9.4

facility can be connected to a smolt station are limited.

Return rates to Súgandafjörður are much inferior to those at the other sites, averaging 2.8 %. This corresponds to almost 100 kg per 1,000 smolts released which is somewhat higher than one would expect from the return rate. This is due to a relatively high ratio of salmon compared to grilse at Súgandafjörður.

Grilse-salmon ratio

The grilse-salmon proportions at the various ranching sites are shown in Fig. 6. At Kollafjörður and Lárós there are considerable differences in
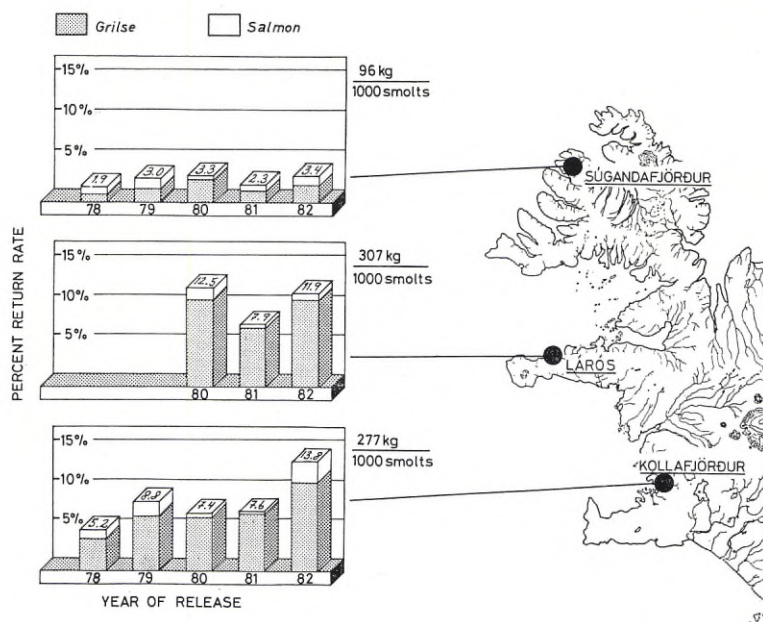
Fig. 5. Return rates to the various ranching sites shown as both percentage of released smolts and as average kgs per 1000 smolts released in the five years.
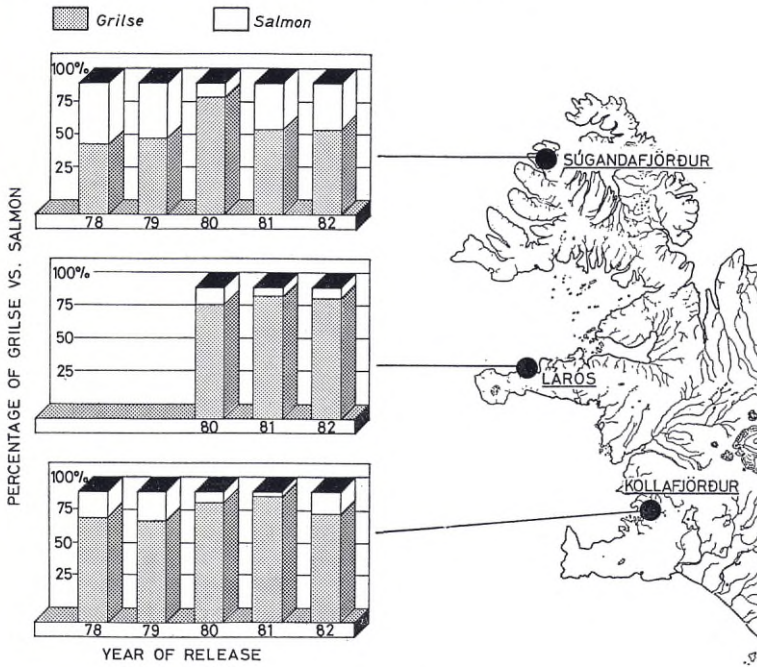
Fig. 6. Difference in grilse-salmon ratio between the three salmon ranching sites.

this proportion between years which is probably caused by variation in various environmental factors at the time of release, such as ocean conditions, freshwater temperature etc. There is, however, a much greater difference in grilse-salmon ratio between Kollafjörður and Lárós on one hand, and Súgandafjörður on the other.

As previously pointed out, Súgandafjörður is in a different climatic zone with the melting of the snow far into the summer and cold current dominat-

ing off-shore. It is therefore very interesting to see if a variation in those factors could be used to explain the differences.

Fig. 7 shows the average freshwater temperatures during the adaptation period (June) at Lárós and Súgandafjörður. The difference of over 3 degrees has been observed to slow down smoltification at Súgandafjörður and normal release period is over a month later than at Lárós. This in itself is sufficient reason for a later maturation of sal-

Fig. 7. Average freshwater temperatures during the one month adaptation period at Lárós and Súgandafjörður.

Table 3. *Some biological and meteorological factors which could influence the grilse-salmon ratio at Súganda-fjörður in the 1978—82 release experiments.*

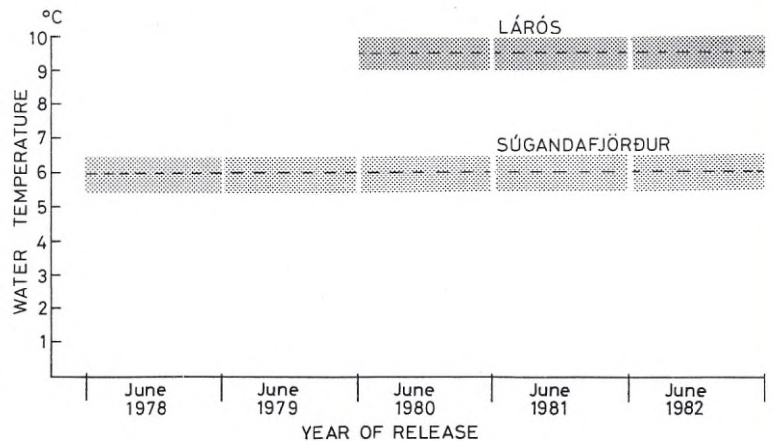| Year of release | % Grilse in return from release | Size of smolts gr. | Averages for the month of June | | | | |
			Air temperature °C	Freshwater temperature °C	Sea temperature °C	Precipitation mm	Snow cover in mountains %
1978	53	20	7.5	6.7	6.3	41	18
1979	57	30	7.6	5.8	5.4	70	11
1980	88	25	8.1	6.3	6.3	31	0
1981	63	25	8.1	6.0	3.7	35	18
1982	67	23	9.0	—	5.6	10	18

mon released at Súgandafjörður. There are further-more differences of ca 1°C in sea temperature at the time of release, 6—7°C at Súgandafjörður v. 7—8°C at Lárós. This would certainly slow down early growth in the sea and enhance late maturation.

There is a pronounced exception from the late maturation pattern at Súgandafjörður in the 1980 release where over 80 % of the fish returned as grilse (Fig. 6). The 1980 spring and summer were exceptionally mild compared to the years before and after. One would therefore have thought that the observed differences could be attributed to some tangible meteorological factors. Table 3 shows some of these factors for the month of June at Súgandafjörður, along with size differences of

smolts at time of tagging. The pronounced grilse ratio in the 1980 release experiment cannot be clearly related to any of these factors. It is, however, apparent that snow has been entirely absent in the mountains surrounding Súganda-fjörður during the month of June in 1980 and sea temperatures have been relatively favourable.

Freshwater release v. salinity adaptation

The freshwater releases and salinity adaptation of smolts at Kollafjörður and Lárós have been described in an earlier section. Fig. 8 shows the results from those experiments. Statistical analysis (chi-square) showed that there was no difference in return rates at either location using the two methods. This is quite surprising, considering that
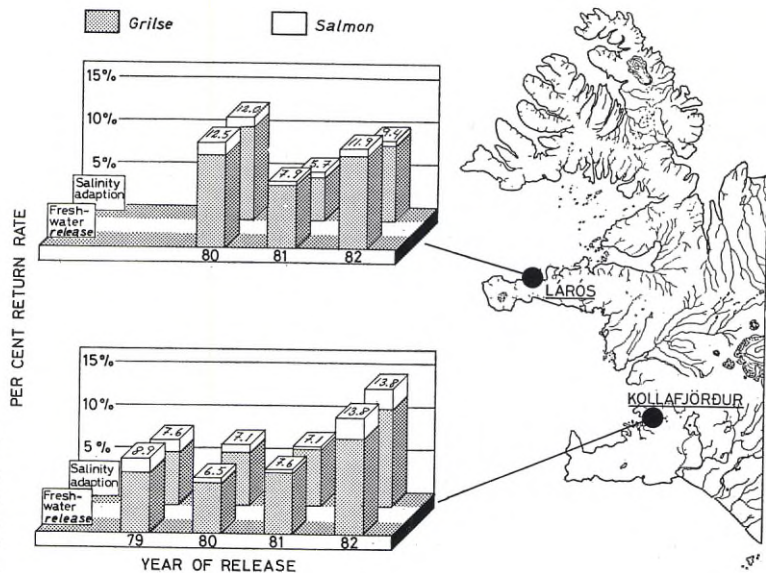

Fig. 8. Difference in return rate depending on the method of release. Smolts adapted to salt water are released during high tide at night. Fish released from freshwater can linger in the release ponds for several weeks.
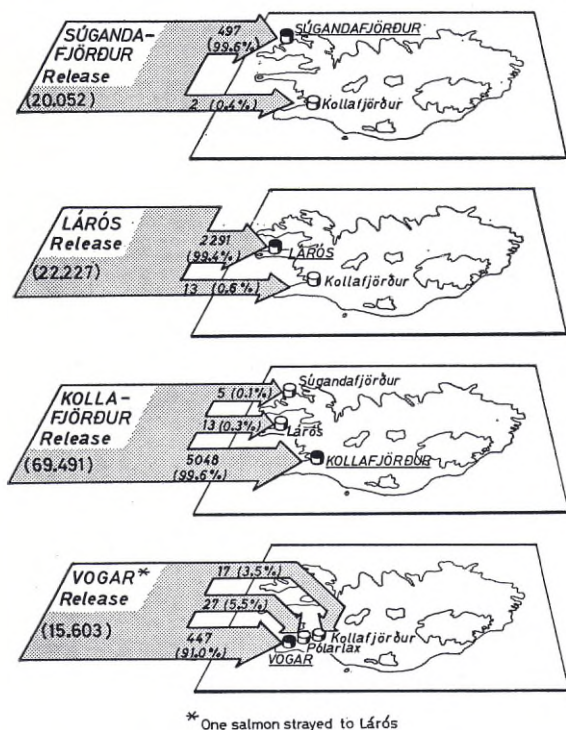
Fig. 9. Straying of salmon to other ranching facilities from the various ranching sites. Also shown are numbers of released smolts and returning salmon.

the freshwater released fish go out over a months period but the adapted smolts are arbitrarily released over a few hours. This indicates that any positive effects of smolts migrating out in large schools as they would do when salinity adaptation is used, is offset by some negative factors, possibly predator attraction. Seawater survival seems in this case to be a fairly constant fraction, as if the smolts have to pass through a bottleneck which is independent of release time, within a certain release window, as well as the magnitude of smolts migrating at any one time. The smolts also do not seem to benefit from controlled acclimatization to saltwater.

Straying between release sites

The salmon ranching experiments have yielded important information on the straying of micro-tagged salmon between release sites (Fig. 9). Additional information from releases at the Vogar ranching site has been included in this analysis

as well as some return information to Pólarlax station. One can safely assume that considerable straying of salmon occurs from the ranching stations to various streams. This information, however, is not complete, as adipose clips, which are only external sign of microtags, are not easily seen by sports-fishermen. Since tag-return effort would be variable between streams it is better not to include this limited material.

Fig. 9 shows that over 99 % of the returning salmon find their way to the place of release, in the case of the three major ranching sites discussed in the paper. Straying to other ranching sites is thus less than 1 %. Somewhat higher fractions strayed to Kollafjörður from Lárós and Súgandafjörður than the other way around but the numbers are quite small and probably of little significance where homing is concerned.

Only 91 % of salmon destined for Vogar ranching site are caught there and 9 % stray to other ranching stations. This high straying rate is probably due to the fact that the Vogar operation is entirely dependent on pumping of well water mixed with sea-water for attracting the adults. No natural watershed is in the area and the site is thus completely unaffected by rain and resulting freshets. Most of the adults must thus be trapped in the estuarine area.

The neighbouring Pólarlax ranching site, although attached to a smolt station, is much of same nature, using similar ground water resources for attraction which may explain why they get most of the strays. It should be pointed out that tag returns from Pólarlax may be incomplete and the presented figures thus a minimum. Strays to Kollafjörður from the Vogar releases are considerably lower than those to Pólarlax and have been quite variable between years. This information is quite interesting, considering that the smolts released were purchased from Kollafjörður Fish Farm and all these sites are fairly close together. It has been noticed that strays from Vogar to Kollafjörður have been considerably reduced when salmon are actively caught in the estuary at Vogar, soon after arrival. This indicates that some of the straying fish may have entered Vogar bay before going off to other sites. Homing may thus be a lot better than indicated by these figures.

On the whole the data in Fig. 9 suggests that

homing to places where smolts are fed for a month before release is quite good. Ranching can easily be carried out at sites where there is no smolt rearing station and smolts can be purchased from distant stations.

IV. DISCUSSION

The ranching experiments have shown that smolts reared at the same facility and released at various ranching stations have a strong impulse to return to the site of release, even when these are located fairly close to the place of origin and rearing. Since the smolts have only been held for a month at the release site it demonstrates clearly that Atlantic salmon smolts can imprint to a release site in a very short time as has been demonstrated many times with the Pacific species and thoroughly reviewed by BRANNON (1982, 1984).

It is interesting that the salmon do not have a greater trend to stray from the release sites to Kollafjörður Fish Farm as their native site and place of rearing than to stray from the station to the various release sites. Admittedly the strays are somewhat more numerous from the Vogar release site which is closest to Kollafjörður but the salmon show a greater preference for the Pólarlax ranching station which is rearing and releasing salmon of different stocks. It should also be pointed out that the Vogar release site is not attached to a natural watershed and uses ground water for smolts acclimatization and adult attraction. The water source is of similar origin as the one at Pólarlax hatchery which could partly explain why the strays from Vogar have a preference for that site. Salmon returning to the Pólarlax facility have earlier shown a curious preference for a ground water flow located 400 metres from the hatchery, having rejected the hatchery run off which was quite open to the fish (ÍSAKSSON 1982). This indicates that the salmon were basically homing to some chemical component in the ground water rather than one associated with the population of salmon parr being reared at the station.

From these observations it is difficult to conclude that the salmon are being guided by population specific pheromones (NORDENG 1977, STABELL 1984). There have, however, been indications that salmon are homing more strongly to salmon streams than those having no salmon (ÍSAKSSON

et al. 1978)· This may suggest that some general salmon pheromones reinforce homing.

These experiments have yielded much information on the salmon ranching potential in Iceland, suggesting that conditions for this are more favourable in the areas warmed by the Gulf stream. In areas affected by colder polar currents the return rates are lower and the salmon tend to mature a year later. This basic difference exists between streams in northern and southern Iceland and the majority of grilse returning to northern streams are males whereas an even sex ratio is found in the south (SCARNECCHIA 1983). Second time spawners also stay a year longer in the sea before returning to the north. The salmon catches in rivers in northern Iceland have been shown to be influenced by the sea temperature when those salmon migrated out as smolts (SCARNECCHIA 1984).

It has earlier been suggested that low return rates to Súgandafjörður could be explained by a drop in returns as one moves away from the stream of origin (ÍSAKSSON 1980). Additional information (Lárós) seems to indicate that this is only a part of the explanation and a major cause could be cold and unproductive seas in the Súgandafjörður area. It is, however, likely that one is getting close to the outer limit of transplanting for the Kollafjörður stock, if migration patterns are partly genetically determined as suggested by various authors (BAMS 1976, CROSS 1984). This should in particular be applicable for transplants of Kollafjörður stock to the northern and eastern coasts of Iceland, where the salmon are entering different ocean current systems and migrating in an entirely different direction compared to the home site.

It seems therefore clear that a single ranching strain could be used in southern and western Iceland within 150 kilometres of the site of original homing. Since release sites seem to be just as suitable as those connected to rearing facilities, one can expect a considerable expansion in ranching from such sites. The technique will probably also be used to enhance salmon fishing in small streams which have limited capacity to produce salmon naturally. With the high prise of rod fishing licences this type of ranching is even more profitable than selling salmon to the market.

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The Choice of Reproductive Tactics as a Mixed Evolutionarily Stable Strategy: the Case of Male Atlantic Salmon (*Salmo salar* L.)

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ABSTRACT

There are two alternative mating tactics in male Atlantic salmon. "Precocious males" mature at small sizes while still in the river. "Migrant males" mature at considerably larger sizes after a varying number of years in the sea, and return to the native river for spawning. The precocious males compete with the migrant males on the breeding ground as sneakers. The two tactics are suggested to coexist in a mixed evolutionarily stable strategy (mESS). Besides the negatively frequency-dependent fitnesses of the two tactics, respectively, the fitnesses of precocious males are assumed to be size dependent. That is, only if the male has a size within a particular size range specific to each river at the time of decision between the two tactics, he should become precocious. We also show how the size dependent fitnesses are influenced by the equilibrium frequencies of precocious males and migrants. Thus, we suggest a mixed ESS not maintained by a behavioural or purely stochastic choice of tactic, but rather an evolutionary adjustment of the genetical material so that each individual will choose one of the two tactics depending on environmental conditions affecting growth rate.

