International Council for the Exploration of the Sea

C.M. 1991/M:34
ANACAT Committee

POSSIBLE EFFECTS OF CLIMATIC CHANGES ON THE ECOLOGY OF NORWEGIAN ATLANTIC SALMON (SALMO SALAR L.)

By

Arne Johan Jensen

Norwegian Institute for Nature Research,
Tungasletta 2, N-7004 Trondheim, Norway

ABSTRACT

Increases in the greenhouse gasses corresponding to a doubling of the CO_2 content of the atmosphere is expected to occur around 2030. The most likely scenario indicates a temperature inrease of 1.5 to 3.5°C in Norway, mainly due to changes in winter temperature and particular in inland areas. The precipitation is expected to increase by 7 to 8 percent. The winter runoff will increase manifold, while the summer runoff will decrease. The spring flood will be considerably reduced in rivers in western and central Norway. Water temperature will increase, except in winter in rivers which will continue to have an ice cover.

Possible effects of the climatic changes on the ecology of Norwegian Atlantic salmon are predicted, the salmon population

in two Norwegian rivers are used as case studies. Hatching of eggs will be accelerated, and initial feeding time for alevins will occur earlier in spring. Due to changes in water temperature and water flow regimes, the initial feeding time may be a critical period in many salmon rivers.

Growth and survival of parr are expected to increase, and smolt age will decrease. Hence, smolt production will probably increase considerably. A higher proportion of mature male parr is expected to occur in many rivers.

Altered temperature and flow regimes in rivers may change the timing of smolt runs. The smolt run may be less concentrated in time, schools may be of smaller size, and predation from marine fish species will probably increase. Hence, survival from smolt to adult is expected to be lower than today.

In the ocean the change in climate may affect distribution, total salmon production, as well as sea age at maturity of the salmon.

The upward migration of adult salmon is expected to be easier in early summer, while in late summer droughts may more frequently prevent salmon ascent. Reduced spring peak flow may probably select for a smaller salmon size in Norwegian rivers.

INTRODUCTION

Evidence from many sources show that the consentration of atmospheric CO_2 is steadily rising (Bohlin 1986, Keeling 1986), and the mean global temperature has increased about 0.5°C the last decennium (Houghton and Woodwell 1989). Scenarios for future climate change in Norway are reported by a Norwegian expert team (Eliassen et al. 1989, Eliassen and Grammeltvedt 1990). The scenarios assume an increase in the greenhouse gasses corresponding to a doubling of the CO_2 content of the atmosphere, which is expected to occur around 2030. Based on these scenarios physical consequences of climatic change on Norwegian water courses and water resourses are also predicted (Sælthun et al. 1990). Changes in water flow and water temperature, in turn, will affect life in rivers and lakes. These consequenses are difficult to predict, partly because of lack of information about the environmental requirements of animals. However, one species by which considerable information about environmental requirements excist, is the Atlantic salmon (Salmo salar L.). Because of its complex life cycle in both freshwater and marine environments, effects of climatic change may be difficult to predict. Nevertheless, the considerable information which excist about its environmental requirements inspire to make a preliminary assess of possible effects of climatic changes on the ecology of this species.

In this paper a theoretical base for predicting effects of changed climate on the different life stages of Atlantic salmon is given. The consequences of a doubling of the CO_2 content in the atmosphere for two Norwegian Atlantic salmon populations are predicted; the river Stryneelva population in western Norway, and the river Altaelva population in northern Norway.

PREDICTED CHANGES IN WATER DISCHARGE AND WATER TEMPERATURE IN NORWEGIAN RIVERS

The base for predictions of change in water discharge and water temperature (Sælthun et al. 1990), as well as the consequences of these changes on Atlantic salmon, are the climatic scenarios for Norway given by Eliassen and Grammeltvedt (1990). These scenarios are given for air temperature and precipitation. The most likely scenario indicates a temperature increase of 1.5 to 3.5°C, mostly in the winter and in the inland. The precipitation is expected to increase by 7 to 8 percent (Table 1).

The runoff has by Sælthun et al. (1990) been simulated for seven Norwegian watercourses over a 30 year period, both for the present climate and for two scenarios. The simulation describes the changes for basins in three elevation bands, a mountainous, an intermediate level and a lowland basin. The model applied for these simulations also predicts changes in the snow cover, soil moisture and ground water regime. These simulations are the basis for the subsequent evaluation of possible consequences.

The most likely scenario indicates a moderate increase in the annual runoff in mountainous districts and districts with high annual precipitation. The annual runoff will decrease in lowland basins and in forested basins in the inland because of increase in the evapotranspiration. The seasonal pattern will change significantly, in particular in basins within the intermediate elevation band. The spring flood will be strongly redused in many basins. The winter runoff will increase manifold, while the summer runoff will decrease. Floods will occur more frequently in autumn and winter. I used Atlantic salmon from the river Stryneelva (61°55'N, 6°33'E) in western Norway in the first simulation. However, simulated annual runoff followed by a climatic change is not available for this river, so I used data from the nearby river Vosso (60°38'N, 6°13'E) (Sælthun et al. 1990) (Fig. 1a), assuming a similar change in water flow in these rivers. As a second case study, I chose river Altaelva (69°58'N, 23°20'E) in northern Norway (Fig. 1b).

According to Sælthun et al. (1990) the duration of the snow cover on the ground will be reduced by one to three months. The soil moisture deficit will increase, indicating an increase in the need for artificial irrigation on most areas except the western coastal zone. Increased irrigation demand and reduced summer runoff can give water shortage in small water courses.

A detailed prediction of water temperature is not given in Sæltun et al. (1990), but they state that the water temperature most likely will increase with the air temperature in summer. The rise in the water temperature from close to 0°C to nearly the air temperature will occur one month earlier because of earlier termination of the snowmelt. Therefore, on the basis of these informations and on meteorological data, I have proposed a new temperature regime after the change in climate for the rivers Stryneelva and Altaelva (Fig. 2).

EFFECTS OF CLIMATIC CHANGE ON ECOLOGY OF ATLANTIC SALMON

Spawning

Photoperiod has been shown to be the major environmental factor in the control of the sequence of endocrine and other physiological changes which ultimately lead to spawning in salmonids (deVlaming 1972, MacQuarrie et al. 1978, Whitehead et al. 1978). However, water temperature during maturation may also play a role in determining the time of spawning in salmonids (Henderson 1963, Morrison and Smith 1986). Within nearby populations of Atlantic salmon in Norway spawning time may differ by two months (Heggberget 1988), indicating that if daylength is the predominant cue for timing of spawning, the salmon populations spawning at different lengths of day are adapted to different lengths of photoperiod.

Mean water temperature in ten Norwegian rivers during peak spawning varied between 1.0 and 4.7°C, showing that spawning occurs at various temperatures in various stocks of Atlantic salmon (Heggberget 1988). Peterson et al. (1977) reported spawning of Atlantic salmon in the Miramichi River when temperatures were about 6°C and falling, indicating that populations of Atlantic salom in Norway spawn at colder temperatures than those in Canada.

Timing of spawning thus seems to be influenced by the thermal regime, in such a way that spawning occur at a time which will result in hatching of eggs, and initial feeding of alevins at a specific and presumably optimal time for survival of fry (Heggberget 1988, Jensen et al. 1991).

Hence, spawning is mainly adapted to a specific photoperiod, which means that in spite of the climatic change predicted, spawning time may probably remain unaltered. However, effects of water temperature on spawning time should be furnished.

Egg incubation period

Hatching of salmonid alevins is a distinctive event and can be determined objectively. Temperature variation during development is a major source of variation in hatching time (Alderdice and Velsen 1978, Crisp 1981, Jungwirth and Winkler 1984, Humpesch 1985, Tang et al. 1987, Elliott et al. 1987, Beacham and Murray 1990). However, additive genetic variation (McIntyre and Blanc 1973, Sato 1980, Beacham 1988), changes in temperature (Heggberget and Wallace 1984), oxygen consentration (Silver et al. 1963, Garside 1966), and light intensity (Kwain 1975) can also influence hatching time.

For Atlantic salmon eggs the development time at different temperatures from fertilization to hatching is described mathematically by Crisp (1981). Results from hatching experiments performed at temperatures between 2.4 and 12°C were available to Crisp (1981). Additional experiments at temperatures between 0.1 and 1.3°C have later been performed by Heggberget and Wallace (1984) and Wallace and Heggberget (1988), who concluded that Crisp`s equation 1b satisfactorily described the time from fertilization to hatching also at temperatures close to zero:

$$(1) \quad \log D = b \log (T-\alpha) + \log a$$
$$= -2.6562 \log (T + 11.0) + 5.1908$$

where d = incubation time (days), T = temperature (°C), and a, α and b are constants (Crisp 1981, equation 1b).

A climatic change will increase water temperature during winter, and hence, accelerate hatching.