I. INTRODUCTION

There is often more than one life history alternative available to individuals within a population, *e.g.* male mating tactics (DOMINEY 1984). This is particularly true for many fish species (GROSS 1984), for example in many salmonids, alternative male reproductive behaviours have evolved. In the Atlantic salmon (*Salmo salar* L.) some males mature at an earlier age and at a size comparable to that of juvenile parrs, such males are regarded to be precocious (JONES 1959). Precocious males mature while still in the native river, as opposed to "normal" males (and females) who migrate to the sea as smolts after 1—7 years depending on the geographical location and nutritional conditions in the river. After having spent a number of years in the sea, the migrants return to the river for spawning. Because of the much lower growth rate in the river compared to the sea, a precocious male will always be much smaller than the mature migrant male, but not necessarily younger.

The reproductive behaviour differs markedly between precocious and migrant males. A migrant male courting a full grown female fertilizes the eggs as soon as they are released. At these moments precocious males rapidly swim to a position under-neath the pair and try to fertilize the eggs (JONES and KING 1952). After one or more seasons as precocious males at least a fraction of them smoltify and participate in the normal smolt run to the sea (ÖSTERDAHL 1969, LEYZEROVICH and MELNIKOVA 1979).

It has been shown that the proportion of precocious males in the total male population varies considerably between rivers. POWER (1973) and DALLEY *et al.* (1983) presented data from some Norwegian and Canadian rivers. Among the Norwegian rivers the proportion of precocious males ranged from 8 to 20 %, whereas the range among the Canadian rivers was 12 to 100 %. However, most studies on the significance of this reproductive alternative have been focused on physiological and behavioural adjustments (ERIKSSON *et al.* 1979, THORPE *et al.* 1980, THORPE *et al.* 1982, LUNDQVIST and FRIDBERG 1982). Surprisingly, very few studies have been done on the evolution and maintenance of the precocious fraction of the male population.

MAYNARD SMITH (1982) and GROSS (1984) put forwards the suggestion that this system of two reproductive alternatives in male salmon could be an evolutionary stable strategy (ESS), in which the reproduction of precocious males was

regulated by negative frequency-dependent success. Moreover, GROSS (1984) provided preliminary evidence for frequency-dependent success in precocious coho salmon (*Onchorhynchus kisutsh*), and GROSS (1985) mathematically demonstrated that the lifetime fitness of precocious and "normal" male is about equal. SCHAFFER and ELSON (1975) have presented a theory concerning at what ages and sizes the migrating males should optimally mature, but did not take into account the mate competition with the precocious males. In the present paper, the choice of reproductive alternative in salmon male parr is further analysed. We evaluate the situation as an ESS model (*cf.* GROSS 1984), and incorporate the size component as well, where each individual will choose one of the two tactics in a stochastic manner, depending on the environmental conditions. The concepts in ESS theory are still ambiguous as has been recently pointed out by DOMINEY (1984). Here, we define a mESS (mixed ESS) as a strategy composed of tactics with equal fitnesses. The choice of tactic might or might not be conditional. On the other hand, if more than one strategy exists in a population they will coexist in an ESSt (evolutionarily stable state; *cf.* also GROSS 1984).

II. THEORY

When dealing with life-histories in age-structured populations, fitness is usually defined by terms of the equation; $1 = \Sigma e^{-rx} l(x) b(x)$, where x is the age, r is the intrinsic rate of natural increase, $l(x)$ is the probability of survival from age x-1 to x and $b(x)$ is the function describing fecundity at age x. Maximizing fitness is the same as maximizing r, given that the population is living in a density-independent environment. Under density dependent conditions, selection favouring a maximization of N (population density) seems to be operating (CHARLESWORTH 1980). The situation becomes less clear if selection is also frequency dependent (*e.g.* CHARLESWORTH and CHARLESWORTH 1975).

The individual fitness of precocious males (W_p) turns out to be a function with age (x), fecundity $b(x)$, survival $l(x)$, frequency (q), size (S) and population size (N) as important elements ($W_p=$
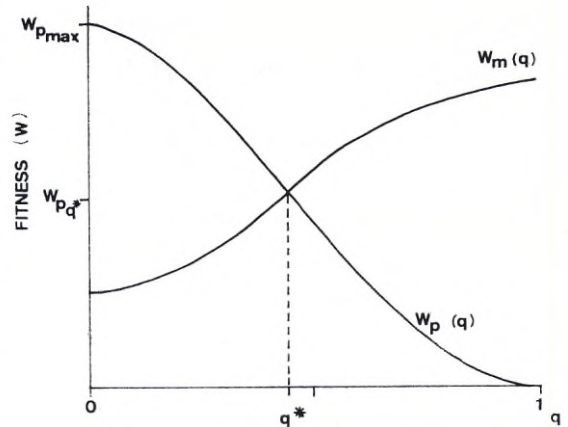

Fig. 1. The frequency-dependent fitness functions of precocious males ($W_{p(q)}$) and migrants ($W_{m(q)}$). q is the proportion of all males reproducing as precocious; 1-q being the proportion reproducing as migrant full size males. At q* both alternatives do equally well.

$f(x,l(x),b(x),q,S,N))$. Yet too little is known about this reproductive system in order to outline a proper fitness function. Instead we suggest a possible mechanism for the evolution and maintenance of the two reproductive alternatives.

We assume that the fitness of precocious males, W_p, is dependent on the reproductive alternatives that all other members in the population have adopted, *i.e.* W_p is inversely frequency dependent. An increase in precocious frequency (q) would increase mate competition as well as food competition in the river, *i.e.* it would tend to reduce W_p. Similarly, the fitness of migrants, W_m, is inversely related to the frequency of migrant males (1-q) in a corresponding manner. The true shapes of the functions $W_p=f(q)$ and $W_m=g(q)$ are very difficult to estimate since no data are available on the frequency-dependent mating success of Atlantic salmon males. However, an illustration of the possible fitness functions is shown in Fig. 1, based on GROSS (1984).

The reproductive success of precocious males is also assumed to be size dependent. A large precocious male would probably have difficulties in performing the sneaking behaviour since he would then be too conspicuous and the full-size courting male would attack him as he would be seen as an intruder. On the other hand, a precocious male

will have less reproductive success if it was too small to produce any significant amount of milt for proper fertilization. Thus, there is a size interval (I) representing the range within which a precocious male can have reproductive success. Fitnesses as a function of size within I is assumed to be approximately normally distributed with a mean at the midpoint of I.

There is a fixed time, t_d, in the year when a male salmon has to decide whether to migrate or to stay in the river. The time of reproduction (t_r) reoccurs annually and always comes later than t_d.

An ESS situation

Since the fitnesses of the two alternatives are assumed to be frequency dependent, this system can be analysed by an ESS model (MAYNARD SMITH 1982). In Fig. 1 such an ESS situation is illustrated. Let q^* be the q value satisfying the equation $W_p(q)=W_m(q)$ (*cf.* Fig. 1). Then the proportion q^* of the reproducing male population should be precocious and $1-q^*$ should be migrant males.

If this system holds for the Atlantic salmon, two possible interpretations follow. One possibility is that the two morphs represent a genetic dimorphism, *i.e.* the two alternatives are genetically determined and thus there are two strategies co-existing at an ESSt (GROSS 1984). Differential reproductive success at different q-values would then balance the frequencies of precocious (q^*) and migrant males ($1-q^*$). The other possibility is that the two alternatives are different tactics within a mixed strategy, *i.e.* the only stable strategy would be one where the probability of choosing the precocious alternative is q^* and the probability of choosing the migrant alternative is $1-q^*$. This, then, would be a mixed evolutionarily stable strategy (mESS) at the individual level with equal fitnesses. A crucial test to discriminate between the two possibilities is to investigate whether the precocious alternative really is inherited or not. We assume that the alternatives probably are not due to a genetic dimorphism, since available data have not shown that the precocious trait is inherited (*e.g.* GLEBE *et al.* 1978; BAILEY *et al.* 1980).

How can such an mESS exist without genetic

regulation of each alternative? In the following section we outline a possible solution to this problem.

Size-dependent choice

If the reproductive success of a precocious male is size dependent, it would be necessary for the male to know that he will reach a size within I in order to be precocious, if he chooses that alternative. We assume that the interval (I) is typical for each population. Since the time of decision, t_d, probably lies several months prior to the spawning period, the male parr has to take the decision before the migrating males have returned to the river. A male parr has to know at that time if his size at t_r is going to fall within the interval I, *i.e.* whether it will, in fact, be able to become precocious or not. This is made possible by a size interval D. This interval D will ultimately be adjusted by I so that an individual within D at t_d will also fit I at t_r. Thus an individual whose size falls within D at t_d will develop gonads and have a decreased growth rate compared with the time before t_d. However, it is not sufficient for the male at t_d to know that he will fit I at t_r. In order to maintain the ESS equilibrium it is also necessary that the appropriate fraction

$$q^* = \frac{\Sigma p_{i,tr}}{\Sigma(p_{i,tr} + m_{i,tr})}$$

becomes precocious, where $p_{i,tr}$ is the number of precocious males of age class i at t_r and $m_{i,tr}$ is the number of full-grown adult males of age class i at t_r. In order to reach q^*, a number of $\Sigma(p_{i,tr}/s_i)$ should fit D at t_d, where s_i is the probability of survival from t_d to t_r for a precocious male in age class i. Since D is also set to determine the proportion that is to become precocious it follows that the size range of precocious males found in the river (I') does not necessarily have to be the same as the interval I, but rather constitute a certain part of it (Fig. 2). When the population is stable, the ESS equilibrium is maintained by means of the size interval D. If the population size changes, q^* probably also changes due to changes in the fitness functions. An increase in population size would for example result
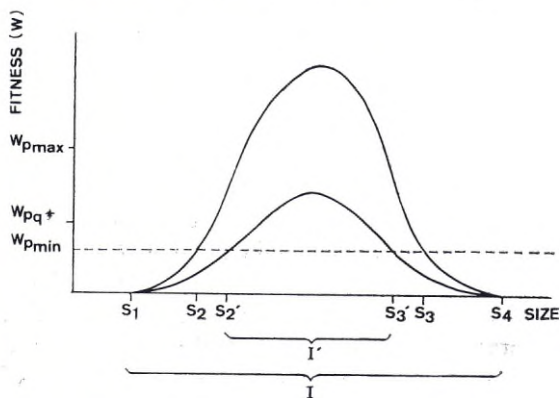
Fig. 2. The size-dependent fitness of precocious males. The outer curve describes the fitness as a function of precocious size in a situation of an infinitely small proportion precocious males. The sneaking behaviour is only possible if the male size lies within the range of I. The precocious alternative is only advantageous if the sizes of the precocious males lie within the range of I and have a fitness value that lies above the threshold (W_{pmin}). On average they will have the

fitness $W_{pmax} = \dfrac{1}{(S_3 - S_2)} \displaystyle\int_{S_2}^{S_3} f(s)\,ds$. At equilibrium the

proportion q^* should choose the precocious alternative

and then the average fitness $W_{pq^*} = \dfrac{1}{(S_3' - S_2')} \displaystyle\int_{S_2'}^{S_3'} g(s)\,ds$

is lower than W_{pmax}. Such a situation is described by the inner curve. As a result of the decreased fitness a small male should only choose the precocious alternative if he reaches a size within I′ at t_r.

in increased food competition and hence affect the fecundity and survival rates of the precocious and their offspring. The fitness function would then change for the precocious males, influencing q^* as well.

Consequently, individual growth rates are crucial for the outcome of this system. Whether an individual is going to fit D at t_d or not is dependent on the growth rate of the individual. In order to illustrate this hypothesis we have analysed the outcome of different growth rates with a given D (7—9 cm) and growth rates described by the von Bertalanffy growth model (Fig. 3). In this example a male should become precocious at least once if $0 < K \leqslant 0.1189$ or $0.1328 < K \leqslant 0.1783$ or $0.2657 < K \leqslant 0.3567$, where K is the parameter determining the growth rate. Out-

$L\infty = 30cm$
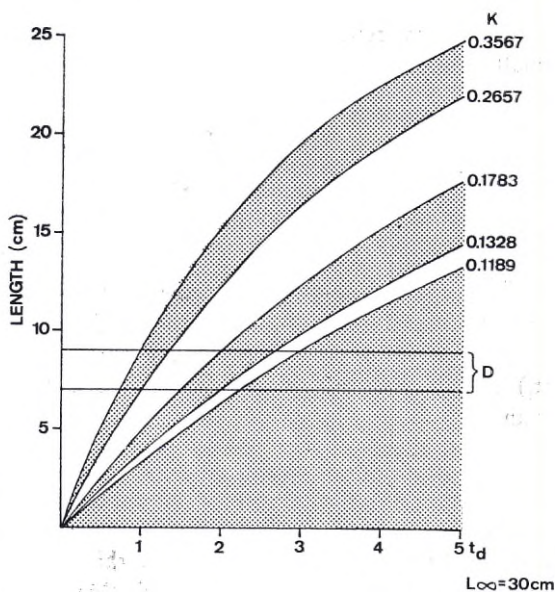
Fig. 3. An example of how D restricts the possibility of becoming precocious depending on growth rate. Only individuals with growth rates within the shaded areas will fit D at t_d, thus becoming precocious at t_r. Growth is described by the von Bertalanffy growth equation: $L = L_\infty (1 - e^{-K(t-t_0)})$, where L is length, L_∞ is the maximum length in the river (here arbitrarily set to 30 cm), K is the parameter determining growth rate and t is year of decision. $t_0 = 0$.

side these ranges no individual should adopt the precocious alternative. Low growth rates will result in individuals becoming precocious several times before migrating to the sea. More generally, the condition for becoming precocious can be expressed as

$$-\frac{\ln\left(1 - \dfrac{D_{min}}{L_\infty}\right)}{t_i - t_0} \leqslant K \leqslant -\frac{\ln\left(1 - \dfrac{D_{max}}{L_\infty}\right)}{t_i - t_0}$$

where L_∞ is the largest possible size a fish can reach in the river, D_{min} and D_{max} are the lower and upper limits of D, t_i is the i:th year (i=1,2, ...,n) when the male has to decide whether to become precocious or not and $t_0 = 0$.

On the basis of this, if D and the average growth rates in the river are known, it would be possible to predict what alternative an individual would choose. Furthermore, a test of the model would be to experimentally change the growth rates to fall outside their normal ranges. Indi-

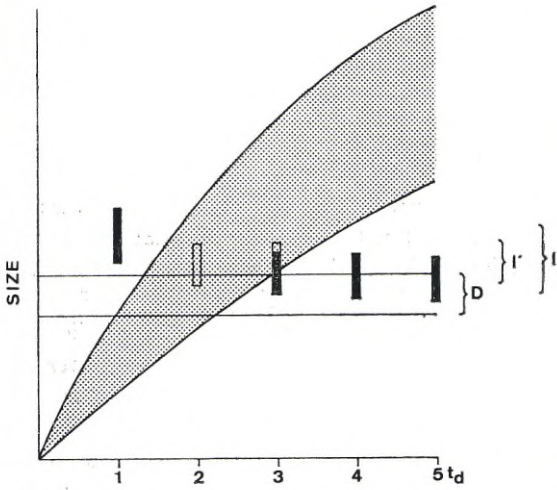Fig. 4. Size intervals for precocious males with growth rates different from the normal in a hypothetical river. The normal growth rates are found within the shaded area. An individual within D at t_d will become precocious and reach a size at t_r within the vertical bar, here for simplicity placed above t_d. Open bar denotes the precocious size interval (I') for the normal situation at equilibrium. Filled bars indicate examples of precocious size intervals for fish with greatly altered growth rates from the normal. Thus altering the growth rates for individuals from a given population will result in precocious males with sizes deviating from the normal.
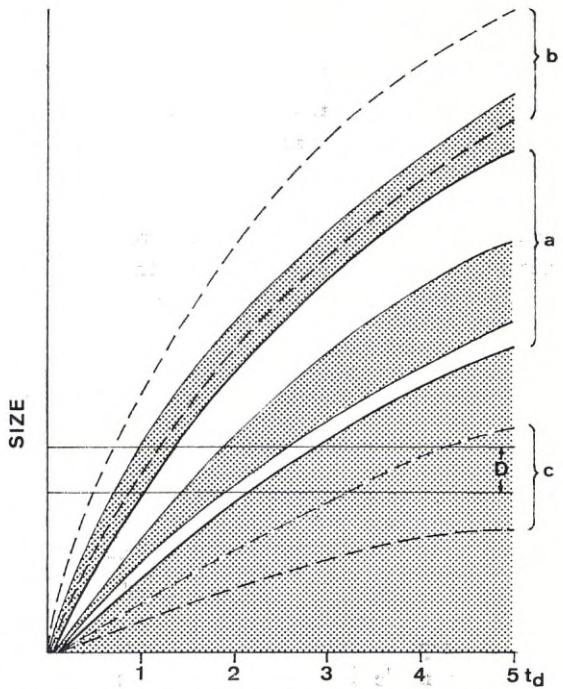

Fig. 5. The frequencies of precocious males are changed as the growth rates are changed from the normal (a). We assume that within the growth rate interval the individual growth rates are normally distributed. In this example higher growth rates than normal (b) result in lower frequencies of precocious males. With lower growth rates (c) all males become precocious. Males become precocious within the shaded areas as in Fig. 3.

viduals should still become precocious, but possibly fall outside I', or even possibly outside I, since D is adjusted to the normal growth situation in the river. That is, the frequencies and sizes of males choosing the precocious alternative will not necessarily remain the same. In Figs. 4 and 5 the effects of greatly altered growth rates are illustrated. No explicit test of this prediction has been made, but GIBSON (1978) has presented data showing that increased growth rates in salmon parr due to altered conditions in the river resulted in higher frequencies of precocious males as well as an increase in size in these males.

III. DISCUSSION

In a stable population at equilibrium, W_p should equal W_m. Measurements of life-time fitness are often extremely difficult to make, but if it is possible to calculate this, and if it can be shown that W_p and W_m approach equality, this would

give support to our assumption of an ESS situation. If such measurements reveal that $W_p \neq W_m$ one might regard the inferior strategy or tactic (apart from if the population is not at equilibrium or if sampling errors are great) as the "best of a bad situation" (BBS, GROSS 1984). In Atlantic salmon this could be the case if slowly growing individuals had seriously lowered survival and reproductive success compared to migrants and they simply want to take the chance to be precocious in order to have at least some reproductive value. Precociousness in the Atlantic salmon is found in a variety of growing conditions and it has indeed been suggested that high growth rates result in male parr becoming precocious (SCHIEFER 1971). Other studies have, however, shown that slowly growing individuals become precocious (POWER 1973). Thus, a BBS situation does not

seem to be applicable to the Atlantic salmon. Moreover, a BBS situation is certainly not a special case of an ESS situation.

Are the two alternatives then tactics in an mESS or strategies coexisting at an ESSt? Since available data indicates that the alternatives are tactics rather than strategies (GLEBE *et al.* 1978, BAILEY *et al.* 1980), the ESSt alternative probably does not apply to the Atlantic salmon. Another argument in favour of the idea that the reproductive alternatives are tactics is that parr from the same population, held under different conditions (temperature and salinity) resulted in unequal proportions of precocious males (6 % vs 50 %) (ERIKSSON unpubl.). Consequently we suggest that the life-history strategy in male Atlantic salmon is a mESS with the tactics being "migrant" and "precocious". By contrast, precocial maturity in coho salmon may have an underlying genetic basis (GROSS 1984). Contrary to this we argue that the choice of reproductive alternative in male Atlantic salmon is made by each individual male. The result of the choice is ultimately due to the relative fitness of the precocious and migrant males. Proximately the decision is due to individual growth rate.

For such a system to exist, there must be some mechanism regulating the frequencies of the two male types in such a way that the ESS equilibrium is maintained. Our size interval hypothesis could be one possibility. Indeed, there are several indications in favour of this hypothesis. In a number of studies it was found that the size of precocious males fell within a rather narrow range at various localities (LEE and POWER 1976 (17—20 cm), BAILEY *et al.* 1980 (10—18 cm), THORPE *et al.* 1982 (10—14 cm, 9—16 cm, 10—18 cm)). A lower limit for being precocious has also been suggested by BAILEY *et al.* (1980). These suggested size ranges would then roughly constitute our I'. There is no reason to believe that this size range should be the same in all rivers. For example, the size of returning full grown migrants and the competition situation in the river might influence the size of the interval.

Previous studies have also suggested that there is a critical time in the year when the males have to decide whether to migrate or become precocious (THORPE *et al.* 1980, LUNDQVIST 1983). This time

is thought to be in spring—early summer prior to the seaward migration and some months in advance of the spawning in autumn. This supports our assumption of t_d.

In the literature much attention has been paid to the smoltification process, *i.e.* the physiological and behavioural preparations for the seaward migration. ELSON (1957) suggested that there may be a lower size limit below which parr do not smoltify and BAILEY *et al.* (1980) gave further support to this idea. Other authors have indicated that it may be growth rate and not size *per se* that is crucial in the smoltification process (MITANS 1973, RANDALL and POWER 1979, SAUNDERS *et al.* 1982). A lower limit for smoltification might well coincide with, or at least be similar to, our upper limit of D, the smoltification limit, however, being regulated by size-dependent mortality when the fish are leaving the river and their first months in the sea. Since the selective forces acting on sizes for smoltification are not the same as those acting on D, the upper limit of D should vary independently of the smoltification limit.

The hypothesis of a mixed ESS equilibrium (MAYNARD SMITH 1982, GROSS 1984) adjusting critical size intervals as evaluated in this paper provides one possible explanation for the precocious phenomenon. STEARNS and CRANDALL (1984) have, however, suggested an alternative hypothesis concerning age and size at maturity in fish. They argue that neither size nor age alone is critical, but that there is an age-size trajectory along which individual fish mature optimally. Such a trajectory is also plastic, *i.e.* its shape varies with environmental conditions, such as mortality. They suggest that this hypothesis can also be applied to the life history alternatives of the Atlantic salmon. The application of this hypothesis to the Atlantic salmon can, however, be questioned. Firstly they do not allow for seasonal reproduction and secondly it should be very difficult to find a single age-size trajectory which takes into account the fact that mortality and growing conditions in the river are quite different from those in the sea.

Further studies aimed at contributing to the understanding of the male reproductive system in Atlantic salmon should be to test whether the fitnesses of the two alternatives are equal, as done

by GROSS (1985) for coho salmon, and whether the reproductive successes are negatively frequency-dependent. The crucial question on whether the precocious alternative is genetically pre-programmed or not remains unanswered.

IV. ACKNOWLEDGMENTS

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The Thermal Biology of Atlantic Salmon: Influence of Temperature on Salmon Culture with Particular Reference to Constraints Imposed by Low Temperature

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ABSTRACT

The Atlantic salmon (*Salmo salar* L.) is well represented in Atlantic subarctic areas and, because of its adaptations for survival in cold environments, is well suited for aquaculture in such areas. Low freshwater and sea temperatures slow growth of cultured salmonids and are a constraint to culture. The lower lethal temperature of *S. salar* is $-0.7°C$ in seawater. Commercial and experimental catches of salmon in offshore areas during fall-spring and growth rates during this period indicate that favorable, if not optimal, temperatures for feeding and growth of salmon during their marine phase are in the $4—12°C$ range, lower than for juvenile salmon in fresh water.

Atlantic salmon exposed to low temperatures ($0—1°C$) not only grow slowly during the juvenile phase but may also suffer osmotic and nutritional damage. The lower lethal temperature precludes culture of *S. salar* in many coastal marine areas. Special locations with safe water temperatures (no lower than $0°C$), together with adequate protection from heavy seas, are required for year-round culture of salmon in sea cages.

In spite of the constraints to salmonid culture under severe winter conditions, growth rates in sea cages in southwest Bay and Fundy, with annual temperatures from $1—14°C$, are as high as free-ranging salmon in nature. Moreover, the winter period at temperatures of $1—2°C$ may delay the onset of sexual maturation, a positive effect since immature salmon reach a larger size end are more valuable than mature individuals. Evidence is presented in support of the suggestion that low winter temperature, not difference in photoperiod, is largely responsible for lower incidence of grilse in northern than in southern sea farms.

Measures to counteract the low temperature constraint to aquaculture include seasonal shifting of salmon from seawater to fresh water, submerged cages, use of thermal effluent to raise temperatures, genetic engineering to produce freezing resistant salmon and manipulation of photoperiod to adjust physiology so as to make best use of periods of suitable temperature.

I. INTRODUCTION

In addition to having the usual biological and economic requirements such as ease of breeding, hatching and rearing all life stages, known nutritional requirements and high market price, candidate species for aquaculture in Atlantic subarctic areas must have tolerance to low temperature and a propensity for reasonable growth at such temperatures. The Atlantic salmon (*Salmo salar* L.) appears to meet these requirements. Its breeding and migratory ranges extend into and beyond Atlantic subarctic areas. The present breeding range is from Maine (Lat. 44°) to Ungava Bay, Quebec (Lat. 58°) in N. America, the Kapisigdlit River (Lat. 64°) in W. Greenland, most rivers in Iceland and, in Europe, from Spain and Portugal (Lat. 41°) to Finnmark, Norway (Lat. 70°) and rivers entering the Barents and Kara Seas (Lat. 69°) (MacCRIMMON and GOTS 1979). Separate breeding units (stocks) of *S. salar* have developed special adaptations, some of them in recognition of environmental extremes, which allow them to occupy places with specific demands (POWER 1981; SAUNDERS 1981; THORPE and MITCHELL 1981). SCARNECCHIA (1984), in discussing the variation in salmon catches from Iceland's north coast rivers where extremes and variations in sea temperature occur, says that "Populations near the edge of their distributions are more likely than those centrally distributed to be regulated by extreme environmental conditions as opposed to internal dynamics". The sal-

mon stocks in the rivers entering Ungava Bay, Quebec exemplify this statement; the climatic and marine conditions are such that smolt and kelt emigration and adult return are frequently delayed as ice lingers outside the river estuaries and passage may be precluded by frigid Arctic water for all but brief periods each year (POWER 1981). During some seasons, these fish do not leave their estuaries until late summer; in extreme cases they may remain in the estuaries or return to fresh water without having gone to sea (POWER 1981; ROBITAILLE *et al.* 1984a, b; ROBITAILLE *et al.* 1986).

The main constraint to aquaculture in Subarctic areas is low temperature and consequent low growth rates and, sometimes, death from freezing. The purpose of this paper is to consider the thermal biology of *S. salar*, how the species responds to low temperature and what measures aquaculturists might take to maximize production in spite of the cold aquatic environment.

II. THERMAL BIOLOGY OF ATLANTIC SALMON

Lower and upper lethal temperatures and optima

S. salar is a eurythermal species; its lower lethal temperature is $-0.7°C$ in seawater of 30 ⁰/₀₀ salinity (SAUNDERS *et al.* 1975) and the ultimate upper lethal temperature is $27.8°C$ (GARSIDE 1973). Although salmon and other marine fishes can live for some time at temperatures below their lower lethal provided they do not come in contact with ice (SCHOLANDER *et al.* 1957) and salmon in fresh water can endure temperatures higher than $27.8°C$ for short periods (HUNTSMAN 1942), these temperatures should not be closely approached during culture operations. The thermal range giving best growth of juvenile salmon in fresh water is $14—18°C$; the optimum for fry is said to be about $16°C$ (JAVAID and ANDERSON 1967; SIGINEVICH 1967). A consideration of optimum temperature for marine growth is in a later section, thermal adaptations during marine life.

Aquaculturists should be aware of thermal optima for growth but should appreciate that seasonal and ecological factors may modify feeding and growth responses to temperature.

Salmonid culturists commonly observe that a given temperature, say $6°C$, elicits a much stronger feeding response as temperature rises to this level in the spring than as it cools to $6°C$ in autumn. This response is likely owing to photoperiod-induced increases in growth hormone (KOMOURD-JIAN *et al.* 1976) and other endocrinological activity. BRETT (1971) suggested that sockeye salmon (*Oncorhynchus nerka*) may derive metabolic benefit during their juvenile residence in lakes by rising from the hypolimnion during summer months (35—45 m, 8—10°C) to feed at dawn and dusk near the surface (15—17°C) and return to the hypolimnion to digest and assimilate their food. This pattern of thermoregulation may have evolved partly in response to predators near the surface.

Influence of temperature on physiology and behavior

Juvenile salmon in nature make an abrupt change in habitat in autumn as temperature falls. ALLEN (1941) observed during the autumn that below $7°C$ *S. salar* in a northern Scottish river appear to lie quiescently in sheltered places feeding and growing little. RIMMER *et al.* (1983) reported that salmon in a New Brunswick stream disappeared from their summer feeding stations in the autumn as water temperature fell to or below $10°C$ and were found sheltered in chambers among and beneath streambed stones in the same areas they occupied during summer. Moreover, the ability to hold position against stream current decreased sharply at temperatures below $8°C$. Critical holding velocity (stream velocity at which fish were unable to stem water currents) of naturally produced fish was much greater than for hatchery-reared fish; values fell sharply below $8°C$ (RIMMER *et al.* 1985). The likely significance of these observations is that energetic demands of salmon in nature during periods of low temperature and reduced feeding are minimized by resting in sheltered places with reduced water currents; hatchery-reared salmon are less able than those naturally produced to stem stream currents. Such thermally induced behavior may also help in avoiding predation. The crowded conditions in artificial culture and the usual smooth concrete or

fiberglass tanks used in most rearing stations permit no energy-saving behavior like that observed in naturally produced salmon. The specially constructed, radial-flow rearing chambers described by THORPE (1977) are clearly superior, in this respect, to most other tanks for rearing salmon.

Although photoperiod is the main environmental variable controlling salmonid parr-smolt transformation (WEDEMEYER *et al.* 1980; SAUNDERS *et al.* 1985), water temperature and river discharge exert the primary influence on migratory behavior (BAGGERMAN 1960; WEDEMEYER *et al.* 1980; JONSSON and RUDD-HANSEN 1985). WHITE (1939), ÖSTERDAHL (1969), BAGLINIÈRE (1976), SOLOMON (1978) and POWER (1981) have reported that Atlantic salmon smolts move downstream as temperature rises to the 8—10°C range. JONSSON and RUDD-HANSEN (1985) stress that the timing of smolt descent is not related to a threshold temperature or number of degree days but to variations in water temperature during April— May. In the rivers entering Ungava Bay, Quebec, salmon may smoltify during successive years and reach an unusually large size before thermal conditions are suitable for them to leave the river or enter the sea (POWER 1959, 1981). Although migratory behavior is not necessary for smolts being produced for aquaculture, this manifestation of the completion of smoltification is a convenient indicator of the readiness to enter seawater. SAUNDERS and HENDERSON (1978), JOHNSTON and SAUNDERS (1981), SAUNDERS *et al.* (1985) and KRISTINSSON *et al.* (1985) suggest how temperature and photoperiod can be manipulated during culture of *S. salar* to maximize growth while still allowing proper smolt development.

Thermal adaptations during marine life

Although temperatures from 14—18°C are ideal for feeding and growth of juvenile Atlantic salmon (JAVAID and ANDERSON 1967; SIGNINEVICH 1967), such temperatures are seldom available to them during their life at sea, at least, not in the N. Atlantic. Relatively warm surface waters are available over the productive banks off Nova Scotia and New England but many salmon choose to move north. Post-smolts from Maine rivers are

frequently taken in the Bay of Fundy and along the coast of Nova Scotia; later marine stages of Maine salmon contribute to fisheries off W. Greenland, Newfoundland and Labrador (MEISTER 1984). Perhaps marine distribution of salmon can tell us something about their thermal requirements and preferences during their marine phase.

The high seas fisheries for feeding salmon near W. Greenland (MAY 1973) and the Faeroe Islands (ANON. 1984) have greatly increased our knowledge of salmon during their marine phase, their diet and their thermal biology. DUNBAR (1982) summarizes the information on climatic changes in the W. Greenland area during the 20th century. DUNBAR and THOMSON (1979) give evidence that *S. salar* has not always been abundant off W. Greenland. Periods of abundance appear to correspond with cooling sea surface temperatures, not warming periods which are associated with abundance of cod (*Gadus morhua*) which migrated there from an area near Iceland. DUNBAR and THOMSON (1979) suggest that northward expansion of the Labrador Sea gyre into Davis Strait, together with the intensification of the W. Greenland Current have shifted the distribution of salmon into this area.

Judging from catches in various sea fisheries and from research vessels, the acceptable temperatures during the marine phase are between 4 and 12°C. ALM (1958) reports that Baltic salmon move to deeper, cooler water when surface temperature exceeds 11—12°C and return to surface layers when they cool to 11—12°C. ALM reports, further, that maturing salmon enter coastal and river waters of much higher temperature; he suggests that maturing salmon are less sensitive to high water temperatures than migrating, feeding salmon. THUROW (1966) suggests that sea temperatures from 2—8°C constitute an optimum range for *S. salar* in the Baltic. Salmon near W. Greenland and in Davis Strait are seldom found in water colder than 2°C (MAY 1973). The best catches have been made in the W. Greenland area during late summer-autumn when water temperatures are from 3—8°C (MAY 1973). CHRISTENSEN and LEAR (1980) have shown a direct correlation between salmon catches and surface temperatures at W. Greenland. TEMPLEMAN (1968) reported on research catches of feeding salmon in the Labrador

Sea during the autumn and spring when surface temperatures were 3.7—6.1°C. TEMPLEMAN speculated that salmon are present year round on bank and shelf areas and probably are found also over oceanic depths off Newfoundland. Surface temperatures of 3—6°C are probably available in the Northwest Atlantic even during winter (TEMPLEMAN 1968; LEAR 1976; REDDIN 1985). During late summer, salmon are found in surface waters of 8.5—9.6°C in the Labrador Sea and near the southern tip of Greenland. Thus, suitable temperatures are available in that area allowing salmon to continue feeding and growing; their scales indicate a slow but significant amount of growth during winter-spring. LEAR (1976) suggests that the area around the southwestern Grand Bank and southwestern St. Pierre Bank, where surface temperatures are 3—6°C, is an overwintering area for N. American Atlantic salmon. More recently, REDDIN (1985) reported large concentrations of salmon over oceanic depths off Newfoundland in the spring where surface temperatures were 4—6°C and that these salmon were feeding on a variety of fish and invertebrates. REDDIN (1985 and pers. comm.) suggested that water temperature, more than abundance of prey, appeared to affect marine distribution. Although stomach contents were five times greater in salmon taken over Grand Bank than those taken in areas farther offshore, catch rates were greater in the more offshore areas where water temperature was higher. REDDIN (1985) reports, further, that the salmon in his catches include 1-sea-winter fish which were maturing (as grilse) together with multiple-sea-winter fish.

REDDIN (pers. comm.) suggests that salmon abundance and their onshore movements from winter-spring feeding grounds and the timing and location of the beginning of the Newfoundland coastal net fishery may be influenced by the location of the 4°C isotherm. The annual beginning of the coastal fishery around insular Newfoundland is often delayed by accumulation of sea ice which is affected by sea and air temperatures together with wind direction and intensity acting with the prevailing Labrador current (O'CONNELL et al. 1985). Annual variations in the distribution of sea ice along the east coast of Newfoundland may have a marked influence on the catch of

mainland (Canadian Maritime Provinces and Maine, U.S.A.) salmon during their onshore migration toward their rivers (REDDIN and BURFITT 1984).