Initial feeding time

After hatching, alevins remain covered by gravel for several weeks, during which time they survive on nutrients in their large yolk sacs. Some time before the yolk is exhausted, alevins begin exogenous feeding, and emerge from the gravel. The duration of the stage from hatching to 50-percent initial feeding is mainly temperature dependent, and this relationship is described mathematically by Jensen et al. (1989b) for temperatures in the range 3.9 - 10.4°C:

$$(2) \quad D = 472\ T^{-1.27}$$

where D = number of days after hatching, T = temperature (°C), and a and b are constants.

Emergence from the gravel is closely related to initial feeding. Alternatively, the time taken from hatching to emergence may be estimated according to Crisp (1988).

The increased winter temperature followed by a climatic change will shorten the period from hatching to 50-percent initial feeding.

Since the duration of both incubation and alevin period depend on the temperature regime, a linking of spawning time to a stream temperature triggers spawning at a time which will result in initial feeding at a specific and presumably optimal time for survival. Due to long time selection it is expected that in each population the majority of alevins start feeding and emerge from the gravel when the environmental conditions are favourable for highest possible survival. In Norwegian rivers initial feeding is avoided during spring peak flow, and before water temperature reach 8°C (Jensen et al. 1991). Two different strategies are indicated: (1) initial feeding may take place before the culmination of the spring flow or (2) after the spring peak flow.

The choise of strategy depends on the temperature and flow regimes in each river. After a change in climate both temperature and flow regimes will be altered. Hence, in some rivers alevins may reach the inital feeding stage at a time when temperature or flow is unacceptable, resulting in high mortality. Therefore, the initial feeding time seems to be a critical period in many salmon rivers with changing climate in the future.

Growth of parr

When the yolk sac is absorbed, growth is mainly dependent on nutrient conditions, water temperature, and fish weight (Donaldson and Foster 1940, Baldwin 1957, Brett et al. 1969, Elliott 1975a, b, Spigarelli et al. 1982). When food is present in abundance, estimated optimum temperatures for growth vary among species (Brett et al. 1969, Elliott 1975a, b, Hokanson et al. 1977). In sockeye salmon (Oncorhynchus nerka) optimum growth occurred at 15°C at excess rations, and progressively shifted to a lower temperature at each lower ration (Brett et al. 1969). A corresponding model for brown trout was developed by Elliott (1975a, b). For brown trout, the optimum temperature for growth at excess rations was found to be 13°C, while growth commences at 4°C.

A similar model for growth of Atlantic salmon is lacking, but the optimum temperature for growth of parr seems to be about 16-17°C at excess food rations (Siginevich 1967, Dwyer and Piper 1987). At temperatures below a certain limit Atlantic salmon parr move from riffles to pools and reduce or stop feeding (Allen 1940, 1941, Gibson 1978, Gardiner and Geddes 1980, Rimmer et al. 1983, 1984). This lower temperature limit for growth is not fixed, but varies from river to river according to the temperature regime (Jensen 1990). In rather cold Norwegian rivers this limit seems to be about 7°C (Jensen and Johnsen 1986), the same as observed in Britain by Allen (1940, 1941) and Gardiner and Geddes (1980). Also a higher temperature limit for growth is probably excisting, and the upper ultimate lethal temperature for

Atlantic salmon has been found to be 27.8°C (Garside 1973).

In expectation of such a growth model for Atlantic salmon, I have used a modified version of the brown trout model (Elliott 1975a, b) to estimate growth of Atlantic salmon parr. I used the same growth rate, but I increased the optimum temperature for growth to 16°C, and excluded growth estimates at temperatures below 7°C. The maximum temperature for growth was increased in parallel with the optimum temperature, i.e. from 19.5°C to 22.5°C. I made the assumption that nutrient conditions for salmon will remain the same after the temperature increase.

A climatic change probably results in increased growth rates of Atlantic salmon parr, and hence, lower smolt age, in rivers where water temperatures will stay below 16-17°C and nutrient conditions are favourable. In rivers where water temperatures in part of the year will be higher than this limit, growth will be retarded in these periods. In rivers with poor nutrient conditions for salmon, the growth will be retarded also at temperatures lower than 16-17°C. Generally, the length of the growth season will increase. As a consequence, the annual growth of parr will be better, and the smolt age lower than today. Annual mortality of salmon parr has been estimated at 40-60 percent (Elson 1975, Symons 1979), and smolt production is inversely related to smolt age (Symons 1979). Therefore, salmon smolt production is expected to increase in most Norwegian rivers.

Since maturation of salmon male parr has been associated with fast growth rate (Thorpe et al. 1982, Dalley et al. 1983, Randall et al. 1986, Thorpe 1986), the proportion of mature male parr is expected to increase in the future.

<u>Effects of increased winter flow and winter temperature on parr</u>

Increased water flow and water temperature in winter is expected to increase survival of salmon parr. In Norwegian rivers discharge is usually lowest in winter, and the area covered by water at that time is probably limiting for bottom fauna production, as well as for hiding places for salmonids. Atlantic salmon parr become photonegative, and hide in shaded areas beneath rocks of the stream bed during winter (Lindroth 1955, Gibson 1978, Rimmer et al. 1983, 1984, Rimmer and Paim 1990). Therefore, the size of habitat available in winter is important for survival of salmonids (Rimmer et al. 1983). Building of weirs increases water level in pools, and increases survival of salmonids in winter (Saunders and Smith 1962, Näslund 1987). Chadwick (1982) reported high mortality of eggs of Atlantic salmon in periods with low water flow, following spawning at high water levels. The river Orkla in central Norway is utilized for hydroelectric purposes, and the flow regime is considerably altered. In winter a minimum flow of 10 m^3/s is now imposed, while flows as low as 1 m^3/s occurred earlier. This is probably the main reason why the production of Atlantic salmon smolts have increased from 4 per 100 m^2 before the hydropower regulation to 5-11 per 100 m^2 today (Hvidsten 1991). Similarily, Wolff et al. (1990) measured a more than twofold increase in brown trout standing stock after increasing minimum low flows in Douglas Creek, Wyoming.

Elevated winter temperature may increase the proportion of downstream migrating previously mature male parr. In a river release experiment Berglund et al. (1991) showed that rearing previously mature males at 4-7°C above the ambient water temperature from December to April increased the number of downstream migrating fish to a level similar to that of immature smolts.

Smolt migration

Photoperiod during spring has been identified as the major environmental variable controlling the transformation from stream-dwelling parr to seaward-migrating smolts (Wedemeyer et al. 1980). After the transformation from parr to smolt, some environmental stimulus triggers the migration, the nature of the stimulus often appearing to differ in different rivers. Water temperature, water flow, cloudiness, and lunar cycle have been suggested to regulate timing of the seaward migration of smolts (Foerster 1937, White 1939, Österdahl 1969, Baglinière 1976, Solomon 1978, Grau 1982, Jonsson and Ruud-Hansen 1985, Hesthagen and Garnås 1986). Some authors have stressed the importance of a threshold water temperature prior to the start of the smolt run, either 5°C (Fried et al. 1978) or 10°C (Elson 1962, Jessop 1975). In the river Imsa in southern Norway the smolt decent was not triggered by a specific water temperature or a specific number of degree-days, but was controlled by a combination of actual temperature and temperature increases in the water during spring (Jonsson and Ruud-Hansen 1985). In the river Orkla in central Norway the smolt run was correlated with changes in water flow. The temperature was only 2-3°C when the smolt run was initiated, suggesting that this factor is of less importance in controlling the onset of the smolt run in that river (Hesthagen and Garnås 1986). Correlations between the smolt run and water level has been observed also in several other rivers (Allen 1944, Hoar 1953, Österdahl 1969, Baglinière 1976, Nott 1973).

Irrespective of which of these factors regulate smolt run, changed temperature and flow regimes in rivers may change the timing of smolt runs, with severe effects on salmon stocks. This is because survival of salmon in the sea depends partly on the time when the smolts enter the sea. Delayed downstream migration of smolts have resulted in decreased survival to adults (Cross and Piggins 1982, Hansen 1987), and successive smolt plantings showed that a short period during spring was the optimal time for smolts to leave freshwater (Larsson 1977, Hansen and Jonsson 1989).

Descending smolts are subject to heavy mortality from fish and birds in the river and estuary (Piggins 1959, Thurow 1966, Larsson 1985, Reitan et al. 1987, Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988). In estuaries and fjords in central

Norway the major mortality is caused by marine fish species, especially cod, _Gadus morhua_, and saithe, _Gadus pollachius_ (Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988). To avoid predation, the smolts leave the river in schools, and at night (Hayes 1953, Thorpe and Morgan 1978, Thorpe et al. 1981, Hesthagen and Garnås 1986). Hvidsten and Hansen (1988) observed that water discharge at release is of great importance for survival of hatchery-reared smolts released within the normal period of smoltification, and that high water discharge at release improves survival to adults. They believed that the main reason for this is reduced mortality due to predation just after release. In the estuary of the river Orkla in central Norway Hvidsten (pers. med.) observed highest mortality from cod and saithe of smolts leaving the river outside the peak migration time, indicating that schooling is important to avoid predation.