Any suggestion that the best thermal range for feeding and growth of *S. salar* during its marine phase is lower than for its juvenile (freshwater) phase is speculative just now but there is a strong suggestion from the foregoing discussion that this is the case. Experimental data on temperature selection and feeding and growth studies with post-smolts at a wide range of temperatures are, to my knowledge, lacking. In addition to the obvious necessity to cope with the change in salinity during the transition from a freshwater to a marine fish, *S. salar* must be prepared to do its feeding and growing at much lower temperatures in the sea than in rivers.

BLAKE et al. (1984) give data which suggest that there is a metabolic adjustment associated with smoltification. The activities of the respiratory chain enzymes, cytochrome C oxidase and succinate dehydrogenase and concentrations of liver mitochondria are greater in smolts than in parr. These and other, so far unexplored, attributes may give smolts a greater scope for metabolism and growth than parr. This metabolic adjustment may or may not be related to thermal adaptations during marine life.

Judging from growth rates of salmon during the marine phase (ALLEN et al. 1972) and catches in various sea fisheries and research fishing, the temperatures between 4—8°C must be acceptable if not, indeed, ideal for marine growth. The smolting process appears to mark a major change in metabolic pattern between the juvenile phase in freshwater and the marine phase (FONTAINE and HATEY 1950; WENDT and SAUNDERS 1973; BLAKE et al. 1984). This suggested change in thermal optima between freshwater and marine phases would be an adaptation by the species allowing it to exploit these two diverse habitats, taking advantage on the one hand of the time of higher productivity in freshwater nursery streams (spring and early summer), and on the other hand the opportunity to exploit a larger and more diverse food supply on a year-round basis but in a cooler environment. This adaptation would allow salmon to reach a large size in the sea, enhancing survival

rates through reduced susceptibility to predation and producing an abundance of spawn.

Thermal behavior in other anadromous salmonids

Sea-running populations of Arctic charr (*Salvelinus alpinus*) and brook trout (*S. fontinalis*) are facultatively anadromous in most, if not all, cases spending only summer weeks or months in the sea and winter in brackish or fresh water (HUNTER 1966; NORDENG 1971; McCORMICK *et al.* 1985). Brook trout appear not to undergo smoltification and develop less hypo-osmotic regulatory ability than Atlantic salmon (McCORMICK *et al.* 1985). Arctic charr and brook trout make limited excursions to sea but apparently do not make long distance migrations as do Atlantic salmon and do not seek suitable temperatures for feeding and overwintering offshore. Anadromous populations of Arctic charr in N. America and Europe return to fresh water in late summer or early autumn (HUNTER 1966, NORDENG 1971). Anadromous populations of brook trout probably do the same although this is not certain. It is likely, however, that anadromous populations of brook trout in Canadian Atlantic provinces overwinter in fresh water or suitable estuaries. An anadromous population of brook trout in the N.W. Miramichi ascend the river each spring during May—June (SAUNDERS, unpubl. observations). These fish may have overwintered in the lower part of the river or estuary, since coastal and offshore waters in this area have lethal temperatures each winter. Brook trout, especially the males, suffer osmoregulatory failure and have reduced salinity tolerance when they become mature (SAUNDERS *et al.* 1975; SUTTERLIN *et al.* 1976; McCORMICK and NAIMAN 1984). Brook trout osmoregulate less well at low temperatures (0—2°C) than Atlantic salmon and rainbow trout (*Salmo gairdneri*) (SAUNDERS *et al.* 1975).

III. PROBLEMS IN SALMON CULTURE

Physiological effects of low temperature

Low winter temperatures can have strong adverse effects on culture of salmon during their juvenile stages in fresh water and during grow-out operations in seawater. For example, smolt production under such conditions usually requires two years, thus reducing plant output and increasing cost of production. Sustained periods of near 0°C temperature in northern rearing stations may lead to depletion of energy reserves and what is referred to as coldwater gill "disease" (JOHANSSON 1968; WENDT and SAUNDERS 1973). This "disease" may be a symptom of malnutrition resulting from bioenergetic demands exceeding or nearly exceeding energy reserves in the form of stored lipids.

A further consequence of long-term exposure of Atlantic salmon to low temperature (ca. 1°C) is osmotic imbalance (BYRNE *et al.* 1972). Osmolality of post-smolt salmon in fresh water was significantly lower at < 1°C than at temperatures from 3—14°C, an indication of possible osmotic imbalance. There was no such imbalance at 15 $^0/_{00}$ salinity but significantly higher osmolality and Na^+ values at 1°C and 30 $^0/_{00}$ salinity than between 3 and 14°C. Forced swimming activity exacerbated osmotic and ionic imbalance in water of 0 and 30 $^0/_{00}$ salinity but had little effect at 15 $^0/_{00}$ which is nearly isosmotic with salmon blood. Depressed levels of Na^+ and Cl^- in juvenile salmon held for long periods in poorly mineralized (soft), cold fresh water may be owing to a net loss of these ions to the environment because the fish are not feeding.

VIRTANEN and OIKARI (1984) report that low temperatures (1.5°C) promoted hyperglycaemia in *S. salar* in both fresh and salt water and suggest that this condition is related to altered energy metabolism owing to the low temperature. *S. salar* and *S. gairdneri* subjected to the lower lethal temperature (−0.7°C) had only moderately elevated osmolalities (ca. 364 Mosmol/kg) which probably did not lead to mortality (SAUNDERS *et al.* 1975). Mortality was owing to formation of ice crystals in the tissues. Brook trout, on the other hand, had osmolalities of ∼ 492 Mosmol/kg at 2°C and probably died at −0.7°C from a combination of severe osmotic imbalance and formation of ice crystals.

Physical constraints to aquaculture in cold climates

The lower lethal temperature of −0.7°C for *S. salar* precludes year-round sea-cage culture in

many suitably sheltered locations in subarctic areas. A north flowing branch of the Gulf Stream along the west coast of Norway permits year-round culture of *S. salar* and *S. gairdneri* from Lat. 59° to 71° where temperature usually remains well above 0°C. The south and east coasts of Norway (MIDTTUN 1975) and the west coast of Sweden are not warmed by the Gulf Stream and sometimes have sea surface temperatures in the lethal range. In spite of keen interest in salmonid aquaculture in eastern Canada, year-round sea-cage culture is limited so far to a small area in S.W. Bay of Fundy where sea surface temperature has, in recent years, fallen no lower than 0°C (SUTTERLIN *et al.* 1981, SAUNDERS *et al.* 1983), and along the S.W. coast of Nova Scotia where sea temperatures are comparable with those in S.W. Bay of Fundy. This is at a latitude of 44—45° which corresponds with that of southern France. Much of eastern Canada's coastline is cooled by the southward flowing Labrador current which precludes overwintering of salmonids in surface floating sea cages in Newfoundland, Quebec and northern Nova Scotia and New Brunswick. Great care must be taken in selecting sites which provide suitable protection from heavy seas and which have suitable winter temperatures. Location of cage farms too close to shore in areas with extreme tidal amplitudes (> 8 m), like those in the S.W. Bay of Fundy, may result in local cooling of seawater to lethal levels in intertidal areas which remain largely ice-free because of the extreme tidal mixing.

Another danger in nearshore areas is from floating ice, particularly in areas near freshwater outflow. The successful sea farms in S.W. New Brunswick and S.W. Nova Scotia are located in limited areas which are influenced mainly by oceanic water and which are protected by islands or headlands extending away from dangerous nearshore conditions. During recent years with relatively mild winters and acceptable sea temperatures, the most serious physical constraint to expansion of the salmonid farming industry in S.W. New Brunswick and S.W. Nova Scotia has been availability of suitably protected places. There is, nevertheless, the threat of lethal temperatures should winter sea temperatures return to the low levels that existed in the 1960's (St. Andrews Biological Station, unpubl. records), before sea farming was started in the S.W. Bay of Fundy area.

IV. POSSIBLE BENEFITS FROM LOW TEMPERATURE

High growth rates at low sea temperatures

It was a surprise to learn that growth of cage-reared Atlantic salmon in the vicinity of St. Andrews, N.B. is as great or greater than that of free-ranging salmon in the N.W. Atlantic. This is in spite of winter temperatures in the 1—3°C range for three to four months (SUTTERLIN *et al.* 1981; SAUNDERS *et al.* 1983). Cage-reared salmon do not grow perceptibly between December and March. The period of growth in Bay of Fundy sea cages is from April to November with maximum sea temperatures seldom reaching 13°C. Since the available evidence is that free-ranging salmon at sea are found in water warmer than 4°C (REDDIN 1985) and those salmon caught during winter months are feeding, it is remarkable that the cage-reared fish, which feed little during three to four winter months, reach greater sizes than their free-ranging counterparts (SUTTERLIN *et al.* 1981; ALLEN *et al.* 1972). Such growth of cage-reared salmon is probably influenced by the abundance of high quality food provided and no expenditure of energy required in searching for and capturing it. Strong tidal currents in the Bay of Fundy area provide rapid exchange of water through sea cages with disolved oxygen remaining near air saturation levels. Sea-cage operators in S.W. New Brunswick begin harvesting salmon of 3.5 kg in October, only 17—18 months after putting 1+ smolts (ca. 50 g) in sea cages. It appears, then, that areas with relatively low sea temperatures are more than adequate for salmonid production in sea cages since growth is fast enough during the eight to nine months when temperature is suitable for feeding to outstrip, on a yearly basis, free-ranging salmon that appear to have suitable temperatures and the opportunity to feed all winter (REDDIN 1985).

Low sea temperatures may delay sexual maturation

There is encouraging evidence that low sea temperatures during winter may further enhance production rates in sea farms by delaying sexual maturation and allowing continued somatic growth. Although there is clear evidence of a genetic component in determination of sea age and size at maturity in *S. salar* (NAEVDAL 1983; GJERDE 1984), there is also a strong environmental effect which modifies the genetic propensity. SAUNDERS *et al.* (1983) reported that two strains of salmon that have high grilse/multi-sea-winter (MSW) salmon ratios under natural conditions had low ratios when reared in sea cages at a New Brunswick farm. One strain which yields grilse to MSW salmon in a ratio of about 1:1 under natural conditions produces few or no grilse when reared in sea cages. The second strain which produces a preponderance of grilse in nature (SAUNDERS and SCHOM 1985) produces significant numbers of grilse in sea cages but at a much lower incidence than in nature. Moreover, both strains show fluctuations from year to year which appear to be related to minimum temperatures during December—January; fewer grilse were produced following winters with temperatures of 0—2°C than following those with 3—4°C. SAUNDERS *et al.* (1983) suggest that low sea temperature at a certain time during winter may result in the fish's making a physiological "decision" not to commence sexual maturation that year. This appears to apply to fish which might otherwise mature as grilse or MSW salmon. The available data on sea temperatures experienced by free-ranging salmon overwintering under natural conditions (REDDIN 1985) suggest that these winter temperatures are considerably higher than those in sea cages in S.W. Bay of Fundy. It is to be expected that not all strains of salmon would respond in the same way to lower winter temperatures than they usually experience at sea. Moreover, perhaps not all strains overwinter in the same sea areas, some naturally experiencing low temperatures similar to those at N.B. cage sites. SCARNECCHIA (1983) provides evidence that sea temperature affects the grilse-larger salmon ratio in Icelandic salmon stocks. Salmon from southern and western Icelandic rivers enter relatively warm ocean

water and return mainly as grilse. Those from northern and northeastern rivers enter colder ocean water and produce fewer grilse. SCARNECCHIA (1983) showed that ocean temperature in June explains much of the variability in the ratio of grilse to MSW salmon in Iceland. He did not report on ocean temperatures encountered at later stages or the possibility that various stocks of Icelandic salmon mix during their marine phase. KORSGAARD *et al.* (1986) have shown that there is a direct correlation with temperature in the vitellogenic response to estradiol treatment in male and female, post-smolt salmon spending their first winter in sea water. Vitellogenin, a yolk precursor produced by the liver, is a useful indicator of maturation in Atlantic salmon (IDLER *et al.* 1981).

It has been clearly demonstrated that members of a strain of salmon reared at a number of locations, each with different environmental conditions, typically have different growth rates and age and size at maturation (NAEVDAL 1983). This phenomenon, called genotypic-environmental interaction, may explain, at least in part, the higher incidence of grilse in Norwegian salmon strains reared in Norway, Scotland, Ireland and France. Irrespective of the strains of salmon being reared, there is a general increase in incidence of grilse when rearing operations are compared from northern to southern Norway, to Scotland, to Ireland and to France. The generality is that fewer grilse are produced in northern Norway and that the ratio of grilse to MSW salmon increases stepwise from northern to southern Norway, to Scotland, to Ireland, to France. GILLES BEOUF (pers. comm.) observed > 80 % grilse using a "grilse strain" and 50—70 % grilse using a "non-grilse" strain from Norway when both strains were grown out in sea cages in Brittany. There are similar, though less dramatic, differences in grilse/MSW salmon ratios comparing Norway with Scotland and Ireland.

Different thermal regimes between northerly and more southerly regions are the most likely environmental variable affecting age at maturation. DAG MØLLER (pers. comm.) observed that the grilse/MSW salmon ratio in Norwegian sea farms varies from year to year, fewer grilse being produced following more severe winters. However,

natural photoperiod regimes also vary greatly between the locations (N. Norway to France) where *S. salar* are being cage reared. SCARNECCHIA (1983) stressed that although sea temperature and latitude were closely correlated, there is clear evidence that sea temperatures off N.W. Iceland, not latitude, affected percentages of grilse. Further support for the contention that winter temperature, more than latitude and related photoperiod, is responsible for low incidence of grilse at northern sea farms is the observation of low and high incidence of grilse in New Brunswick and Brittany respectively, both at approximately the same latitude. However, different stocks of salmon were reared at these two locations. It remains to be demonstrated whether sea temperature or photoperiod (in relation to latitude) is more important as an influence on maturation as grilse. At any rate, it appears that salmon culturists at high latitudes can expect to produce grilse-to-MSW salmon at lower ratios than their counterparts to the south.

V. MEASURES TO COUNTERACT CONSTRAINTS FROM LOW ENVIRONMENTAL TEMPERATURE

Temperatures for incubation and early rearing

Subarctic conditions are unlikely to result in serious constraints during incubation of Atlantic salmon for aquaculture. Spawning in nature takes place at temperatures from slightly above 0°C to as high as 10°C. PETERSON *et al.* (1977) incubated newly fertilized salmon eggs at 2° intervals between 2 and 12°C with transfer of subgroups after eyeing and after hatching to the same 2° intervals between 2 and 12°C. Observations on survival and alevin and fry size were made following incubation under the resulting large number (66) of temperature regimes. There was higher mortality prior to eyeing at temperatures below than above 4°C. The results show that, although eggs can be incubated over a wide thermal range and with changing temperature, alevin size at hatching is reduced as incubation temperature increases. Sudden decrease in temperature induces severe edema which may result in reduced growth and death. The optimum temperature from fertil-

ization to eyeing was judged to be ca. 6°C, based on time to eyeing and size of alevins at hatching. Compromises are necessary in choosing the best temperature for the stage between eyeing and hatching. High temperature (12°C) results in most rapid development but encourages fungus infections; lower temperatures (< 2°C) result in maximum alevin size but later hatching. Similar compromises must be made when choosing temperature for the stage from hatching to first feeding.

HEGGBERGET and WALLACE (1984) investigated effects of low incubation temperatures (means: 1.31, 1.10 and 0.65°C) on time to hatching in *S. salar* in consideration of the effects of hydroelectric development on the River Alta in northern Norway. It was concluded that such development and consequent elevated temperatures would result in earlier hatch (about wo weeks) in the river. Of perhaps greater importance would be time of swim-up and first feeding in relation to other biota in the river.

Since incubation requires relatively little water, it is economically feasible to heat water to achieve the desired rate of embryonic development and time of hatching. However, it is of utmost importance that the time of first feeding should be planned to coincide with availability of water at 10—14°C, temperatures at which Atlantic salmon successfully start feeding. GOFF and FORSYTHE (1979) have experienced best success with survival and growth of Atlantic salmon fry at the Mersey Fish Culture Station, Nova Scotia, by orchestrating embryology, hatching and alevin growth so that first feeding does not precede the thermal rise in hatchery water supply to 12°C.

Thermal manipulation to enhance juvenile growth

A partial solution to the low temperature problem in northern latitudes is to locate hatcheries and grow-out facilities in places where they can take advantage of thermal effluent. Few areas have the advantage of geothermal water available for salmonid culture. One such place is Iceland where this natural resource has already resulted in significant developments of subarctic salmonid culture (GUDJONSSON 1973, ÍSAKSSON 1980, 1985) and is sure to see more such activity in the coming years. Two symposia have been devoted

to the technology of using thermal effluent for aquaculture. These were "Waste Heat and Nutrient-Loaded Effluents in Aquaculture" sponsored by the North Atlantic Treaty Organization (NATO) and "New Developments in the Utilization of Heated Effluents and Recirculation Systems for Intensive Culture" sponsored by the European Inland Fisheries Advisory Committee (EIFAC). These meetings brought out many reports on studies showing benefits to be derived from thermal effluent. Some examples of particular interest are use of heated brackish water to speed growth of juvenile Atlantic salmon (VIRTANEN *et al.* 1981; TUUNAINEN *et al.* 1981); recirculation systems to minimize volume of water required and to reduce heating costs by minimizing thermal exchange (MØLLER and BJERK 1981); direct use of cooling water or in conjunction with a heat exchanger (SAUNDERS 1976; KITTELSEN and GJEDREM 1981; INGEBRIGTSEN and TORRISSEN 1981), extracting heat from large bodies of water (WANDSVIK and WALLACE 1981) and use of heat pumps. However, culturists should be cautioned not to use high temperatures ($> 12°C$) in late winter-early spring because these can interfere with some aspects of smoltification in *S. salar* (JOHNSTON and SAUNDERS 1981).

Grow-out arrangements where winter conditions are marginal

The obvious, though undesirable, procedure to follow in areas where low winter temperature precludes overwintering in sea cages is to harvest Atlantic salmon post-smolts after one summer and autumn. This strategy is probably unacceptable because post-smolts would reach, at most, only ca. 2 kg which is smaller than the desired market size. Considering the high cost of smolts, it is unlikely that marketing fish smaller than 2 kg would be profitable. Perhaps a special marketing effort could create a demand for salmon of this size. Other salmonid species may be more attractive for rearing and harvesting after one summer and autumn.

It is technically feasible, although perhaps not financially acceptable, to move salmon from sea cages to fresh water for the winter and back to seawater for continued rearing to market size.

Mariculture operators in at least two North American areas, Quebec and St. Pierre et Miquelon, are using this strategy of seasonal movement between seawater and fresh water.

Some potential locations for salmonid mariculture have acceptable temperatures deeper in the water column, either under cold surface water or below an ice cover which often prevents further cooling and may help to preserve the deeper, thermally stratified layers. ANDERSON (1983) suggests a strategy using the relatively warm seawater trapped below layers of ice and brackish water in Kennebecasis Bay, New Brunswick. He suggests pumping the relatively warm water to floating cages or onshore tanks. Atlantis Sea Farms of Clifton Royal, N.B., are using pumped seawater from Kennebecasis Bay to speed smolt production in onshore tanks. Another strategy is to hold fish in submerged cages at levels where temperature is acceptable. This has been done satisfactorily in two locations in eastern Canada, in S.E. Newfoundland and Cape Breton, Nova Scotia. However, MIKHEYEV *et al.* (1970) have reported that rainbow trout lost equilibrium and developed ulcers or died after prolonged confinement in submerged cages. It is suggested that these difficulties are owing to the fish being denied access to the surface from which to gulp air for maintenance of swimbladder volume. ERIKSSON (1983) reported similar difficulties with *S. salar* but that these can be overcome by bubbling compressed air into sea cages to keep the surface open for feeding and to allow the fish access to the surface. Moreover, salmonids could maintain swimbladder volume by ingesting air bubbles in the water column.

Genetic engineering for resistance to freezing

FLETCHER (pers. comm.) and his colleagues are conducting research on the possibility of improving freezing resistance of Atlantic salmon by introducing from winter flounders (*Pseudopleuronectes americanus*) the gene or genes involved in production of polypeptide antifreeze compounds (DUMAN and DeVRIES 1974, 1976; DAVIES and HEW 1980; FLETCHER and SMITH 1980). FLETCHER and his colleagues use recombinant DNA technology to amplify antifreeze genes which are inserted

by microinjection into fertilized salmon eggs. Recently, they have obtained evidence that the introduced flounder genes are present in Atlantic salmon reared for about a year following injection. Expression of the gene will be determined by presence of the antifreeze compounds and freezing resistance of the salmon. Further aspects of the study are whether or not and under what conditions the gene or genes will be activated or expressed. If individuals are found to have increased freezing resistance, these will be bred with normal salmon to determine if freeze-resistance is heritable. This would be followed by development of freeze-resistant strains for culture in locations that are presently unacceptable because of the high probability of encountering lethal temperatures.

Photoperiod manipulation to take best advantage of suitable temperatures

It has been clearly demonstrated that photoperiod exerts a strong influence on parr-smolt transformation in salmonids with particular reference to *S. salar* (SAUNDERS and HENDERSON 1970; WAGNER 1974; KOMOURDJIAN *et al.* 1976; BRAUER 1982; ERIKSSON and LUNDQVIST 1982; CLARKE *et al.* 1985; KRISTINSSON *et al.* 1985). *S. salar* reared for all or much of their freshwater growth phase under long, unchanging daylength or continuous light grow faster than those reared under a simulated natural photoperiod (KOMOURDJIAN *et al.* 1976; SAUNDERS *et al.* 1985). However, we found that salmon reared under photoperiods other than the simulated natural one for our latitude (45°N) did not develop smolt characteristics or grow as well following transfer to sea water as smolts produced under simulated natural photoperiod. Recently, we have demonstrated that it is feasible to use extended daylength during two to three months in autumn to enhance growth rates and still promote smoltification by restoring and maintaining simulated natural photoperiod until the following spring (SAUNDERS, unpubl. data). This procedure may be useful in places where short growing seasons usually preclude production of 1+ smolts. It is important to provide the growth-stimulating, long daylength before temperatures fall below ca. 10°C in autumn. It is likely that long daylength or continuous light stimulates growth at that time of naturally, decreasing daylength, three months or more past the summer solstice. KOMOURDJIAN *et al.* (1976) observed that imposition of long daylength beginning at the winter solstice stimulated growth of pre-smolt. Atlantic salmon and resulted in increased size, number and apparent activity of pituitary growth hormone cells. However, this was done in the laboratory at elevated (10°C) temperature.

Manipulation of photoperiod as a means of enhancing growth may be equally effective during the marine phase. It may be feasible to use artificial light to extend daylength in a sea-cage operation. Sea water temperatures in S.W. New Brunswick and S.W. Nova Scotia often remain in the 8—10°C range until early December. Based on the above observations with juvenile salmon in fresh water, there may be a similar growth response of post-smolt salmon to artificially extended daylength during the autumn when natural daylength, and presumably growth hormone activity, are rapidly decreasing. The period for effective photoperiod treatment may develop earlier in subarctic areas where daylength decreases much faster during summer and autumn than in areas to the south. If this is so, mariculturists could provide artificially long daylength while sea temperatures are still high enough to allow heavy feeding and rapid growth. Studies should be conducted to learn if such photoperiod manipulation produces enhanced growth without undesirable early maturation.

VI. CONCLUSIONS

Atlantic salmon are commonly found in Atlantic subarctic areas and, because of their adaptations for survival in cold environments, are well suited for aquaculture in such areas. Separate breeding units (stocks) of *S. salar* L. have developed special adaptations, in recognition of environmental extremes, which allow them to occupy places with specific demands. The chief constraint to aquaculture in subarctic areas is low temperature and consequent low growth rates and, sometimes, death from freezing.

The lower lethal temperature of *S. salar* is

−0.7°C in sea water; the optimum for growth during the juvenile phase in fresh water is 14—18°C. Temperatures below 8—10°C elicit energy saving behavior in juveniles in fresh water. Smolt development is completed at temperatures of 8—10°C and downstream movement is timed by variations of river water temperature during April—May.

S. salar appears to have a lower thermal optimum during its marine than during its juvenile phase. Acceptable temperatures for feeding and growth appear to be between 4 and 12°C, based on catches in various sea fisheries and from research vessels. Movements in the N.W. Atlantic appear to be influenced by the location of the 4°C isotherm. It is suggested that smoltification marks a change in metabolic pattern, allowing salmon to exploit two diverse habitats, one, in fresh water, with food available mainly during periods of high temperature and the other, in the sea, with lower temperatures prevailing year-round but with food available most of the year.

Low rearing temperatures result in slow juvenile and marine growth. Lethal marine seawater temperatures limit sea cage culture to relatively small areas of Eastern Canada, in S.W. New Brunswick and S.W. Nova Scotia. The combined requirements of acceptable temperature and protection from heavy seas further limit suitable cage sites. However, salmon grow well in this area during the eight to nine months when temperature is in the 4—12°C range. Growth of cage reared salmon in the Bay of Fundy area is faster than in free-ranging salmon in the N.W. Atlantic. Moreover, low winter temperature appears to result in a physiological "decision" to postpone sexual maturation. This leads to greater production through maintenance of somatic growth. In Europe there is an increase in the incidence of early maturity of cage reared salmon from north to south, probably owing more to the increase in winter sea temperature north to south than to differences in photoperiod.

Low winter temperatures for incubation and early rearing can be overcome by heating water during this period of minimal water requirements. Various technological measures can be used to provide heated water during the juvenile phase. These include use of geothermal water, water recycle systems, use of industrial thermal effluent, heat exchangers and heat pumps.

Marine grow-out is ideally conducted in sea cages. Where lethal temperature precludes overwintering, operators are forced to harvest after one growing season or move fish to land-based facilities for overwintering. Some areas have suitably warm water overlain by colder water or ice. Submerged cages can be used to hold fish in the relatively warm water or it can be pumped to onshore facilities.

An attempt is being made to develop freeze-resistant strains of salmon by introducing genes from other fishes for production of antifreeze proteins. Recent studies have shown that photoperiod manipulation can be used to stimulate growth of juvenile salmon during autumn when growth is usually slow. Careful timing of such manipulation permits normal smoltification. Artificially long daylength may also have growth-promoting benefits in marine grow-out operations.

VII. ACKNOWLEDGMENTS

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Some Biological Problems in Ranching Salmonids

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ABSTRACT

Ranching salmonids, as an exploitation system assumes that:

a: cultivation to the smolting stage can be achieved such that individual fish are behaviourally and physiologically equivalent to wild migrants;

b: cultivated fish can adjust to the wild environment rapidly, behave and develop normally within it;

c: the marine environment can support additional salmonids, without detriment to existing wild stocks in growth or survival;

d: homing of ranched stocks will be as accurate as that of wild stocks, and will thereby ensure minimal risk of adverse genetic impact on wild stocks;

e: international management measures can be so arranged as to ensure maximal harvests of ranched fish to the benefit of the original cultivators.

The paper will explore some of the biological problems inherent in these assumptions.

I. INTRODUCTION

Ranching salmonids, as an exploitation system, assumes that:

(1) cultivation to the smolting stage can be achieved such that individual fishes are behaviourally and physiologically equivalent to wild migrants;

(2) cultivated fish can adjust to the wild environment rapidly, behave and develop normally within it;

(3) the marine environment can support additional salmonids, without detriment to existing wild stocks in growth or survival;

(4) homing of ranched stocks will be as accurate as that of wild stocks, and will thereby ensure minimal risk of adverse genetic impact on wild stocks; and

(5) management measures can be so arranged as to ensure maximal harvests of ranched fish to the benefit of the original cultivators.

To what extent are these assumptions warranted, what are the biological problems inherent in them, and what are the priorities for research into areas where improvement of the practice is most needed?

II. CULTIVATION

Salmonids, as other organisms, have evolved patterns of development which ensure their successful reproduction. Growth is a means to this end, but in growing the fish become vulnerable as human prey. Cultivation ensures some control over growth and development. These developmental patterns, while encoded in the genome, have evolved in relation to the environments in which that development takes place. In principle, provided enough is known about these genetic-environmental interactions and their sequencing, rearing salmonids in captivity provides the chance to maximise the opportunities for their rapid development while at the same time eliminating the dangers and disadvantages facing them in the wild environment. For example, food can be provided in abundance at precisely the right time for the fishes needs, and predators completely excluded. However, is it known yet what are the real needs of the fish? By what means do they meet these in the wild environment? Do present cultivation practices make use of these means? To what extent are practices still imposed on them, which are designed for the physical and economic convenience of the grower, but which may be at odds with the fishes demands? Are these practices really achieving the goals desired?

For example, acceleration of development through to smolting reduces the length of time fish have to be maintained in hatcheries (DONALD-SON and BRANNON 1976, ÍSAKSSON 1985), and so increases the turnover of production through such facilities — clearly desirable economically. Acceleration is possible by appropriate manipulation of temperature and photoperiod, so inducing the fish to hatch early and grow rapidly to a size equivalent to that at which wild fish would smolt and emigrate from freshwater. The assumption seems to be that a critical size for smolting is all-important, and the sooner that it can be achieved the better. But, as SIMPSON (1985) has noted, all that has been achieved with certainty is a fish of a particular size. Has that fish been given the appropriate environmental signals to permit it to develop all the other capacities and changes requisite for life at sea? As importantly, has the acceleration process provided other signals which may have interfered with the smolting process?

In general, increased rates of growth are accompanied by decreased age to first maturity (ALM 1959; FRYER and ILES 1969, THORPE and MORGAN 1980, THORPE et al. 1983; THORPE 1986). There is mounting evidence that since sexual maturation implies the retention of freshwater adaptations and smolting implies their abandonment (THORPE 1982, 1984), they are mutually inhibitory processes (EVROPEITSEVA 1959; THORPE and MORGAN 1980, ERIKSSON and LUNDQVIST 1982, SAUNDERS et al. 1982; THORPE et al. 1982, LUNDQVIST 1983, AIDA et al. 1984; LANGDON and THORPE 1985, MIWA and INUI 1985, IKUTA et al. 1985, VILLARREAL and THORPE 1985, RANDALL et al. 1986, THORPE 1986).

So, acceleration towards smolting implies the risk of early maturation, and possibly the inhibition of smolting, which would defeat the original objective. The risk is particularly great among those species which show a strong tendency to complete the whole life-cycle in freshwater, such as the trouts (Salmo spp.) and charrs (Salve-linus spp.). As male salmonids tend to mature at one or more years earlier than females, this risk is greater among males. The phenomenon is not simply an artefact of cultivation, but occurs in the wild also (e.g. BAGLINIERE and MAISSE 1985).

In Newfoundland, MYERS (1984) found that when densities of juvenile Atlantic salmon (Salmo salar) on the nursery grounds were very low, developmental rates were correspondingly high, and the incidence of mature male parr was so high as to imply a reduction of up to 60 % in the potential harvest of adults of that year-class. In Oncorhynchus masou, the cherry salmon of Japan, 80 % of the males do not smolt but mature as parr (YAMAZAKI pers. comm. 1985). Experiments are now being carried out there to try to increase the proportion smolting, by slowing down development during the freshwater phase. By a similar approach it is hoped to produce sockeye (sea-run) smolts from hime (landlocked) salmon (O. nerka), (SHIRAHATA 1985, KOBAYASHI pers. comm. 1985).

What determines which tactic the fish will employ — to smolt, delay maturation, grow large at sea, and spawn at a large size; or to mature and spawn as a parr, and very probably remain at small size in freshwater? PAULY (1984) has suggested that the surface area of the gill lamellae may ultimately be inadequate to permit fishes to meet their metabolic oxygen demand, and that this limitation may provide the developmental cue to initiate maturation. Whereas this may be contributory to the decision to mature, it probably plays its part only if it limits the storage of surplus energy above a genetically determined threshold level, at that precise season when the hypothalamo-hypophysial system is capable of setting in train the events which lead to gonad growth and maturation (THORPE 1986). Whatever the exact nature of the physiological decision, it appears to take place in late winter or early spring (papers in Aquaculture 43, 1984). A second type of decision, relating to the maintenance or the arrest of growth, takes place in July (THORPE et al. 1982, VILLARREAL 1983, HIGGINS 1985, HIGGINS and TALBOT 1985), resulting in the familiar bimodal frequency distribution of fish size (THORPE 1977), and determines whether or not the fish will smolt. It seems probable that both decisions are based on the rate of acquisition of surplus energy at the appropriate time, and hormone kinetics related to its storage (THORPE 1986). The endocrine regulation of energy usage in each case will differ.

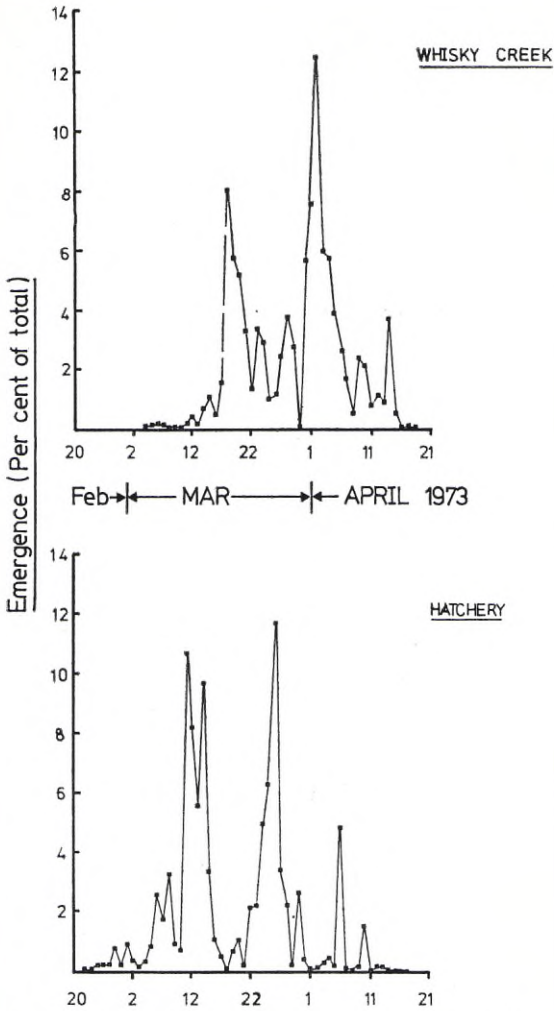LANNAN (1980) found a slightly different "accel-

Fig. 1. Comparison of downstream runs of chum salmon fry (*Oncorhynchus keta*) from the Netarts Bay Hatchery and Whiskey Creek (from LANNAN 1980).

eration" effect in chum salmon (*O. keta*). He compared the timing of outmigration of fry from the hatchery incubation unit at Netarts Bay, Oregon, with that of fry from the same parent population which had incubated in the adjacent Whiskey Creek, and showed that peaks of emigration occurred 6—7 days earlier from the hatchery population than from the stream (Fig. 1). He suggested that this was an effect of selecting early running fish as parents for the hatchery population, biassing the subsequent hatchery pro-

duction towards early developers. Over subsequent years he noted a progressive slowing of the embryonic development rate among fish in the hatchery. He suggested that early entry to the estuary of the fry was maladaptive, and that natural selection had resisted this trend by favouring genotypes with slower developmental rates. This had forced the hatchery to use broodfish which gave rise to fry which migrated at the optimal time. Such a natural corrective to hatchery misjudgement may only be possible in small-scale cases like that at Netarts Bay/Whiskey Creek, where the total adult chum population averaged only 280 fish.