A climatic change will reduce the spring peak flow in many Norwegian rivers. In rivers where water flow is the triggering mechanism to initiate smolt migration, the smolt run will probably be less concentrated in time, schools will be of smaller size, and predation from cod and saithe as well as from birds will increase. Hence, survival from smolt to adult is expected to be lower.

Ocean life

A climatic change according to the levels given in Table 1 is expected to give a general warming of the sea outside Norway of about 2°C (Øiestad 1990). Øiestad (1990) expects that this warming of the sea will give increases in populations of species like cod, herring and capelin north of 62°N to a level similar to historic maximum values. The predictions for invertebrates as well as fish fauna indicates that food supply for salmon on the feeding areas will increase or at least be the same as today (Øiestad 1990).

Once the Atlantic salmon smolts have entered the sea little is known about their movements. Knowledge about the biology of postsmolts is scarce (conf. Reddin and Short 1991), and we have no information about Norwegian populations from they leave the coastal areas to they are found on the feeding areas. The feeding areas for the Norwegian salmon are in the North Norwegian Sea, and the fish are found both off the Faroes and off the Norwegian coast (Mills 1989).

Although temperatures of 16-17°C seem to be optimal for feeding and growth of juvenile Atlantic salmon (Siginevich 1967, Dwyer and Piper 1987), such temperatures are seldom available to them during their life at sea. Judging from catches in various fisheries and from research vessels, the acceptable temperatures during the marine phase are between 4 and 12°C (Saunders 1986). Temperatures at the feeding areas of Norwegian strains of Atlantic salmon are sparce. However, salmon near West Greenland and in the Davis Strait are seldom found in water colder than 2°C (May 1973). The best catches have been made on and east of the Grand Bank in May at temperatures of 5-8°C (Reddin 1985), and in the West Greenland area during late summer/autumn when water temperatures are from 3 to 8°C (May 1973). Alm (1958) reported 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. According to Thurow (1966) sea temperatures from 2 to 8°C constitute an optimum range for Atlantic salmon in the Baltic.

The Atlantic salmon may face the warmer sea either by staying in the same feeding areas as today, and hence, accept a 2°C increase in sea temperature, or they may move northward to new areas with temperatures similar to those preferred today. However, the feeding areas may be closely linked to gyres or rotating ocean currents (Stewart 1978). Changes in the climate may affect the strength of the ocean currents, and thereby the location and distribution of the gyres. A hypothesis that the migration of salmon is directly or indirectly pre-programmed, and thus under influence of a circannual rhythm is also proposed.

If so, the travelled distance could be seen as a result of a temporal migratory activity sequence, rather than being a result of a direct goal orientation (Eriksson et al. 1982, Eriksson 1989).

That climatic changes can affect the distribution and abundance of many species of marine fish have been shown by Cushing (1983). Dunbar and Thomson (1979) attributed the presence and absence of salmon at West Greenland to climatic change. Periods of abundance appear to correspond with cooling sea surface temperatures, not warming periods. They suggest that northward expansion of the Labrador Sea gyre into Davis Strait, together with the intensification of the West Greenland Current have shifted the distribution of salmon into this area. The northeastern limit of salmon distribution was until recently the Pechora River and Varandei Island in the USSR (MacCrimmon and Gots 1979). However, appearently because of a gradual warming trend in the climate from 1919 to 1938, enhanced by a strong inflow of warm Atlantic water, salmon penetrated eastward into the Kara Sea and spawned in the Kara River from 1932 onwards (Jensen 1939, Berg 1948).

Temperature conditions in the ocean may have some influence on total salmon production. Scarnecchia (1984) obtained significant correlations between low April-July sea temperatures and declines in primary production, standing crop of zooplankton, reduced abundance and altered distribution of pelagic forage fishes and salmon catches in the northeast Atlantic. Reddin (1988) suggested similar relations in the northwest Atlantic.

Temperature may also be linked to sea age at maturity. Scarnecchia (1983) pointed out that salmon from southern and western Islandic 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. He showed that ocean temperature in June explains much of the variability in the ratio of grilse to multi-sea-winter (MSW) salmon in Iceland. Similarily, Saunders et al. (1983) showed that cold winters inhibited maturation of cage-reared salmon and significantly reduced the grilse to MSW salmon ratio. However, results obtained by Martin and Mitchell (1985) contrast completely with those of Scarnecchia (1983) and Saunders et al. (1983). Martin and Mitchell (1985) examined possible influence of sea temperature upon the age of return salmon using the catch and weight data of grilse and MSW salmon of the vicinity of the River Dee, and found that increase in temperature in the subarctic is associated with larger numbers of fish returning as MSW salmon and fewer as grilse. Martin and Mitchell (1985) speculated that the distinction between the salmon observed by Scarnecchia (1983) and Saunders et al. (1983) and those returning to the River Dee is that the former, either by capture or circumstances, are forced to endure cold sea temperatures while the latter are free to avoid such conditions.

From this overview I conclude that a warmer ocean will affect the distribution area of the salmon, the total salmon production, as well as the grilse to MSW salmon ratio. However, the present knowledge is too scarce to predict details.

River ascent of adult salmon

River flow is the factor most frequently cited as controlling the rate of upstream migration of salmon in rivers. But its effects are often modified by others, like water temperature, cloud cover, atmospheric pressure, turbidity, water quality, and general weather, wind and tide (Banks 1969). Increases in flow stimulate salmon to ascend a river, in cases with and without physical obstacles (Huntsman 1939, 1948, Hayes 1953, Harriman 1961, Jensen et al. 1986). However, salmon may be able to ascend an obstacle at certain water flows only (Stuart 1962, Jensen et al. 1989a).

Water temperature is an important factor for salmon ascent, especially in early summer. Even small obstacles are difficult to ascend when water temperature is below about 5-8°C (Menzies

1939, Pyefinch 1955, Jackson and Howie 1967, Jensen et al. 1989a). Salmon are not able to ascend the first obstacle in river Vefsna in Norway before the water temperature has increased to 8°C, and the river discharge is reduced to 300 m^3/s. Ascent is delayed in the upper reaches of Vefsna in wet years compared with dry years, indicating that water discharge in periods may be too high for ascending some of the falls. However, also at too low discharge the ascent stopped (Jensen et al. 1986, 1989a).

In the river Vefsna increases in water temperature increased the ascent of salmon (Jensen et al. 1986). On the contrary, Hayes (1953), MacKinnon and Brett (1953) and Jackson and Howie (1967) concluded that when water temperature increased to above the critical temperature necessary for ascending obstacles, it appeared to have little effect on the initiation of runs.

Too high water temperatures may decrease the intensity of upward migration. Elson (1969) concluded that the intensity of Atlantic salmon ascent in the North-West Miramichi River increased with increasing water temperature up to 22°C, and then decreased. In the River Dee Alabaster (1991) estimated the rate of migration to be reduced to about 0.5 of the average at a mean weekly maximum water temperature of 19.5°C, and reduced to about 0.25 of the average at 25.5°C.

The percentage of grilse is found to be inversely related to discharge of river and length of river (Schaffer and Elson 1975, Power 1981, Scarnecchia 1983). High water discharge during the upstream spawning migration seems more essential for large than small salmon. In the River Imsa in Norway the larger, multi-sea-winter salmon were more dependent on high water levels when migrating than smaller one-sea-winter fish (Jonsson et al. 1990). Some of the largest salmon strains in Norway are, probably because of long time selection, found in rivers with high peak spring flow as well as a high mean flow (for example the rivers Altaelva, Eira, Stryneelva, and Drammenselva). Hence, the reduced peak spring flow followed by a climatic change probably selects for a reduced salmon size in Norwegian rivers.

A change in climate results in an earlier temperature rise in spring, as well as a reduction in peak spring flow (Fig. 1, Fig. 2). For both reasons it will be easier for the salmon to ascend obstacles in early summer, and it is expected that the upward migration in some rivers will take place earlier than today. On the contrary, in July and August water flow will be reduced, and periods with too low flow for ascent in these months will occur more frequently than today.

CASE STUDY NO. 1; THE RIVER STRYNEELVA ATLANTIC SALMON

Life history

The river Stryneelva has a catchment area of 546 km^2, and the annual water flow is 33 m^3/s. Atlantic salmon can migrate 27 km upstream from the river mouth, including the 13 km lake Strynevatnet. The annual catch is about 2 tons. Also sea-run brown trout (Salmo trutta L.) and stationary Arctic char (Salvelinus alpinus L.) are present in the watercource.