LUNDQVIST (1983) found that several components of the smolting process in Atlantic salmon show circannual patterns of change, and suggested that successful smolting occurs when these are synchronised by photoperiod cues. LANGDON (1983) and LANGDON and THORPE (1985) showed that smolting and non-smolting fish differ chiefly in the intensities of response in these components in the spring, and that the degree of synchrony in one-year-old "smolts" was poorer than in two-year-olds. Was this an "acceleration" effect, and if so, what environmental cues had been presented at the wrong time? SAUNDERS and HENDERSON (1970) found that seawater tolerance among smolt-sized Atlantic salmon was influenced by the photoperiod regime experienced in the immediately preceding months. WAGNER (1974) showed that the downstream migration behaviour of steelhead trout (*Salmo gairdneri*) was also affected by their prior photoperiod experience, and ÍSAKSSON (1982) found that Atlantic salmon exposed to abnormal photoperiods over the winter prior to release showed poorer return success as adults than did control fish which experienced natural day-length changes.

It is clear that cyclically changing environmental variables synchronise physiological and behavioural events in salmonid development, but the precise times at which the fish receive this environmental information, and the critical physiological states at these times which then determine the direction of developmental decisions taken, are less clear. Such information is vital if culture systems are to operate efficiently.
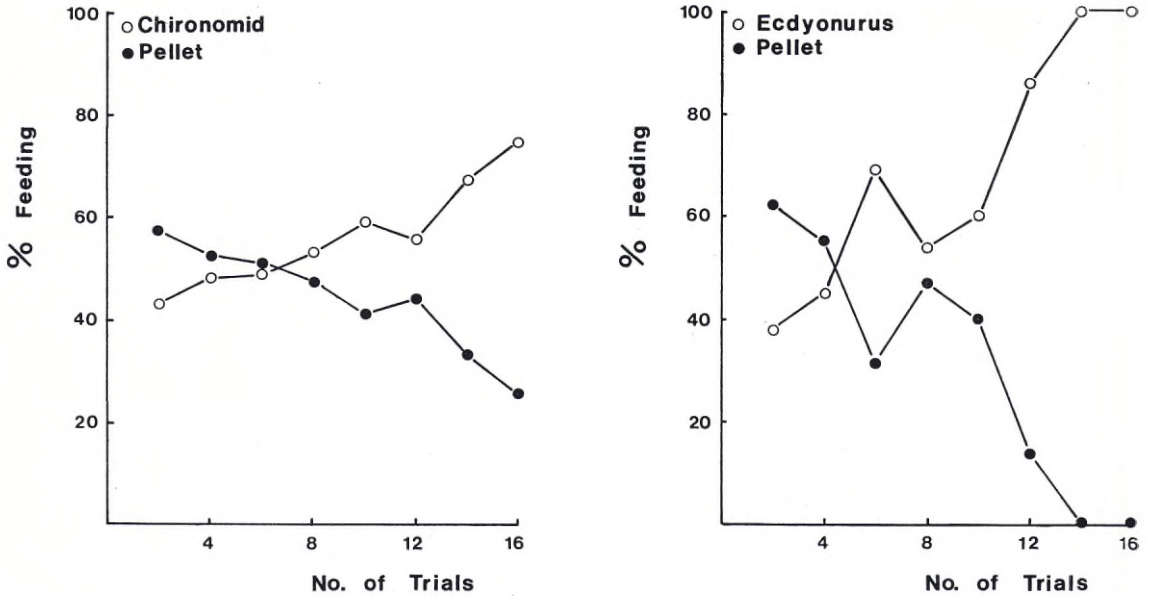
Fig. 2. Change in preference from pelletted food (solid circles) to live invertebrate prey (open circles) in hatchery-reared Atlantic salmon (*Salmo salar*) parr. A: chironomid larvae; B: ephemeropteran larvae (*Ecdyonurus*) (from STRADMEYER 1985).

III. ADAPTATION

However, it will not be of much value to produce a fish which is physiologically sound if it is at the same time behaviourally inadequate, and consequently highly vulnerable to predation.

LARSSON and LARSSON (1975) found that hatchery Atlantic salmon showed prompt escape reactions to overhead (avian) predators, but had to learn to recognise predatory fish, especially pike (*Esox lucius*) and burbot (*Lota lota*). Is that learning process continuous, or if not, at what developmental stage does it take place most effectively in the wild? At migration the plasma thyroxine (T4) levels in salmonids tend to be relatively high (for review see DICKHOFF et al. 1982). High T4 levels imply increased sensitivity to external stimuli, which is a precondition for effective learning, and enhances their responsiveness to both predators and prey in novel environments. Since T4 has also been shown to be implicated in the elaboration of neurons associated with long term memory (SCHOLZ et al. 1985), and thyroid stimulating hormone (TSH) to be associated with successful imprinting of

home-stream cues (HASLER and SCHOLZ 1983), high levels of both these hormones at or just before downstream migration should enhance the precision of homing of the returning adults. However, YOUNGSON and SIMPSON (1984) found that plasma T4 levels in May in Atlantic salmon from a commercial hatchery were significantly lower than those in similarly sized wild fish. This implies that the reared salmon were less sensitive to external stimulation than were the wild fish at this critical time, so that on release they were less well equipped to memorise the characteristics of their release site and were more vulnerable to predators. High risk of predation close to freshwater or coastal release sites has been demonstrated recently for Atlantic salmon in Norway (JENSEN 1979, HANSEN 1982) and Sweden (LARSSON 1982), and for coho salmon (*O. kisutch*) in Oregon (McNEIL MS 1985).

HORWOOD and CUSHING (1978) noted that a fish "in the sea avoids death by growing". To grow it must eat, and to eat it must capture prey successfully. Much research has focussed on the production of nutritionally adequate and convenient dry pelletted diets for juvenile salmonids

(see, for example, papers in HALVER and TIEWS 1979), but can they convert from such food to live prey animals quickly and effectively? Are they conditioned to respond only to inanimate pellet shapes? In some recent work OLLA (pers. comm. 1984) found that smolting coho salmon from a hatchery, when given a choice of live wild prey or pellets, responded to both, but a few fish continued to prefer pellets. In a similar study on hatchery-reared Atlantic salmon, STRADMEYER (1985) has found that after only 4—6 trials, lasting 30—45 minutes in total, these fish changed preference from pellets to live insect larvae as prey. They responded more rapidly to the wriggling live prey than to the passively displaced pellet, and after 14 trials (105 minutes) with pellets and the larval ephemeropteran *Ecdyonurus* they showed 100 % preference for live prey (Fig. 2). Following FENDERSON *et al.* (1968), STRADMEYER suggested that as these experimental fish were progeny of wild parents they retained genetically determined responses towards wild food organisms. It has yet to be established whether "domestication" (*i.e.* the selection of traits favouring successful development in captivity) results in a loss or weakening of these innate responses to wild food organisms, but this has been suggested to account for the poor survival of "domestic" versus wild brook trout (*Salvelinus fontinalis*) (ERSBAK and HAASE 1983) and brown trout (BACHMAN 1984) when released to the wild.

IV. OCEAN CARRYING CAPACITY

Assuming that the released fish are appropriately responsive to both predators and prey, can the coastal areas into which they have been introduced support them?

WALTERS *et al.* (1978) suggested that the successive waves of juvenile Pacific salmon emigrating from the Fraser and other British Columbia rivers had evolved this discontinuity of arrival in the coastal environment in response to short-term fluctuations in the availability of zooplankton prey. The first wave of salmon imposed a heavy demand on the standing crop of plankton, but by growing they graduated to larger food particles (*e.g.* WANKOWSKI and THORPE 1979), and the

short time interval before the next influx of smolting salmon arrived permitted a restoration of high biomass of zooplankton, which ensured high availability for the second wave in its turn. Coastal production of zooplankton was apparently more than adequate to support these waves of juvenile salmon, as zooplankton biomasses were not lower in 1966 and 1968 when pink salmon juveniles (*O. gorbuscha*) were present, than in 1967 when they were absent (STEPHENS *et al.* 1969). However, COONEY (1984) has calculated from data in the literature that the ability of the Alaska coastal current's production to feed the juvenile salmon populations was marginal at all seasons, and that environment was only adequate in spring and summer if forage species from the bordering ocean areas were transported across the continental shelf and augmented the food supply. HARGREAVES (1984), challenging this conclusion, and using other published data, suggested that advection of zooplankton organisms from the open ocean into coastal waters was not necessary to support salmon there, but might still be utilised by the fish. He emphasised that all such calculations were really guesses, and that much more information was needed on the regulators of oceanic production.

Rapid growth reduces vulnerability to predation (HORWOOD and CUSHING 1978, LASKER and ZWEIFEL 1978, WALTERS *et al.* 1978, THORPE 1980) and SCARNECCHIA (1984) has shown that in years when productivity along the North coast of Iceland was relatively poor due to low spring temperatures, the generation of smolting Atlantic salmon entering the sea gave rise to relatively poor catches as adults in subsequent years. Work currently in progress by PEARCY and his colleagues at Oregon State University has shown that coho salmon disperse into waters within 37 km (20 nautical miles) of the coast, and continue to live as solitary individuals and not in shoals as has often been suggested (OLLA pers. comm. 1984). OLLA has also observed pronounced aggressive behaviour towards other coho among such fish after 2 months at sea. Given evident competition for food in this juvenile environment, density-dependent growth and mortality effects are to be expected. PETERMAN (1984) has shown density-dependent growth among sockeye salmon (*O.*
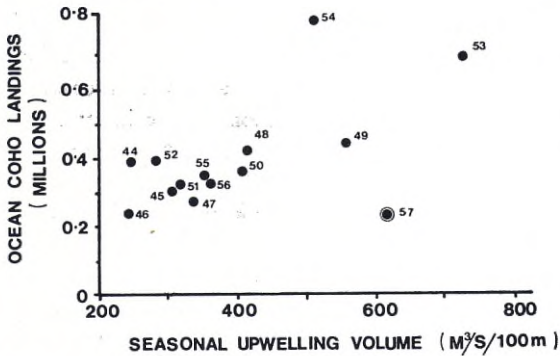
Fig. 3. Relationship between Oregon coastal upwelling volume in spring, and landed catch of adult coho salmon (*Oncorhynchus kisutch*) in the following year (from NICKELSON and LICHATOWICH 1984).

nerka) in the Gulf of Alaska, both in the total species population there, and within separate stocks. He found that this was established during the first 16 months at sea. NICKELSON and LICHATOWICH (1984) showed that the ocean landings of coho salmon in Oregon were correlated with the coastal upwelling volume in the previous spring and summer, which were the first months after entry of the migrants to the sea (Fig. 3). MATHEWS (1984) reviewed data on interannual variation in post-smolt survival and environmental factors at sea for a number of salmonids in the North Pacific, and showed that this relationship between Oregon coho survival and coastal upwelling was the only strongly correlated consistent pattern that had been found. He cautioned that its biological meaning was obscure: was food supply for juvenile coho plentiful in years of high upwelling volume, or was predation pressure low in these years? PEARCY (1984) also posed these questions, and added: does the strength of upwelling influence the water movement patterns, and so the orientation or the migratory patterns of the coho? He was unable to show differences in early marine growth of coho between years of weak and strong upwelling, but this may have implied that in weak years it was only the faster growers which had survived (*cf.* WALTERS *et al.* 1978). Management measures to improve coho yield would differ according to which interpretation was put on the relationship. Recent high recapture rates (McNEIL pers. comm.

1985) from releases of coho at distances up to 25 km (15 miles) offshore, into warm clear and relatively unproductive "El Nino" waters suggest that predation or water movement at this time may normally be just as critical as food supply. However, it is the latter which must determine coastal carrying capacity for young salmonids and it is therefore of high importance that methods be developed to estimate the quantity of food organisms available to newly released salmon on a day to day basis, in order that releases may be matched precisely to periods of relative food abundance.

This begs the question of what are those food organisms likely to be? From experiments on food selectivity among Atlantic salmon during freshwater development WANKOWSKI and THORPE (1979) found that food particles of width equal to 2.5 % of the fork length of the fish were selected preferentially and resulted in maximal growth. Assuming that this preference was still exercised after entry to the sea, the likely optimal prey width for salmon throughout their first year at sea was calculated (ANON. 1983), based on an estimated salmon growth curve derived from catch data. This revealed that 0-group herring (*Clupea harengus*), and 0-group sand-eels (*Ammodytes* sp.) were potentially important prey animals for at least the salmon's first growing season at sea (Fig. 4). It would be profitable to search for evidence of correlations between the year-class strengths of 0-group herring, and growth and survival of salmon in the same year, in relatively confined environments such as the upper Baltic Sea.

But this begs a series of other questions: where are the young salmon at this time, how rapidly do they disperse away from their release point, and by what is their movement directed, if at all? Passage of Atlantic salmon through estuaries is chiefly by passive transport (LaBAR *et al.* 1978, McCLEAVE *et al.* 1978, TYTLER *et al.* 1978), and movement away from the estuaries was found to be non-directed at first, followed by movement with the surface current (HOLM *et al.* 1982). From the speed of downstream travel (4—28 km/day) (DAWLEY *et al.* 1981, in SIMENSTAD and WISSMAR 1984) it seems likely that chinook salmon (*O. tshawytscha*) are also displaced passively through the
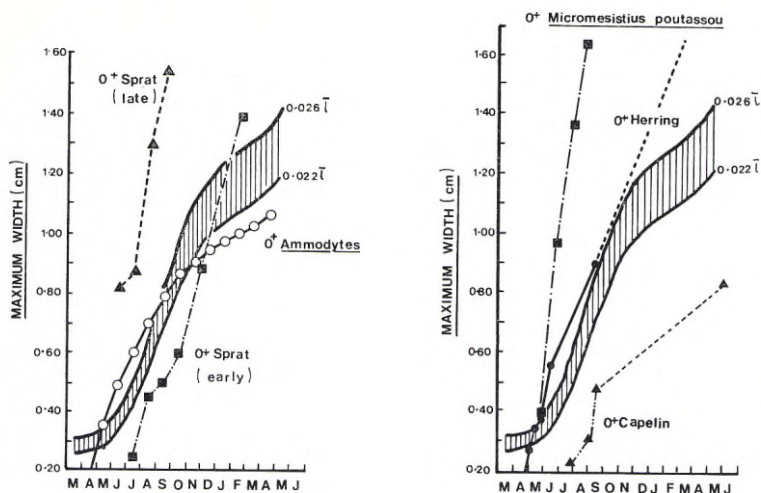
Fig. 4. Width growth of potential prey fishes of Atlantic salmon (*Salmo salar*), in relation to predicted optimal food particle width to achieve observed salmon growth. a: sprat and *Ammodytes*. b: herring, capelin, and blue whiting (from THORPE 1984).

Columbia River estuary. LARSSON and ATESHKAR (1979) recorded movements averaging c. 50 km/wk among Baltic salmon released from the Lule River mouth into the Bay of Bothnia. When combined with measurements of surface water velocity in these areas, such movements could scarcely be interpreted as directed migrations, but were rather the resultant displacement of fish moving randomly in a region with a predominantly southerly current vector, while others appeared to have been displaced across to the Finnish coastal areas on the anticlockwise surface circulation (Fig. 5). Similarly, coho, pink (*O. gorbuscha*) and chum salmon entering the Strait of Georgia from the Fraser River ride the current across the Strait and disperse with surface currents among the Gulf Islands or along the mainland and Vancouver Island shores (HEALEY 1980, TABATA 1984). Movements of some coho salmon, after release on the Oregon coast, are consistent with random dispersal influenced by wind-driven surface water movement and upwelling patterns, but tend to be confined to regions of relatively high productivity within 37 km (20 nautical miles) of the coast during the first 4—5 months (HARTT 1980, PEARCY 1984). (But the same authors suggest that there are other coho which move away from the release area more rapidly.) Maximal displacement distances of about 7 km/day were remarkably similar to those of Atlantic salmon in the Baltic (Fig. 6). PEARCY (1984) found evidence of directional trends in

movement which differed from month to month, and he concluded that some coho post-smolts showed weak migrational tendencies. HARTT (1980) noted that many coho and chinook salmon remain in "inside" waters (*e.g.* Puget Sound; Johnstone Strait) for a year or more, and juvenile sockeye, chum and pink salmon were found in Hecate Strait in November. So-called residual chum salmon in Puget Sound were 23 cm in length in November, suggesting that feeding conditions were good there. HARTT (1980) suggested that although food availability for these individuals had been adequate, for the bulk of the population at an earlier time density and food competition could have been the impetus for seaward migration. Similarly in chum salmon fry, HEALEY (1979, 1980, 1982) found that residence in the Nanaimo River estuary was dependent on the abundance of their preferred harpacticoid prey, and emigration occurred as the copepod supply declined. HEALEY (1980) found further that in May and June these fish in deeper water encountered food shortages and competed with pink and sockeye salmon, and suggested that they left Georgia Strait at this time in response to poor feeding conditions. Coho and chinook salmon fed on larger invertebrates and on fish, and showed no evidence of reduced feeding success until late summer, at which time they too began to leave.