The salmon in river Stryneelva spawn in November and December. Peak spawning occurs between 15 November and 25 November (Heggberget 1988). Peak hatching is estimated to take place the last days of April, and peak initial feeding in early June (Fig. 3) (Jensen et al. 1991).

The mean smolt age is 3.3 $\pm$ 0.1 years (range 2-5), and mean smolt length 124.7 $\pm$ 1.4 mm. The mean length of a one year old parr is 45 mm. Annual growth rate for 1+ and 2+ parr averages 28 mm, and since the growth season (defined as the number of days with a water temperature at or above 7°C) is 149 days (range 119-178), the mean daily increment is 0.19 mm (Jensen and Johnsen 1989).

Density of Atlantic salmon parr is estimated to 54-102 per 100

m^2, while numbers of brown trout parr, the only other species of interest, were 6-10 parr per 100 m^2 (Jensen and Johnsen 1989).

The salmon in the river Stryneelva are typical for populations of large salmon. About 75 percent of all males and females remained 3 winters at sea before they returned to the river to spawn. The average weight of salmon remaining one, two and three winters in the sea was 1.9, 6.9, and 10.3 kg, respectively (Jensen and Johnsen 1989).

Possible effects of climatic change

The elevated winter temperature in Stryneelva (Fig. 2a) is expected to accelerate hatching by about 32 days. Hence, peak hatching is expected to take place about 19 March, compared to 20 April today. Initial feeding time will occur about 31 days earlier than today (about 5 May vs. about 5 June today). Since both temperature rise in spring and initial feeding are expected to occur one month earlier than today, water temperature seems to be about the same at this stage (about 8°C) also after the climatic change (Fig. 2a). The water flow will be considerably lower than today at initial feeding. Therefore, the initial feeding stage will probably not be more critical than today in this population.

An increase in the summer temperatures as predicted in Fig. 2a will, according to the growth model, result in an increase in the annual growth rate of 0+ salmon from 45 mm to 65 mm, and of 1+ parr from 28 mm to 46 mm, corresponding to a new smolt age of about 2.0 years. Since the normal annual mortality of salmon parr is about 40-60 percent (Elson 1975, Symons 1979), this lower smolt age is expected to give a doubling of the smolt production in Stryneelva.

As we do not know neither the time for smolt migration nor the environmental factors which regulate smolt run in Stryneelva, effects of climatic change on smolt migration are inpredictable.

After the climatic change prespawning migrants will meet a river with a different flow regime than today (conf. Fig. 1a). The spring flood will probably be considerably reduced, and when the migrants arrive (usually in June/July today), the river discharge will be only about 50 percent of today. Hence, large salmon, which are in majority today, will hesitate in ascending the river. The reduced discharge in this period probably selects for a smaller salmon size in Stryneelva.

CASE STUDY NO. 2; THE RIVER ALTAELVA ATLANTIC SALMON

Life history

The river Altaelva has a catchment area of 7 400 km^2, and the annual water flow is about 77 m^3/s. Atlantic salmon can migrate 46 km upstream from its outlet to the sea. Salmon is the dominant fish species in Altaelva, and mean annual catch the last ten years was about 19 000 kg. Female spawners are dominated by 3 sea winter fish, while male spawners are dominated by two groups, 1 sea winter fish and 3 sea winter fish. Mean weight of the salmon after one, two, and three winters at sea are 2.1, 6.7 and 10.7 kg, respectively (Saksgård and Heggberget 1987, Heggberget 1989).

The Altaelva salmon spawn between 10 November and 15 December, with peak spawning the last days of November (Heggberget 1988). Peak hatching is estimated to take place the first days of June, and peak initial feeding about 10 July (Fig. 4).

Both density and growth of parr is highest in the upper third of the river, and in that area mean smolt age and size are 3.85 $\pm$ 0.07 years, and 153 $\pm$ 3 mm, respectively (Heggberget 1989). Mean length of a one year old parr is 43 mm, and annual growth rate of 1+ and 2+ parr averages 31 mm (Heggberget et al. 1986). The growth season (days > 7°C) is 98 days (range 82-112), and hence, daily growth increment is 0.32 mm.

Possible effects of climatic change

In spite of the elevated winter temperatures the river will probably remain covered by ice for several months. However, this period will be shorter than today. Hatching of salmon eggs is expected to be accelerated with 23 days (peak hatching at 18 May vs. 10 June today), and initial feeding will probably also occur 23 days earlier than today (17 June vs. 10 July). Both rise in water temperature and river flow in spring will occur about three weeks earlier than today, and therefore initial feeding is expected to take place at about the same water temperature (12-13°C, Fig. 4) and river discharge as today (about 50 percent of peak spring flow, Fig. 1b). Hence, survival of alevins at initial feeding is expected to be similar to today.

According to the growth model, the increased summer temperature (Fig. 2b) results in increased annual growth of 0+ salmon to 54 mm, and the annual growth of 1+ and 2+ parr is estimated to increase to about 43 mm. This corresponds to a new smolt age of slightly less than 3 years, compared to 3.85 years today. The lower smolt age is expected to give a doubling of the smolt production (Symons 1979) in the river Altaelva.

Today the main smolt run takes place in the river Altaelva in late June/early July. The smolts decend at decreasing water flow and at a water temperature of about 10°C. The water temperature is probably the triggering mechanism to initiate migration (T.G. Heggberget pers. com.). If this is the case, the smolt run will be accelerated with about three weeks after the climatic change. Irrespective of such an acceleration, the water discharge will be lower at the smolt run than today (Fig. 1b). As a consequence, predation from fish in the estuary will probably increase.

The upstream migration of adult salmon takes place mainly in June and July. After a change in climate, the spring peak flood will occur earlier, and the water discharge in June/July will be lower than today (Fig. 1b). Because of the low river flow it will probably be more difficult for large salmon to ascend the river in June/July in the future. Therefore, a selection against a smaller size, or a selection against an earlier ascent (May/June), or a combination of these alternatives, is expected.

CONCLUSION

A change in the climate corresponding to a doubling of the CO_2-content of the atmosphere will alter the water discharge and water temperature regimes in Norwegian rivers. The flow will increase in winter, and the spring flood will be considerably reduced in most rivers. Water temperature will increase both summer and winter.

Hatching of Atlantic salmon eggs as well as initial feeding of alevins will be accelerated, and occur earlier in spring. Dependent on temperature and flow, the initial feeding time may be a critical period in many salmon rivers.

Increasing length of the growth season, combined with elevated summer temperatures, is expected to increase annual growth of parr in most rivers. Increased water discharge and water temperatures in winter is expected to increase parr survival. Hence smolt age will decrease, and smolt production probably increase considerably. A larger proportion of mature male parr is expected to occur in many rivers.

Due to changed temperature and flow regimes, the timing of the smolt run may be changed, and may be a critical period in some rivers. The smolt run may be less concentrated in time, schools may be of smaller size, and predation from marine fishes will probably increase. Hence, survival from smolt to adult is expected to be lower than today.

After the change in climate the salmon may choose feeding areas in the ocean other than today. Temperature conditions in the ocean may influence total salmon production, and may also be linked to sea age at maturity. However, the present knowledge is too scarce to predict details.

The ascent of adult salmon in rivers is expected to be easier in early summer, while in late summer droughts may more frequently prevent upward migration. Reduced spring peak flood may probably select for a smaller salmon size in Norwegian rivers than today.

LITERATURE

Alabaster, J.S. 1991. The temperature requirements of adult Atlantic salmon, Salmo salar L., during their upstream migration in the River Dee. J. Fish Biol. 37: 659-661.

Alderdice, D.F. and F.P.J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (Oncorhynchus gorbuscha). J. Fish. Res. Board Can. 35: 69-75.

Allen, K.R. 1940. Studies on the biology of the early stages of the salmon (Salmo salar). I. Growth in the river Eden. J. Anim. Ecol. 9: 1-23.

Allen, K.R. 1941. Studies on the early stages of the salmon (Salmo salar). III. Growth in the Thurso river system, Caithness. J. Anim. Ecol. 10: 273-295.

Allen, K.R. 1944. Studies on the biology of the early stages of the salmon (Salmo salar). 4. The smolt migration in the Thurso River in 1939. J. Anim. Ecol. 13: 63-85.

Alm, G. 1958. Seasonal fluctuations in the catches of salmon in the Baltic. J. Cons. int. Explor. Mer 23: 399-433.

Baglinière, J.L. 1976. Étude des populations de Saumon atlantique (Salmo salar L., 1766) en Bretagne - Basse-Normandie. II. Activite de devalaison des smolts sur l'Elle. Ann. Hydrobiol. 7: 159-177.

Baldwin, N.S. 1957. Food consumption and growth of brook trout at different temperatures. Trans. Am. Fish. Soc. 86: 323-

328.