Collectively these studies provide strong circumstantial evidence for food shortage as a main
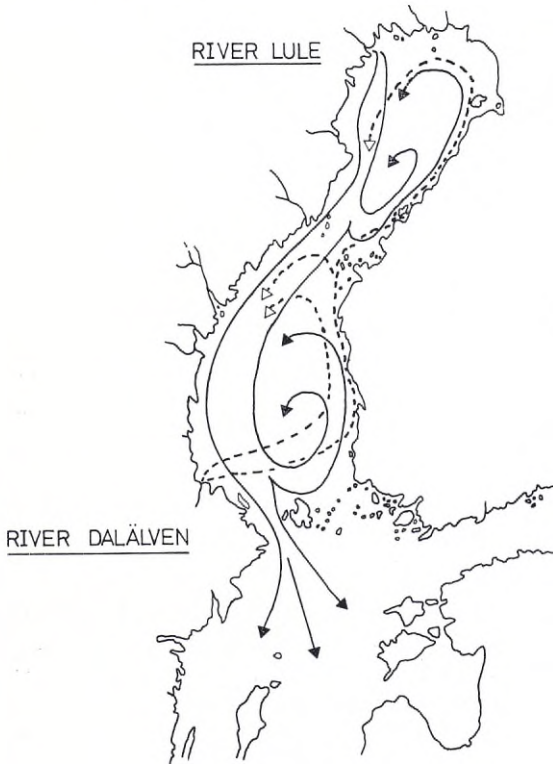
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Fig. 5. Patterns of movement of Atlantic salmon post-smolts (*Salmo salar*), migrating from the Rivers Lule and Dalälven, Sweden (from LINDROTH *et al.* 1982).

motivator for migration among many salmonid species, and emphasise the importance of obtaining detailed information on the requirements and behaviour of juvenile salmon at entry to the sea, and on the availability of potential prey, if releases are to be carried out effectively.

V. HOMING

The efficiency of ranching as an exploitation system depends heavily on the accuracy with which the fish home to the release/recapture site.

Salmonid stocks have evolved in relation to breeding and nursery environments which differ in physical and biological characteristics, eliciting differences in developmental timing and responses, morphology and reproductive characteristics in the fishes (see reviews in STOCS SYMPOSIUM 1981). Such characteristics can only be maintained in a stock if the range of appropriate genotypes is preserved, precisely matched with its particular environment. Such genetic discreteness has been demonstrated in stocks of most salmonid species, especially in those with complex age structures, and less so in those with less variant life-history strategies (STOCS SYMPOSIUM 1981, OKAZAKI 1982). That preservation of discreteness is assured, by segregation of maturing fish into component
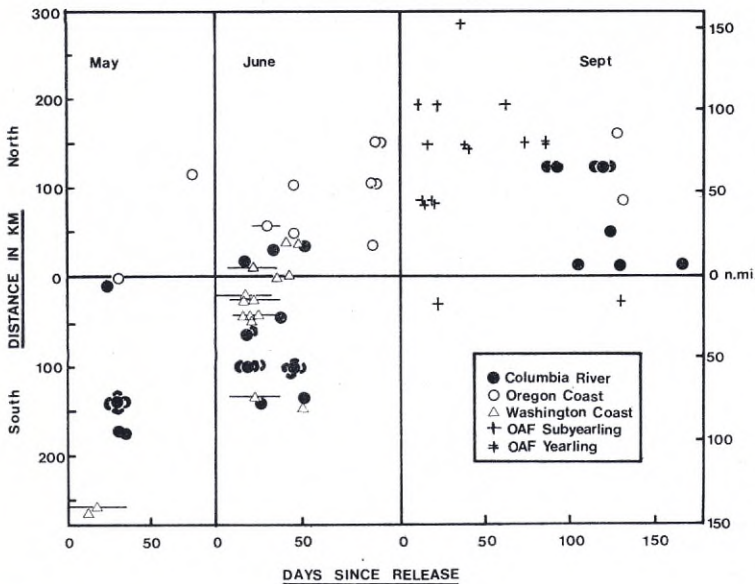

Fig. 6. Distance north and south of the point of ocean entry, versus days since release for marked juvenile coho salmon (*Oncorhynchus kisutch*) from Oregon, 1982 (from PEARCY 1984).

stocks from mixed populations, and return migration with precise homing to natal streams.

Numerous studies have demonstrated that this occurs, but there are few estimates of its precision. For Atlantic salmon a recent review (ANON. 1983) concluded that homing was approximately 97 % accurate to the home stream. For chinook salmon, QUINN and FRESH (1984) recorded 98.6 % accuracy of homing of the Cowlitz River Hatchery stock. The orientation mechanisms at sea are unknown. Some recent evidence implies that Atlantic salmon are able to maintain a compass course (SMITH *et al.* 1981), and QUINN and GROOT (1984) have argued that a very high degree of orientation is required for a fish to cover the 1,000—2,000 km in 1—4 weeks that Pacific salmon tagging studies have shown happens.

However, there is abundant evidence for the use of olfactory cues once the fish are close to, or in, the home river. The use of such cues implies their recognition, and it has been demonstrated that imprinting of home-stream information is acquired by the juvenile fish at critical periods before entry to the sea (HASLER *et al.* 1978, HARA 1970, SHIRAHATA 1973, UEDA 1973, STABELL 1984), such that introduced fish return to their release point rather than to their ancestral home. However, the learning process is not equally effective at all stages of development. Using hime salmon (landlocked *O. nerka*) in Lake Chuzenji, Japan, SHIRAHATA (1973) found that hatchery reared fish released as juvenile migrants at 6 or 18 months after hatching into a stream which had no salmon, returned to that stream at maturity and formed a new spawning population there. However, fish at 23 months and older, when they were acclimatised to the "new" stream for 10 months, failed to return to it as mature adults. He concluded that hormonal activities associated with sexual maturation governed the fishes ability to imprint or not, and that releases were preferable at ages 6 or 18 months, but not any older.

SCHOLZ (1980) and HASLER and SCHOLZ (1983) have found that coho salmon exposed to synthetic chemicals at the time of high thyroid hormone activity in the spring, became imprinted to those chemicals, whereas exposure during the parr stage when thyroid levels were low did not result in imprinting.

Furthermore, when thyroid stimulating hormone (TSH) was injected into parr to increase thyroid hormone output at 5 months before normal smolt migration, and the fish were exposed simultaneously to synthetic chemicals, they became imprinted to these. Hence, in coho at least, high thyroid hormone activity, which is seasonal and episodic, is a prerequisite for successful imprinting. HASLER and SCHOLZ (1983) showed further that formation of permanent long-term olfactory memory resulted from the TSH treatment, and suggested this was due to thyroid induction of structural changes in neurons. SCHOLZ *et al.* (1985) have now shown that thyroid hormones are taken up selectively in brain nuclei of steelhead trout at smolting.

It is therefore vital that reared fish be exposed to the environment of their release site at a time when they can memorise its characteristics. This time needs to be defined for each species and stock, but in most instances there are reliable data from wild runs of migrants indicating when this critical season is. Failure to imprint adequately would result in inability to home precisely, which poses two problems: firstly, it would be economically inefficient; and secondly, and more important overall, it would lead to straying of released fish to other sites at maturity, and to the risk of their breeding with fish of other stocks. Data from SAKHALIN (ALTUKHOV 1981) showed what can happen in an extreme case. When chum salmon from the Kalininka River were introduced on a large scale into the Naiba River the genetic characteristics of the resultant population were radically changed from those of the original Naiba stock, and the population was reduced to less than 5 % of its former numbers over a 12-year period. More optimistically, in Iceland ÍSAKSSON (1985) recorded that when broodstock for future generations was selected from Atlantic salmon returning successfully to the release site at Kollafjörður, the recorded rates of straying to nearby sites declined steadily as the return rate increased.

VI. MANIPULATION

Understanding the physiological, behavioural and genetic mechanisms regulating development opens

the door to manipulating them for human benefit.

Findings about the timing of developmental events emphasise the importance of season in regulating the behaviour of salmonids. The life-cycle is an ordered sequence of stages, but the genetic programme runs under environmental instruction. Altering timing has been attempted in several ways. Accelerating development towards smolting and the problems that this raises, have been discussed above. Changing the migratory patterns has been a dramatically successful result of altering the fishes' time-tables. Delaying the release of smolting Pacific salmon, by holding them in seawater for varying periods after the wild smolt movements had been completed, resulted in changes in their growth, survival to maturity, and distribution at sea (BILTON 1980, NOVOTNY 1980). ERIKSSON et al. (1982) argued that migratory patterns themselves were seasonally regulated, in the sense that the propensity for a fish to be displaced varied seasonally. On this basis ERIKSSON and ERIKSSON (1985) predicted that by delaying releases of Atlantic salmon for 1—6 months, by first retaining them in cages at a marine release site in the Gulf of Bothnia, the fish would not penetrate as far south into the Baltic main basin as would their siblings released at the normal migration period in May/June. Recoveries of marked individuals in the fishery supported this prediction. In addition, the delay also resulted in 5- to 8-fold increases in recapture rates, and 6-fold increases in weight yields to the fishery. These findings have two main implications for exploitation: firstly, the salmon yield from the Baltic could be achieved much more efficiently with the production of one sixth of the number of smolts from hatcheries (or possibly increased considerably), if the delayed release technique was employed; and secondly, the demonstration that the delayed fish are less widely distributed in the Baltic than those which migrated at the usual time lends further support to the idea that local stocks could be retained within nationally controlled waters (EEZs) (THORPE 1980).

In an even more dramatic way, the production of chum salmon in Japan has been increased by similar means. Chum salmon migrate to sea directly on emergence from the spawning gravel,

as fry. They therefore enter the sea at a very small size, and are consequently highly vulnerable to predation. By rearing them on in hatcheries for one month, to increase their size before release, recovery rates as adults have been increased 4-fold (from 1.1 to 4.3 %) over a 15-year period (KOBAYASHI 1980). The extra costs involved in the additional rearing process are of little significance, as the benefit: cost ratio of the chum industry is 70: 8 (HIROI, pers. comm., 1985).

Releases at sea, to reduce coastal predator impact, have shown promise. HANSEN (1982) and LARSSON (1982) found improved yields to sea fisheries for Atlantic salmon released offshore in Scandinavia. However, yields to the home river only improved when the smolting fish were floated out of that river in a cage, in which imprinting of local information could be maintained right up to the time of release. McNEIL (MS 1985) achieved similar results with coho releases off the Oregon coast. A new experiment there is designed to measure the effect of such releases on the straying rate into non-natal streams at spawning.

VII. INFORMATION NEEDS

In summary, provided that the biological problems of rearing salmon to the release stage can be overcome, and that rational release techniques are devised to time those releases optimally in relation to the capacity of the immediate local marine environment to support them, ranching salmon can be a valuable and efficient means of extending exploitation of the oceans by harvesting a predator which returns to the doorstep to give itself up. To achieve this requires more detailed information on the following major topics:

(1) What is the nature of regulation of growth of juvenile salmonids (particularly the role of growth hormone), and how does it relate to the onset of smolting and sexual maturity?

(2) What is smolting; what are its component processes; and how are these regulated?

(3) What is the nature of the physiological conflict between smolting and sexual maturity?

(4) Are hatchery rearing methods adequate to ensure full responsiveness of reared fish to predators and prey organisms at release?

(5) When precisely is the critical period for imprinting the characteristics of home, and for how long is exposure necessary?

(6) Can the coastal environments support the young salmon released into them, and is there evidence of density-dependent growth effects at sea?

(7) On what do they feed at sea, and where?

(8) What role do they play in the coastal eco-system?

(9) What regulates the decision to mature, and when is it taken?

(10) What is the nature of migration at sea, and of homing from the open ocean?

(11) What is the extent of straying among returning adults?

(12) Does this have any genetic impact on the recipient populations?

(13) How are the migratory patterns changed as a result of delayed releases?

(14) How is the length of delay related to subsequent growth, survival, and age at return?

VIII. ACKNOWLEDGMENTS

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Effects of Photoperiod and Temperature on Emergence Pattern in the Baltic Salmon

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ABSTRACT

Newly hatched salmon fry were kept in "emergence aquaria", where the emergence from the gravel was recorded with respect to temperature and photoperiod. The emergence is nocturnal at most temperatures studied, but diurnal at higher temperatures. The peak of emergence is more concentrated during shorter nights than during longer ones. The time the yolksac fry spend in the gravel is negatively time dependent. A high temperature yields a more concentrated emergence period. The relationship between body and yolksac dry weight at emergence is calculated for different temperatures. An optimal temperature for keeping yolksac fry is discussed.

Growth and Development of Seawater Adaptability by Juvenile Coho Salmon (*Oncorhynchus kisutch* WALBAUM) in Relation to Temperature and Photoperiod Phase

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ABSTRACT

A 3×3 factorial experiment was conducted to determine the influence of ponding date and freshwater temperature on growth and development of seawater adaptability in underyearling coho salmon. Coho fry were ponded into 3 simulated natural photoperiod regimes phased at late December, January, and February daylengths. Subsequently, daylength increased at the natural rate for 49°N. Water temperatures were 8, 11 and 14°C. Periodic seawater challenge tests revealed that all groups except those ponded at 8°C into late February photoperiod developed a high degree of seawater adaptability typical of smolts. Transfer of coho reared at 8°C into seawater in late July or August demonstrated that fry ponded into December or January photoperiod were capable of rapid growth in seawater. However, the fish ponded into February daylength grew poorly in seawater, reaching less than half of the size of fish in the other two photoperiods. These results indicate that early ponding is conducive to induction of smolting in underyearling coho salmon.

Environmental Impact of Cage Fish Farming

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ABSTRACT

The environmental impact of cage fish farming in lakes has been studied, both by theoretical calculations and by direct measurements in cage cultures. During the period 1981—84 the phosphorus and nitrogen load from fish farms in two south-Swedish lakes, of different trophic status, has been investigated together with studies of the structure and function of the sediments. The total load of P and N is 12—13 kg P and 86—91 kg N per ton of produced fish and season, respectively. The total load consists of two fractions; a dissolved and a particulate form. For P 15—20 % (2—4 kg/ton produced fish and season) of the load is in the dissolved form, *i.e.* directly affecting the water quality. The remaining part of the P is in the particulate form and sedimented to the bottom and was incorporated to the sediment. Laboratory- and *in situ*-experiments have shown that 5—10 % of the sedimented P can be recycled to the water by anaerobic release and by biological processes. About 85 % (73—77 kg/ton produced fish and season) of the total N load is in a dissolved form, predominately urea and ammonia from the fish excretion. Only 15 % of the N-load is bound as particulate matter, mainly the food losses. Equipment for collecting the sedimenting matter, food losses and feaces, from cage fish farms, has been designed and tested. The technique, is satisfactory (80—95 %), regarding the P reduction while the N removal is not so efficient (10—20 %). The fact that the N load is predominately in the dissolved form and the P load in a particulate form, means that the enviornmental problems are quite different. If the cage farm is situated in a lake where P is the limiting substance for production a removal of the sedimenting matter is motivated. If the farm is situated on the Swedish coast where N is found to be limiting, a removal of the particulate matter is ecologically unmotivated.

Experiments with Net-pen Rearing and Delayed Release of Atlantic Salmon (*Salmo salar* L.) at the Coast of Gotland, Baltic Main Basin

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ABSTRACT

The experiments have been performed during the summers 1983 and 1984. In the net-pen have been kept both one-year-old and two-year-old salmon. For direct release in the sea have been used both two-year-old and three-year-old salmon.

Growth in the net-pen has been excellent, one-year-olds increased from around 13 cm at input in the end of May to around 26 cm at tagging in the end of August. Corresponding growth for two-year-olds was from around 17 cm to around 28 cm.

The obtained results of taggings, so far, show excellent growth and survival for all groups, most remarkable for the three-year-olds released in spring 1984. After 8—10 months in the sea they have gained weight from around 0.3 kgs to almost 3 kgs and a reported recapture rate of near 10 %.

Circadian and Circannual Rhythms in Salmonids: Possibilities of Modulation by External Cues

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ABSTRACT

Evidence of endogenous about 24-h and about 1-year (circadian and circannual) cycles, respectively, in salmonids are reviewed.

Circadian systems in salmonids seem to be quite flexible and the indication of rigid endogenous regulation is weak, probably due to the multi-oscillatory fasion of the system.

Indications and evidence of circannual systems in salmonids appear to be strong. There is also to be expected a strong interaction of circadian and circannual systems by photoperiod regulation of seasonal events like spawning, migration and growth.

The action of external cues like photoperiod and temperature on the dynamics of circadian and circannual systems in salmonids is discussed.

Special questions to be discussed are:
— possibilities to inhibit the expressions of certain events like maturation
— range of entrainment of circadian and circannual cycles.

Prospects of a One-Year Rearing Cycle for Arctic Char

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ABSTRACT

Lack of broodstock and relevant fry rearing techniques, sensitivity to high temperatures, and a normally 3-year rearing cycle to pansize (≈ 300 g) in suitable natural water conditions in northern Scandinavia have so far been limiting the development of aquaculture undertakings with Arctic char (*Salvelinus alpinus* (L.)). Nevertheless, Arctic char is a high-price fish and shows some characteristics that are highly promising if it can be utilized properly:

— early autumn spawning
— exceptional growth rates of fry at optimum temperatures
— volume-dependent rather than area-dependent in rearing facilities.

A theoretical model for a one-year rearing cycle is presented. It includes a combination of indoor hatching and breeding in heated and/or recirculated water systems to produce a 20— 50 g fish during winter and subsequent rearing in net-pens in suitable areas.

Energetics in the Food Particle Size Selection of Arctic Char

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ABSTRACT

This study was initiated as a first attempt to elucidate the prey size selectivity in Arctic char (*Salvelinus alpinus* (L.)). In a first series of experiments caged char were given a surplus supply of pelleted feed of different sizes.

The most positive weight development in char was found in groups supplied with food having a diameter of 2—2.5 % of the fork length of the fish in the experiment.

In a further analysis in the laboratory, reaction time (r) and handling time (h) for different diameters and lengths of feed pellets in char were studied.

r was found to be inversely related to feed particle size in char, while h, as aspected, increased with size of the food. The number of dismissed food increased at both ends of the sizes used in the experiment.

r+h were found to reach lowest values in tests with pellets of a diameter of 2.25 % and a length of 2—3 % of fish fork length. The highest net energy profit (J/time unit) by char in a surplus food situation was calculated to be by utilizing feed particles with a diameter of 2.25 % of their own body length.