Banks, J.W. 1969. A review of the literature on the upstream migration of adult salmonids. J. Fish Biol. 1: 85-136.

Beacham, T.D. 1988. A genetic analysis of early development in pink (Oncorhynchus gorbuscha) and chum salmon (O. keta) et three different temperatures. Genome 30: 89-96.

Beacham, T.D. and C.B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: A comparative analysis. Trans. Am. Fish. Soc. 119: 927-945.

Berg, L.S. 1948. Freshwater fishes of the U.S.S.R. and adjacent countries. Vol. 1. 4.th. ed. Academy of Sciences of the U.S.S.R. Zoological Institute, Moscow. 504 p. (Transl. from Russian by Israel Program for Sci. Transl., Jerusalem, No. 792, 1962).

Berglund, I., L.P. Hansen, H. Lundqvist, B. Jonsson, T. Eriksson, J.E. Thorpe, and L.-O. Eriksson. 1991. Effects of elevated winter temperature on seawater adaptability, sexual rematuration, and downstream migratory behaviour in mature male Atlantic salmon parr (Salmo salar). Can. J. Fish. Aquat. Sci. 48: 1041-1047.

Bohlin, B. 1986. How much CO2 will remain in the atmosphere? pp. 93-156 In the Greenhouse Effect, Climatic change and Ecosystems. Bohlin, B., B.R.O. Doos, J. Jager and R.A. Warrick (eds). Scope 29. Chinchester. Wiley.

Brett, J.R., J.E. Shelbourn and C.T. Shoop. 1969. Growth rate and body composition of fingerling Sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Board Can. 26: 2363-2394.

Chadwick, E.M.P. 1982. Stock recruitment relationship of Atlantic salmon (Salmo salar) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496-1501.

Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for eggs of five species of salmonid fishes. Freshw. Biol. 11: 361-368.

Crisp, D.T. 1988. Prediction, from temperature, of eyeing, hatching and "swim-up" times for salmonid embryos.

Freshwater Biol. 19: 41-48.

Cross, T.F. and D.J. Piggins. 1982. The effects of abnormal climatic conditions on the smolt run of 1980 and subsequent returns of Atlantic salmon and sea trout. I.C.E.S. C.M. 1982/M:26: 8 p.

Cushing, D. 1983. Climate and Fisheries. Academic Press, London.

Dalley, E.L., C.W. Andrews and J.M. Green. 1983. Precocious male Atlantic salmon parr (Salmo salar) in insular Newfoundland. Can. J. Fish. Aquat. Sci. 40: 647-652.

DeVlaming, V.L. 1972. Environmental control of teleost reproductive cycles: a brief review. J. Fish Biol. 4: 131-140.

Donaldson, L.K. and F.J. Foster. 1940. Experimental study of effect of various water temperatures on growth, food utilization, and mortality rates of fingerling sockeye salmon. Trans. Am. Fish. Soc. 70: 339-346.

Dunbar, M.J. and D.H. Thomson. 1979. West Greenland salmon and climatic change. Medd. Grønl. 202: 109-113.

Dwyer, W.P. and R.G. Piper. 1987. Atlantic salmon growth efficiency as affected by temperature. Prog. Fish.-Culturist 49: 57-59.

Eliassen, A. and A. Grammeltvedt. 1990. Scenarier (2*CO_2) i Norge. Notat til Den interdepartementale klimagruppen. 1.2.1990. (In Norwegian).

Eliassen, A., A. Grammeltvedt, M. Mork, K. Pedersen, J.E. Weber, G. Braaten and H. Dovland. 1989. Klimaendringer i Norge ved økt drivhuseffekt. Rapport til Miljøverndepartementets klimautredningsgruppe. (In Norwegian).

Elliott, J.M. 1975a. The growth of brown trout (Salmo trutta L.) fed on maximum rations. J. Anim. Ecol. 44: 805-821.

Elliott, J.M. 1975b. The growth of brown trout (Salmo trutta L.) fed on reduced rations. J. Anim. Ecol. 44: 823-842.

Elliott, J.M., U.H. Humpesch, and M.A. Hurley. 1987. A comparative study of eight mathematical models for the relationship between water temperature and hatching time of eggs of freshwater fish. Archiv für Hydrobiologie 109: 257-277.

Elson, P.F. 1962. Predator-prey relationship between fish-eating birds and Atlantic salmon (with a supplement on fundamentals of merganser control). Bull. Fish. Res. Board Can. 133: 1-87.

Elson, P.F. 1969. High temperature and river ascent by Atlantic salmon. Int. Council Explor. Sea. C.M.1969/M: 12, 9 pp.

Elson, P.F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural productions. Int. Atl. Salmon Found. Spec. Publ. Ser. 6: 96-119.

Eriksson, L-O., H. Lundqvist, E. Brännäs and T. Eriksson. 1982. Annual periodicity of activity and migration in the Baltic salmon, Salmo salar L. pp. 415-430 In: K. Müller (ed). Coastal research in the Gulf of Bothnia. Dr. W. Junk, the Hague, Netherlands.

Eriksson, T. 1989. The effect of release time on the migratory behaviour of Baltic salmon (Salmo salar): influence of an annual time program. Behaviour 108: 10-22.

Foerster, R.E. 1937. The relationships of temperature to the seaward migration of young sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can. 3: 421-438.

Fried, S.M., J.D. McCleave and G.W. LaBar. 1978. Seaward migration of hatchery-reared Atlantic salmon, Salmo salar, smolts in the Penobscot River estuary, Maine: riverine movements. J. Fish. Res. Board Can. 35: 76-87.

Gardiner, W.R. and P. Geddes. 1980. The influence of body composition on the survival of juvenile salmon. Hydrobiologia 69: 67-72.

Garside, E.T. 1966. Effects of oxygen in relation to temperature on the development of embryos of brook trout and rainbow trout. J. Fish. Res. Board Can. 23: 1121-1134.

Garside, E.T. 1973. Ultimate upper lethal temperature of Atlantic salmon Salmo salar L. Can. J. Zool. 51: 898-900.

Gibson, R.J. 1978. The behavior of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) with regard to temperature and to water velocity. Trans. Am. Fish. Soc. 107: 703-712.

Grau, E.G. 1982. Is the lunar cycle a factor timing the onset of salmon migration? p. 184-189. In E.L. Brannon and E.O. Salo (ed.) Salmon and trout migratory behavior symposium, 1981. School of Fisheries, University of Washington, Seattle, WA.

Hansen. L.P. 1987. Growth, migration and survival of lake reared juvenile anadromous Atlantic salmon Salmo salar L. Fauna norv. Ser. A, 8: 29-34.

Hansen, L.P. and B. Jonsson. 1989. Salmon ranching experiments in the River Imsa: Effect of timing of Atlantic salmon (Salmo salar) smolt migration on survival to adults. Aquaculture 82: 367-373.

Harriman, P. 1961. Water control and artificial freshets = Atlantic salmon. Maine Atlantic Salmon Federation Document No. 2, 14 p.

Hayes, F.R. 1953. Artificial freshets and other factors controlling the ascent and population of Atlantic salmon in Le Have River. N. S. Bull. Fish. Res. Board Can. 99, 47 p.

Heggberget, T.G. 1988. Timing of spawning in Norwegian Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 45: 845-849.

Heggberget, T.G. 1989. The population structure and migration system of Atlantic salmon Salmo salar, in the River Alta, North Norway. A summary of the studies 1981-1986. pp. 124-139 In: E. Brannon and B. Jonsson (eds.). Proceedings of the Salmonid Migration and Distribution Symposium. Trondheim, Norway 23-25 June 1987.

Heggberget, T.G. and J.C. Wallace. 1984. Incubation of the eggs of Atlantic salmon, Salmo salar, at low temperatures. Can. J. Fish. Aquat. sci. 41: 389-391.

Henderson, N.E. 1963. Influence of light and temperature on the reproductive cycle of the eastern brook trout, Salvelinus fontinalis (Mitchill). J. Fish. Res. Board Can. 20: 859-897.

Hesthagen, T. and E. Garnås. 1986. Migration of Atlantic salmon smolts in River Orkla of Central Norway in relation to management of a hydroelectric station. North Am. J. Fish.

Managem. 6: 376-382.

Hoar, W.S: 1953. Control and timing of fish migration. Biol. Rew. Cambr. Phil. Soc. 28: 437-452.

Hokanson, K.E., C.F. Kleiner and T.W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, Salmo gairdneri. J. Fish. Res. Board Can. 34: 639-648.

Houghton, R.A. and G.M. Woodwell. 1989. Global climatic change. Scientific American 260 (4): 18-26.

Humpesch, U.H. 1985. Inter- and intra-specific variation in hatching success and embryonic development of five species of salmonids and Thymallus thymallus. Arch. Hydrobiol. 104: 129-144.