Performance of Ranched Baltic Salmon in a Delayed Release Experiment

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ABSTRACT

Non-river based sea-ranching experiments with delayed releases were carried out in the Ulvö-strait, Bothnian Sea (63°04′ N, 18°40′ E). During normal time of smolt run in late May, Baltic salmon (*Salmo salar* L.) smolts were transferred to sea and kept in net-pens 30 km NE of the mouth of River Ångermanälven. Groups of 2000 fish were sequentially released in June, August and in September.

The results showed that delayed releases of Baltic salmon post-smolts affected both temporal as well as spatial aspects of the migration. Furthermore, delayed released experimental fish groups showed a drastically reduced mortality resulting in a manifold increase of recaptured fish. The results are discussed in view of the run-off of an endogenous annual program suggested to affect time of smolt run as well as migration distance in salmon.

Accelerated Growth and Production of Zero Aged Atlantic Salmon (*Salmo salar* L.) Smolts in Iceland

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ABSTRACT

This presentation provides data on growth rates of Atlantic salmon (*Salmo salar* L.) parr at temperatures between 12 and 16°C, in water heated (either directly or by heat exchange systems) by geothermal or industrial cooling waters. In addition, results of attempts to rear and release 30 g smolts within eight months of first feeding are discussed. Specifically, as long as food and life support parameters were not limiting, no significant difference in growth rate could be found for parr reared at either 13 or 15°C. Elevated temperatures were, however, thought to be effective in early selection of upper mode fish and thereby an effective means of passively separating potential zero aged smolts from S1 or S2 smolts. Although, approximately 25 % of the original brood population was released into salt water after 7.5 months of rearing (in mid August), this may have been too late for proper survival and adaption to the ocean. Consequently, this study emphasizes the need to advance spawning by at least one month in a typical Icelandic brood stock in order to allow release of zero aged smolts by July of the first summer.

Salmon Ranching and Smolt Production Facilities in Iceland, 1984

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ABSTRACT

This poster depicts the location of eleven major salmon ranching sites and four additional smolt production facilities in Iceland. Photographs were selected to describe typical site topography, water use, facility design and smolt releasing tactics. Emphasis is placed on various uses of geothermal energy, hydropower, and natural land forms for adult trapping sites. In addition, a brief description of the advantages Iceland offers for sea ranching are discussed and a summary of the 1984 smolt production and adult ranching returns is presented.

Experiment with Fish Oils Made from Capelin in Dry Salmon Feed for Use at Low Seawater Temperatures

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ABSTRACT

Three fish oils produced from capelin raw material were tested as the sole oil addition in dry diets to Atlantic salmon (*Salmo salar* L.) during the winter season.

One fish oil was produced from wintercapelin. The two remaining fish oils were separated out from capelin caught in the summer season. One of these oils was further refined and winterized at 0°C.

The growth experiment conducted over a period of 7 months showed no differences between the dietary groups.

Evaluation of the Seawater Challenge Test on Sea Trout (*Salmo trutta* L.)

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ABSTRACT

Performing seawater survival tests is a traditional way to check the smolt status before the fish are released into rivers or net-pens (CONTE and WAGNER 1965). The 24 h seawater challenge test, developed by CLARKE and BLACKBURN (1977), is a far more sensitive test for estimating seawater survival. In this test the plasma sodium concentration is measured after 24 h in seawater, which provides an index of the degree of smolting. Application of the seawater challenge test on several salmonid species shows that it is a useful method for determining the time of maximum smoltification.

In the present study, a seawater challenge test was developed and evaluated for the sea trout (*Salmo trutta* L.).

Changes in hypo-osmoregulatory ability in smolting sea trout were monitored by performing a seawater challenge test in the beginning of every month from February to May and in late July. In these tests the sea trout were challenged with 25 $^0/_{00}$ seawater for 24 h before sampling. Seawater tolerance increased during the spring, as indicated by a progressive decrease in plasma sodium levels, and was fully developed in April. A high capacity to regulate magnesium ions after transfer to seawater correlated well with the smoltification and culminated in May.

Plasma electrolytes, in sea trout challenged to seawater for 0 to 48 h, reached high and stable levels 24 h after seawater entry. In order to discriminate between parr and smolt, this time should be the most effective exposure period in seawater.

A seawater challenge test performed in 33 $^0/_{00}$ seawater gave a better separation between parr and smolt than the lower salinity (25 $^0/_{00}$) generally used in this study. However, it was found that such a high salinity could not be used due to some mortality of fish still in the parr stage. Stress of shorter duration had no influence on the outcome of the seawater challenge test, whereas a 2 1/2 h transport affected the seawater performance.

Genetic Variation in *Mytilus edulis* L. from Sweden Revealed by Allozyme Electrophoresis

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ABSTRACT

Electrophoretic analysis of 12 enzyme loci in specimens of *Mytilus edulis* L. shows a large within population heterogeneity. Furthermore, large differences in 4 of the 12 loci are found between west and east coast populations from the Swedish coast. Mean genetic identity is similar to values obtained in other species of mussels. This implies either a strong differential selection of juveniles and larvae which migrate through the Sound, or that no genetic exchange takes place due to restricted larval flow between the Baltic and the Kattegatt. On the other hand, the genetic differentiation between the west coast populations over a distance of 300 km is obscure. These results indicate that west coast populations of *Mytilus edulis*, wild or cultured, are not influenced by larvae from the Baltic, as has been proposed.

Effects of Temperature and Photoperiod on Bimodal Growth and Smoltification in Juvenile Atlantic Salmon

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ABSTRACT

In July 1984 groups of 0+ juvenile Atlantic salmon, ranging from 4 to 8 cm in length, were subjected to different photoperiod and temperature regimes. Two temperature regimes were used: 9.5°C and 12.5°C (constant temperature). All groups were under simulated natural photoperiod for the first few months. At those conditions growth rates were low and the entrance into the faster growing phase was slow, but growth was faster at 12.5°C than at 9.5°C. One group was subjected to continuous light in October which, in November/December, resulted in an increase in salinity tolerance and coloration characteristics of smoltification in the upper and lower mode fish, but the entrance into the faster growing phase (lower mode fish becoming upper mode fish) halted at the same time. In January 1985 four additional groups were transferred from simulated natural photoperiod to continuous light. This also resulted in similar changes as those noticed for the previous group in November/December. The experiment was terminated earlier than planned (in March 1985) as bacterial kidney disease (BKD) was found at the farm from which the fish came. The observed mortality (very little) could not be related to this disease and no infected fish was found after inspection of 60 fishes. The data are still being analysed.

Pond Rearing of Fish Fingerlings

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ABSTRACT

The main species used in pond rearing of fingerlings for stocking into natural waters in Finland are: whitefish (*Coregonus lavaretus* (L.), *C. peled* GMELIN), pike (*Esox lucius* L.), grayling (*Thymallus thymallus* (L)), and perch-pike (*Stizostedion lucioperca* (L.)), the last one in central and southern Finland.

The newly-hatched whitefish young are stocked in May or early June (in the north), and the collecting starts in late August, continuing until early October. The body length of fingerlings at collection varies generally between 9 and 13 cm.

The total area of these so-called natural-food ponds is some 5500 hectares in Finland, each pond varying in size between 0.2—200 hectares. Four-fifth of the ponds are situated in the northern part of the country, the northernmost at 69° N.

The management of these ponds takes several forms: the ponds may be drainable or non-drainable, and the food for fish comes naturally (*e.g.* zooplankton). The collection of fish takes place with passive collection devices or by poundnets (non-drainable ponds). In some ponds artificial feeding with dry food may be practiced, also cage cultures with artificial light and artificial feeding with both live and dry food have been built.

Yields in natural food ponds of whitefish reach 100 kg/ha even in Lapland and 200 kg/ha in central Finland, though occasionally through inadverdent conditions the stock in a pond may be lost altogether. Artificial (additional) feeding of whitefish may give even 350 kg/ha. Generally, the pond yields are 10 to 30 times higher than the fish yields in nearby natural waters. Yet year-to-year variation even in the same pond may be great.

In the district of Kuopio the average yield in 1982 was 9000 whitefish fingerlings per hectare, but 15500 in 1983. In cage culture and through artificial feeding the whitefish yield varies between 250 and 1000 individuals/m³ (2.5—10 kg/m³).

New management techniques are being developed to obtain higher yields of high quality fingerlings and to avoid the risks that may destroy the whole pond stock in some years.

The Effect of Temperature and Thyroid Hormones on Fish Physiology and Biochemistry

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ABSTRACT

Earlier studies in our laboratory have shown that at low temperature the cellular effects of thyroxine and triiodo-l-thyronine are not effectively manifested. Therefore, in order to determine if the inability of thoryxine to induce these effects at low temperature is mediated through a temperature-sensitive system for the translocation of T_4 into the nucleus the effect on the uptake of this hormone into body tissues and subcellular fractions was examined.

Injections of ^{125}I-T_4 were given to fish maintained at different temperatures. Uptake was shown to be rapid. All tissues exhibited maximal radioactivity within two hours. Peak activities were temperature dependent. However, transfer of T_4 from the cytoplasm to the nucleus was not blocked at low temperature. Actinomysin-D, an inhibitor of RNA synthesis, decreased RNA and protein in liver and muscle. But in contrast to the effect in mammals T_4 and Actinomysin-D completely antagonise the cellular effects of each other. Timing is an important factor in this effect which may be a temperature dependent phenomenon. Muscle nuclei have more radioactivity than liver nuclei when expressed as radioactivity/g tissue. As there are comparable amounts of radioactivity in the nuclei at differing temperatures then some mechanism/s other than a simple block in transport from cytoplasm must be operating. Our preliminary published observations along with results of other workers are taken to establish an hypothesis.

Food Search Behaviour in Arctic Charr (*Salvelinus alpinus* (L.)) Induced by Food Extracts and Amino Acids

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ABSTRACT

Food search behaviour in Arctic charr (*Salvelinus alpinus* (L.)) to extracts of food pellets (Astra-Ewos) was quantified and compared with the response to solutions of amino acid (aa) mixtures. The concentration of each of 18 aa was analysed in the food extract and similar pure amino acid solutions were prepared. The 18 aa were divided into two groups, one group containing 7 aa with presumed high stimulatory effect and the other group the remaining 11 aa. The solutions of 7, 11 and 18 aa elicited similar responses at concentrations between $2-5 \cdot 10^{-6}$ M, they were stimulatory but not at $2-5 \cdot 10^{-9}$ M. This can be compared with the food extract which elicited response at all concentrations tested, at $5 \cdot 10^{-9}$, $5 \cdot 10^{-8}$, $5 \cdot 10^{-7}$, and $5 \cdot 10^{-6}$ M. The response to the 18 aa mixture was compared with the food extract and was shown to be significantly lower at $5 \cdot 10^{-9}$ M but not at $5 \cdot 10^{-6}$ M. These results show that amino acids induce food search behaviour in Arctic charr but there are also other substances in the food extract which are important.

The Use of Heated Water for Salmon Hatcheries in a Cold Environment — a Case Study in Scotland

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ABSTRACT

The idea of using heated water, either in the form of a heated effluent or in a recirculating system, for the early rearing of Atlantic salmon is not new. Indeed the origins of this idea can be traced to the early or mid-1960's. However, despite the frequent advocation of their use by academics over the last two decades very few such farms exist and the technology has barely been tested on a commercial scale. Indeed, in Scotland only some 4—6 attempts have been made but none has been sustained.

This paper reviews the "optimum temperatures" recommended in the literature for the early stages of Atlantic salmon from the newly stripped egg to first feeding. The actual water temperatures experienced on a number of salmon hatcheries in Scotland together with River Purification Board data have been examined. A case study for a particular recirculating system is then presented and a full economic assessment made. This paper therefore attempts to identify the requirements of the fish, the actual temperature conditions occurring in Scotland and the economic cost of maintaining a simple recirculating system.

Possibilities of Making Forecasts For the Time of Settlement of Blue Mussel (*Mytilus edulis* L.) Larvae on the West Coast of Sweden

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ABSTRACT

One of the main problems when cultivating blue mussel (*Mytilus edulis* L.) with long-line techniques, is to know when to put out the poly-propylene spat collectors.

A study was performed at Tjärnö Marine Biological Laboratory, from May to August 1983, to investigate factors that may be used as indicators of settlement time. We selected three sampling stations with different hydrographical conditions. The following factors were considered: (1) Maturation of gonads, (2) Size and numbers of planktonic larvae, (3) Number of newly settled juveniles, (4) Hydrography (temperature and salinity).

A general correlation time between spawning, planktonic stage, and settlement was found at all three sampling stations, although they differed in onset of spawning and span of planktonic life between places. It seems as if it is mainly the local adult mussel population that produces the new recruits of young mussels. This implies that the local conditions, probably mainly the temperature, are important in determining the time of development. Also, a correlation between the proportion of mature larvae, "eyed" larvae, in the plankton and settlement of larvae was found, with a fortnight between the peak of abundance of "eyed" larvae in the plankton and the peak of settlement. The results indicate that the presence and number of "eyed" larvae in the plankton could be used as a measure to predict settlement. The reliability of this is discussed.

Causes of Variation in Viability of Reared Atlantic Salmon Broodstocks and Eggs

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ABSTRACT

An adequate supply of eggs for smolt production is a serious problem in the Norwegian salmon farming industry. The survival of reared eggs is very variable and significantly lower than that of wild eggs. Several factors concerning insufficient care in broodstock husbandry, nutrition and environment are believed to cause this situation. Genetic inbreeding is supposed to be of minor importance. The seawater environment during the later part of the maturation process is shown to cause high prespawning mortality probably as a result of increased suscepti-bility to bacterial diseases and parasites (*i.e.* sea lice). Diseased fish also have increased pro-blems with osmoregulation which add to other stresses. Mortality during maturation in sea-water also seems dependent on size or age at first maturity. Younger and consequently smaller fish show the highest survival rate. Experiments indicate that prespawning mortality can be considerably reduced by moving the broodfish from seawater netpens to a brackish water environment (dams or netpens) 4—5 months prior to spawning. High quality food is important based on health of the fish and adequate nutrient supply to the eggs. Normal production feed seem to cover the need for protein and fat. Concerning vitamins and minerals our knowl-edge is limited, but vitamin C is believed to be essential in salmonid reproduction.

There seemed to be no negative effect of not feeding the fish the last 4 1/2 months prior to spawning on fecundity, survival of fish or survival of eggs.

The influence of stripping fish from seawater, brackish water or fresh water on subsequent mortality during incubation is still unclear based on experiences that eggs stripped directly from full-strength seawater may have excellent survival in the hatchery.

An important threat to the hatching success is the risk of damaging eggs during stripping, fertilization and transport to the hatchery. The sensitivity of newly fertilized eggs to handling seems to increase rapidly with time but quantifying this mechanism has been difficult.

In Southern Norway acid rain constitutes a principal problem to hatchery management and this factor is suspected to be a very important contributing factor resulting in the low smolt output from hatcheries.

Developmental Rates of Salmon and Charr at Low Temperatures

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ABSTRACT

The temperatures of the water in Arctic, sub-Arctic and high altitude lie within a few degrees of freezing for most of the incubation period of the eggs of the salmonid fishes which spawn in these environments. The incubation period of salmon (*Salmo salar* L.) eggs is dependent while that of charr (*Salvelinus alpinus* (L.)) appears to be independent of temperatures within the range 0.1—2°C. It is, therefore, suggested that the more northern distribution of the latter species is due, at least in part, to the ability of fry to exploit a very short first feeding season efficiency enough to survive the long winter

The Development of Aquaculture in Northern Norway: Ten Years of Experience

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ABSTRACT

Fish farming in northern Norway was started in the early 1970's by a few, usually established businessmen. The initiative was entirely private. At the same time the institutions of higher education in the area began teaching and research in subjects, usually biological subjects, which were relevant for some aspects of the new profession. Between these two activities, fish farming and higher education/research, no apparata existed, neither statefinanced nor private to help the developing profession. One of the results of this lack of "back-up" was that university teachers and researchers were often called upon to assist fish farmers in tasks they were not particularly qualified to carry out. In the 10 years that have followed most of the "back-up" apparata have been established and are in the process of further development. The role of the institutions of higher education has been much more significant in the establishment of the intermediate support systems for fish farming than it was in the provision of direct help to farmers.

Potential Species in Sub-Arctic Aquaculture

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ABSTRACT

If aquaculture is to develop in sub-Arctic areas in competition with temperate zone aquaculture it must either develop a technological superiority in the farming of temperate-zone species or utilize species which are especially suited to sub-Arctic conditions. If the latter strategy is chosen, species of fish, molluscs, crustaceans and algae must be selected which have the potential to thrive under sub-Arctic conditions and at the same time are acceptable to one or several export markets, since human populations in sub-Arctic areas are not high enough to support a large consumption of aquaculture products. Some examples of potential culture species are given and possible investigation methods discussed in relation to the desired research input both temporal and financial.

Individual Growth and Maturation Patterns of Four Net-pen Reared Arctic Char Populations

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ABSTRACT

Four different populations of Arctic char (*Salvelinus alpinus* (L.)) were reared in net-pens in freshwater at Storuman (65° 6′ N, 17° 7′ E). Individual growth and maturation patterns as well as mortality patterns were studied. Char from Lake Hornavan (an N-type char) showed the best growth. Torrö char (an S-type char) showed the worst growth, while the two otherrs (Kvesjön/Rensjön- and Tinnsjö-char) were intermediates. A wide variation in individual body weight was observed in all populations at the end of the investigation period.

In all four populations males matured one year earlier and at smaller sizes than did females. Nearly all chars, 93 %, in the Hornavan population had matured at least once at an age of five years. Repeated maturation was an exception rather than a rule, at least in males.

During the spawning period a high mortality in male char was noticed. Symptoms were in most cases fungus infection. On the other hand no signs of mortality were found in fish kept in brackish water during two seasons.

The results are discussed in relation to the prospect of utilizing Arctic char in aquaculture activities in northern Sweden.

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