Huntsman, A.G. 1939. Salmon for angling in the Margaree River. Bull. Fish. Res. Bd Can. 57, 77 p.

Huntsman, A.G. 1948. Freshets and fish. Trans. Am. Fish. Soc. 75: 257-266.

Hvidsten, N.A. 1991. High winter discharge after regulation increases production of Atlantic salmon (Salmo salar) smolts in the River Orkla, Norway. (manus.).

Hvidsten, N.A. and L.P. Hansen. 1988. Increased recapture rate of adult Atlantic salmon, Salmo salar L., stocked as smolts at high water discharge. J. Fish Biol. 32: 153-154.

Hvidsten, N.A. and R.A. Lund. 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, Salmo salar L., in the estuary of River Orkla, Norway. J. Fish Biol. 33: 121-126.

Hvidsten, N.A. and P.I. Møkkelgjerd. 1987. Predation on salmon smolts, Salmo salar L., in the estuary of the River Surna, Norway. J. Fish Biol. 30: 273-280.

Jackson, P.A. & D.I.D. Howie. 1967. The movement of salmon (Salmo salar) through an estuary and a fish-pass. Irish Fish. Invest. Ser. A. 2, 1-28.

Jensen, A.J. 1990. Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (Salmo salar) and brown trout (Salmo trutta). A summary of studies in Norwegian streams. Dr.

Philos. thesis. Univ. of Trondheim, Norway.

Jensen, A.J. and B.O. Johnsen. 1986. Different adaptation strategies of Atlantic salmon (Salmo salar) populations to extreme climates with special reference to some cold Norwegian rivers. Can. J. Fish. Aquat. Sci. 43: 980-984.

Jensen, A.J. and B.O. Johnsen. 1989. Laks og sjøaure i Stryneelva 1982-1988. Norwegian Institute for Nature Research. Forskningsrapport 4: 27 p. (In Norwegian with English summary).

Jensen, A.J., T.G. Heggberget and B.O. Johnsen. 1986. Upstream migration of adult Atlantic salmon, Salmo salar L. in the River Vefsna, northern Norway. J. Fish Biol. 29: 459-465.

Jensen, A.J., B.O. Johnsen and T.G. Heggberget. 1991. Initial feeding time of Atlantic salmon (Salmo salar L.) alevins compared to river flow and water temperature in Norwegian streams. Env. Biol. Fish. 30: 379-385.

Jensen, A.J., B.O. Johnsen and L.P. Hansen. 1989a. Effect of river flow and water temperature on the upstream migration of adult Atlantic salmon Salmo salar L. in the River Vefsna, northern Norway. pp. 140-146 in: E. Brannon and B. Jonsson (eds.). Proceedings of the Salmonid Migration and Distribution Symposium. Trondheim, Norway.

Jensen, A.J., B.O. Johnsen and L. Saksgård. 1989b. Temperature requirements in Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic char (Salvelinus alpinus) from hatching to initial feeding compared with geographic distribution. Can. J. Fish. Aquat. Sci. 46: 786-789.

Jensen, A.S. 1939. Concerning a change of climate during recent decades in the Arctic and Subarctic regions, from Greenland in the west to Eurasia in east, and contemporary biological and geophysical changes. Det Kgl. Danske Videnskabernes Selskab. Biol. medd. 14 (8), 75 p.

Jessop, B.M. 1975. Investigation of the salmon (Salmo salar) smolt migration of the Big Salmon River, New Brunswick, 1966-72. Tech. Rep. Ser. No MAR/T-75-1: 1-57.

Jonsson, N., B. Jonsson and L.P. Hansen. 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. Anim. Behav. 40: 313-321.

Jonsson, B. and J. Ruud-Hansen. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (Salmo salar) smolts. Can. J. Fish. Aquat. Sci. 42: 593-595.

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

Keeling, C.D. 1986. Atmospheric CO2 concentrations. Mauna Loa Observatory, Hawaii 1958-1986. NDP-001/R1. Carbon dioxide information analysis center. Oak Ridge, Tenn. Oak Ridge Natl. Lab.

Kwain, W. 1975. Embryonic development, early growth, and meristic variation in rainbow trout (Salmo gairdneri) exposed to combinations of light intensity and temperature. J. Fish. Res. Board Can. 32: 397-402.

Larsson, P.-O. 1977. The importance of time and place of release of salmon and sea trout on the results of stockings. I.C.E.S. C.M. 1977/M:42: 4 p.

Larsson, P.-O. 1985. Predation on migrating smolt as a regulating factor in Baltic salmon, Salmo salar L., populations. J. Fish Biol. 26: 391-397.

Lindroth, A. 1955. Distribution, territorial behaviour and movements of sea trout fry in the River Indalsälven. Rep. Inst. Freshw. Res. Drottningholm 36: 104-119.

MacCrimmon, H.R. & Gots, B.L. 1979. World distribution of Atlantic salmon, Salmo salar. J. Fish. Res. Bd. Can. 36: 422-457.

MacKinnon, D. & J.R. Brett. 1953. Fluctuations in the hourly rate of migration of adult coho and spring salmon up the Stamp Falls fish ladder. Fish. Res. Bd Can., Pac. Prog. Rep. No. 95: 53-55.

MacQuarrie, D.W., J.R. Markert and W.E. Vanstone. 1978. Photoperiod induced off season spawning of coho salmon (Oncorhynchus kisutch). Ann. Biol. Anim. Biochim. Biofys.

18: 1051-1058.

Martin, J.H.A. and K.A. Mitchell. 1975. Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (Salmo salar) caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. Sci. 42: 1513-1521.

May, A.W. 1973. Distribution and migrations of salmon in the Northwest Atlantic. Int. Atl. Salmon Sympos., 1972. Spec. Publ. Int. Atl. Salmon Found., 4: 373-382.

Menzies, W.J.M. 1939. In Conference on Salmon Problems (F.R. Moulton, ed.). Publs. Am. Ass. Advmt Sci. 8: 100-101.

McIntyre, J.D. and J.M. Blanc. 1973. A genetic analysis of hatching time in steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 30: 137-139.

Mills, D. 1989. Ecology and management of Atlantic salmon. Chapman and Hall. London. New York. 351 pp.

Morrison, J.K. and C.E. Smith. 1986. Altering the spawning cycle of rainbow trout by manipulating water temperature. Prog. Fish-Cult. 48: 52-54.

Näslund, J. 1987. Effekter av biotopvårdåtgärder på öringpopulationer i Lektabäcken. Information från Sötvattenslaboratoriet, Drottningholm, Sweden. No. 3-1987. 27 p. (In Swedish).

Nott, F.J. 1973. Production of salmon smolts under natural conditions in Devon rivers. Int. Atl. Salmon Found. Spec. Publ. Ser. 4: 157-168.

Øiestad, V. 1990. Konsekvenser av klimaendringer for fiskeri- og havbruksnæringen. Bidrag til den interdepartementale klimautredningen. Fisken og Havet No. 2-1990. (In Norwegian with English summary).

Österdahl, L. 1969. The smolt run of a small Swedish river, p. 205-215. In T.G. Northcote (ed.) Symposium on salmon and trout in streams. H.R. MacMillan Lectures of Fisheries, University of British Columbia, Vancouver, B.C.

Peterson, R.H., H.C.E. Spinney and A. Sreedharan. 1977. Development of Atlantic salmon (Salmo salar) eggs and alevins under varied temperature regimes. J. Fish. Res.

Board Can. 34: 31-43.

Piggins, D.J. 1959. Investigation on predators of salmon smolts and parr. Salmon Research Trust Ireland 5, Appendix 1.

Power, G. 1981. Stock characteristics and catches of Atlantic salmon (Salmo salar) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38: 1601-1611.

Pyefinch, R.A. 1955. A review of the literature on the biology of the Atlantic salmon. Sci. Invest. Freshwat. Fish. Scot. No. 9, 24 p.

Randall, R.G., J.E. Thorpe, R.J. Gibson and D.G. Reddin. 1986. Biological factors affecting age at maturity in Atlantic salmon (Salmo salar). In: Salmonid age at maturity (D.E. Meerburg, ed.), pp. 90-96. Can. Spec. Publ. Fish. Aquat. Sci. 89.

Reddin, D.G. 1985. Atlantic salmon (Salmo salar) on and east of the Grand Bank. J. Northw. Atl. Fish. Sci. 6: 157-164.

Reddin, D.G. 1988. Ocean life of Atlantic salmon (Salmo salar L.) in the northwest Atlantic. In: Atlantic salmon: Planning for the future (D. Mills and D. Piggins, eds.). Croom Helm, London, pp. 483-511.

Reddin, D.G. and P.B. Short. 1991. Postsmolt Atlantic salmon (Salmo salar) in the Labrador Sea. Can. J. Fish. Aquat. Sci. 48: 2-6.

Reitan, O., N.A. Hvidsten and L.P. Hansen. 1987. Bird predation on hatchery reared Atlantic salmon smolts, Salmo salar L., released in the River Eira, Norway. Fauna Norv. Ser. A. 8: 35-38.

Rimmer, D.M. and U. Paim. 1990. Effects of temperature, photoperiod, and season on the photobehaviour of juvenile Atlantic salmon (Salmo salar). Can. J. Zool. 68: 1098-1103.

Rimmer, D.M., U. Paim and R.L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon (Salmo salar) in a small river. Can. J. Fish. Aquat. Sci. 40: 671-680.

Rimmer, D.M., U. Paim and R.L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (Salmo salar) at the summer-autumn transition in a small river.

Can. J. Fish. Aquat. Sci. 41: 469-475.

Saksgård, L. and T.G. Heggberget. 1987. Fiskeribiologiske undersøkelser i Alta-Kautokeinovassdraget før utbygging. Direktoratet for Naturforvaltning. Reguleringsundersøkelsene. Rapport No. 8-1987. 98 pp. (In Norwegian).

Sælthun, N.R., J. Bogen, M.H. Flood, T. Laumann, L.A. Roald, A.M. Tvede and B. Wold. 1990. Klimaendringer og vannressurser. Bidrag til den interdepartementale klimautredningen. NVE-Vassdragsdirektoratet. No. V-30 (In Norwegian, with English summary).

Sato, R. 1980. Variations in hatchability and hatching time, and estimation of heritability for hatching time among individuals within the strain of coho salmon (<u>Oncorhynchus kisutch</u>). Bull. Nat. Res. Inst. Aquac. 1: 21-28.

Saunders, R.L. 1986. The thermal biology of Atlantic salmon: influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. Inst. Freshwater Res. Drottningholm Rep. 63: 77-90.

Saunders, J.W., E.B. Henderson, B.D. Glebe and E.J. Loudenslager. 1983. Evidence of a major environmental component in determination of the grilse : larger salmon ratio in Atlantic salmon (<u>Salmo salar</u>). Aquaculture 33: 107-118.

Saunders, J.W. and M.W. Smith. 1962. Physical alteration of stream habitat to improve brook trout population. Trans. Am. Fish. Soc. 91: 185-188.

Scarnecchia, D.L. 1983. Age at sexual maturity in Islandic stocks of Atlantic salmon (<u>Salmo salar</u>). Can. J. Fish. Aquat. Sci. 40: 1456-1468.

Scarnecchia, D.L. 1984. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (<u>Salmo salar</u>). Can. J. Fish. Aquat. Sci. 41: 917-935.

Schaffer W.M. and P.F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56: 577-590.

Siginevich, G.P. 1967. Nature of the relationship between increase in size of Baltic salmon fry and the water temperature. (Gidrob. Zhurnal 3, 43-48); Fish Res. Board

Can. Transl. Ser. No. 952. 14 p.

Silver, S.J., C.E. Warren and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Trans. Am. Fish. Soc. 92: 327-343.

Solomon, D.J. 1978. Some observations on salmon smolt migration in a chalk stream. J. Fish Biol. 12: 571-574.

Spigarelli, S.A., M.M. Thommes and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. Trans. Am. Fish. Soc. 111: 199-209.

Stewart, L. 1978. Why no southern hemisphere salmon? The gyre theory. Salmon and Trout Magazine 213: 46-50.

Symons, P.E.K. 1979. Estimated escapement of Atlantic salmon (Salmo salar) for maximum smolt production in rivers of different productivity. J. Fish. Res. Board Can. 36: 132-140.

Tang, J., M.D. Bryant and E.L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Prog. Fish.-Cult. 49: 167-174.

Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, Salmo salar: freshwater period influences and conflicts with smolting. In: Salmonid age at maturity (D.J. Meerburg, ed.). pp. 7-14. Can. Spec. Publ. Fish. Aquat. Sci. 89.

Thorpe, J.E. and R.I.G. Morgan. 1978. Periodicity in Atlantic salmon Salmo salar L. smolt migration. J. Fish Biol. 12: 541-548.

Thorpe, J.E., L.G. Ross, G. Strulthers and W. Watts. 1981. Tracking Atlantic salmon smolts, Salmo salar L., through Loch Voil, Scotland. J. Fish Biol. 19: 519-537.

Thorpe, J.E., C. Talbot and C. Villarreal. 1982. Bimodality of growth and smolting in Atlantic salmon, Salmo salar L. Aquaculture 28: 123-132.

Thurow, F. 1966. Beiträge zur Biologie und Bestandeskunde die Atlantichen Lachses (Salmo salar L.) in der Ostsee. Ber. dt. wiss. Kommn. Meeresforsch. 18 (3/4): 223-379.

Wallace, J.C. and T.G. Heggberget. 1988. Incubation of eggs of Atlantic salmon (Salmo salar) from different Norwegian streams at temperatures below 1 °C. Can. J. Fish. Aquat. Sci. 45: 193-196.

Wedemeyer, G.A., R.L. Saunders and W.C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42: 1-14.

White, H.C. 1939. Factors influencing decent of Atlantic salmon smolts. J. Fish. Res. Board Can. 4: 323-326.

Whitehead, C., N.R. Bromage, J.R.M. Forster and A.J. Matty. 1978. The effects of alterations in photoperiod on ovarian development and spawning time in the rainbow trout (Salmo gairdneri). Ann. Biol. Anim. Biochim. Biophys. 18: 1035-1043.

Wolff, S.W., T.A. Wesche, D.D. Harris, and W.A. Hubert. 1990. Brown trout population and habitat changes associated with increased minimum low flows in Douglas Creek, Wyoming. Biological Report 90(11): 1-20.

Table 1. Expected change in air temperature and precipitation in Norway due to a doubling of the CO_2-content (Eliassen and Grammeltvedt 1990).

	Coast	Inland
Air temperature (°C):		
winter	+3.0	+3.5
summer	+1.5	+2.0
Precipitation (%):		
spring	+15	+10
summer	+10	+10
autumn	+ 5	+ 5
winter	+ 5	+ 5

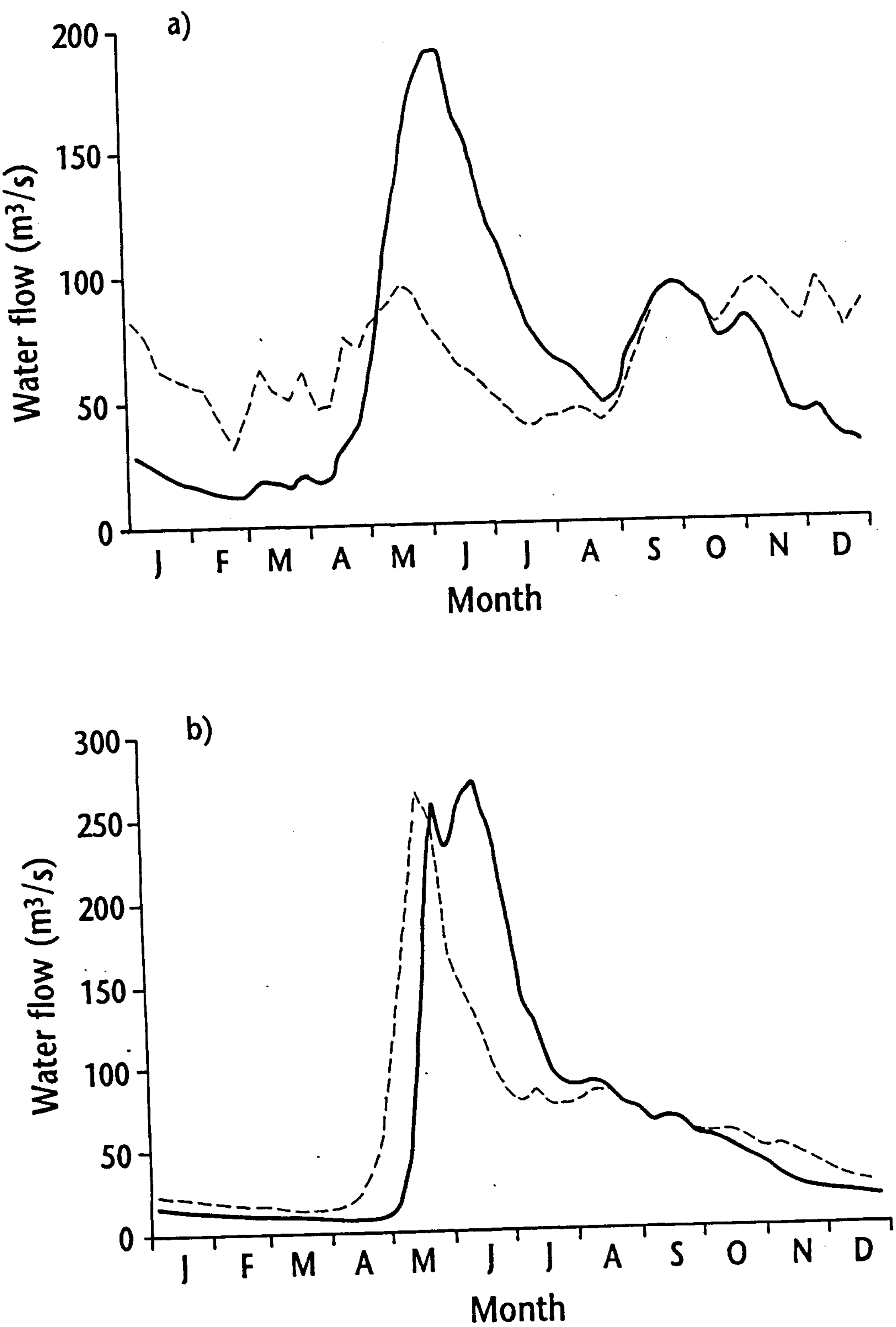

Figure 1. Annual water discharge in a) river Vosso (61°N), and b) river Altaelva (70°N); present regime (solid line) and predicted regime after doubling of the CO_2 content of the atmosphere (stipled line) (redrawn from Sælthun et al. 1990).

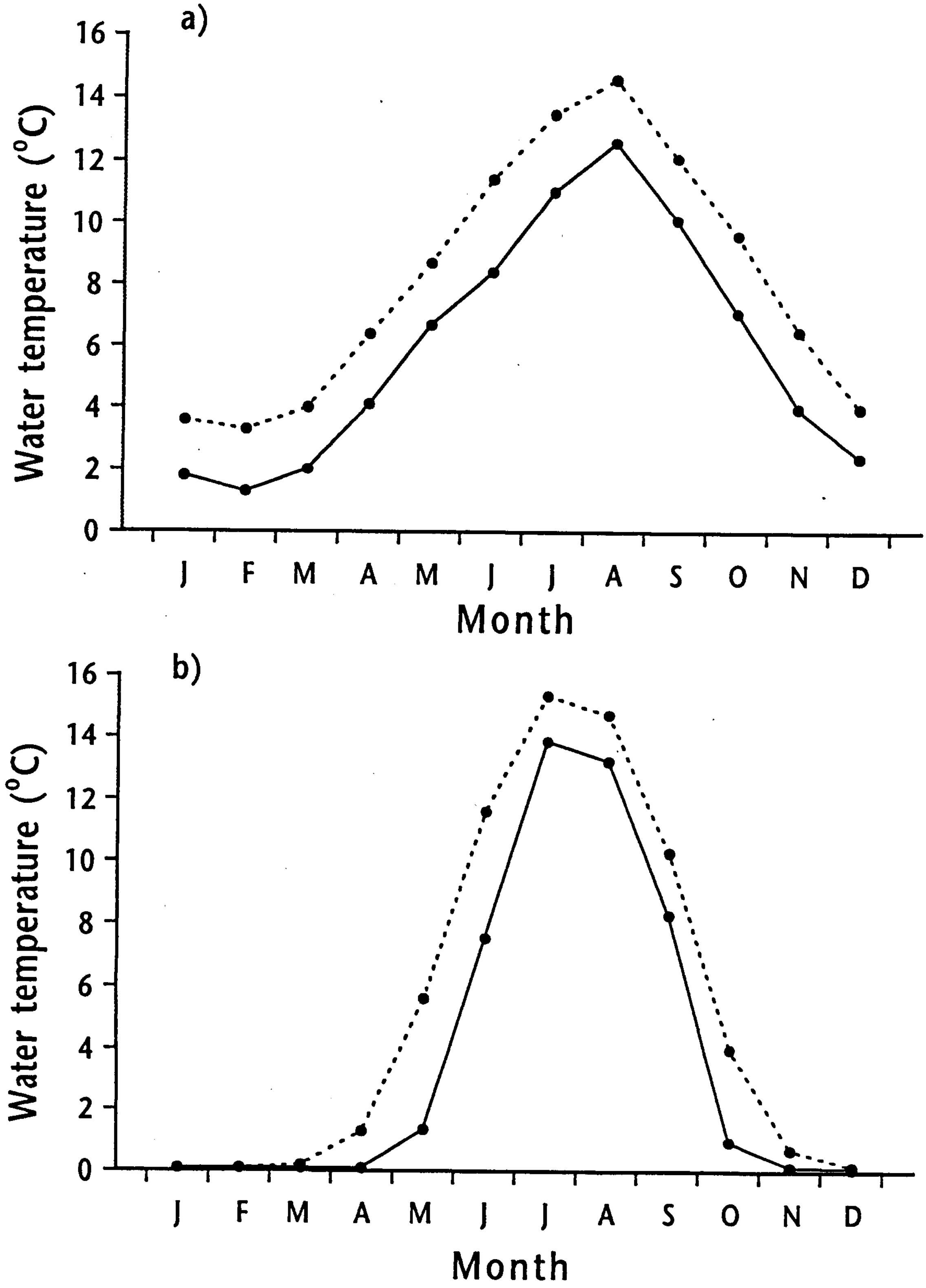

Figure 2. Water temperature in a) river Stryneelva, and b) river Altaelva; present regime (solid line), and expected regime after doubling of the CO_2 content of the atmosphere (dotted line).

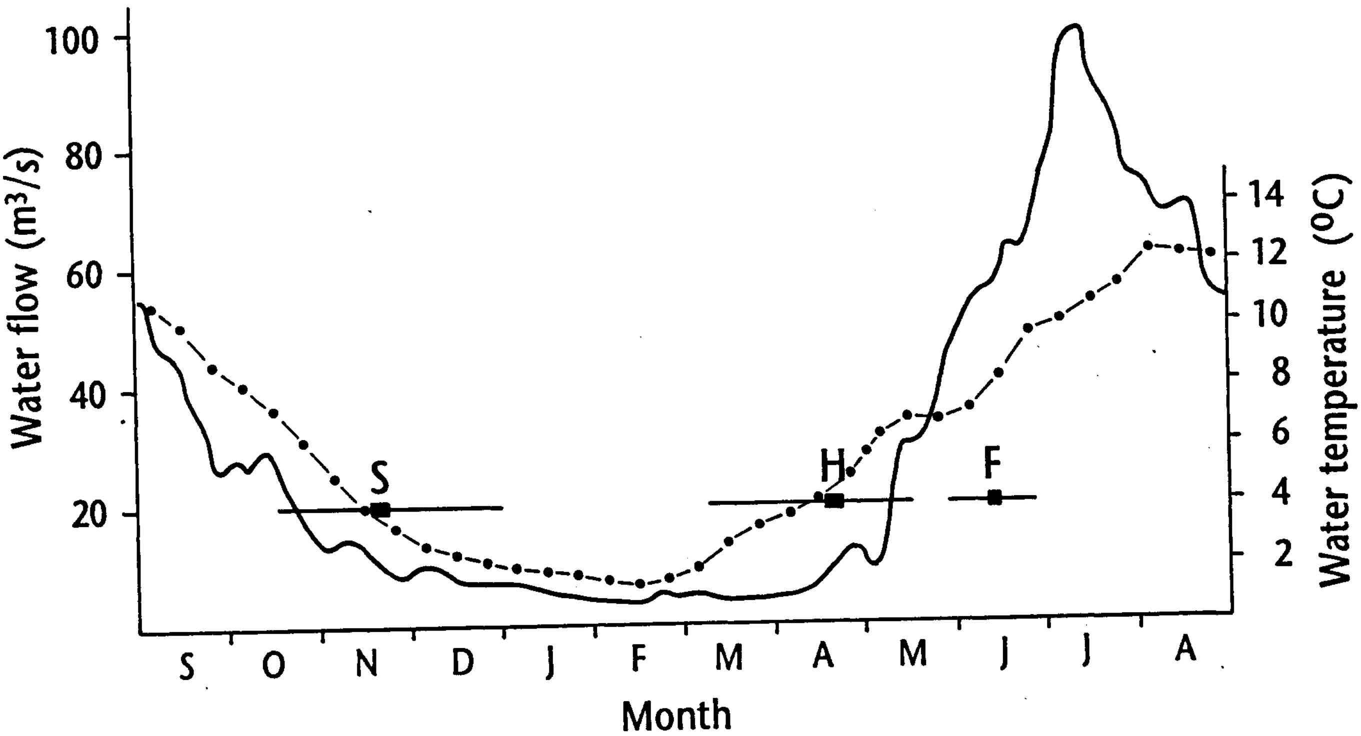

Figure 3. Present water discharge (solid line) and water temperature (stippled line) regimes in the river Stryneelva. Spawning time (S), hatching time (H) as well as time for initial feeding of alevins (F) are also given.

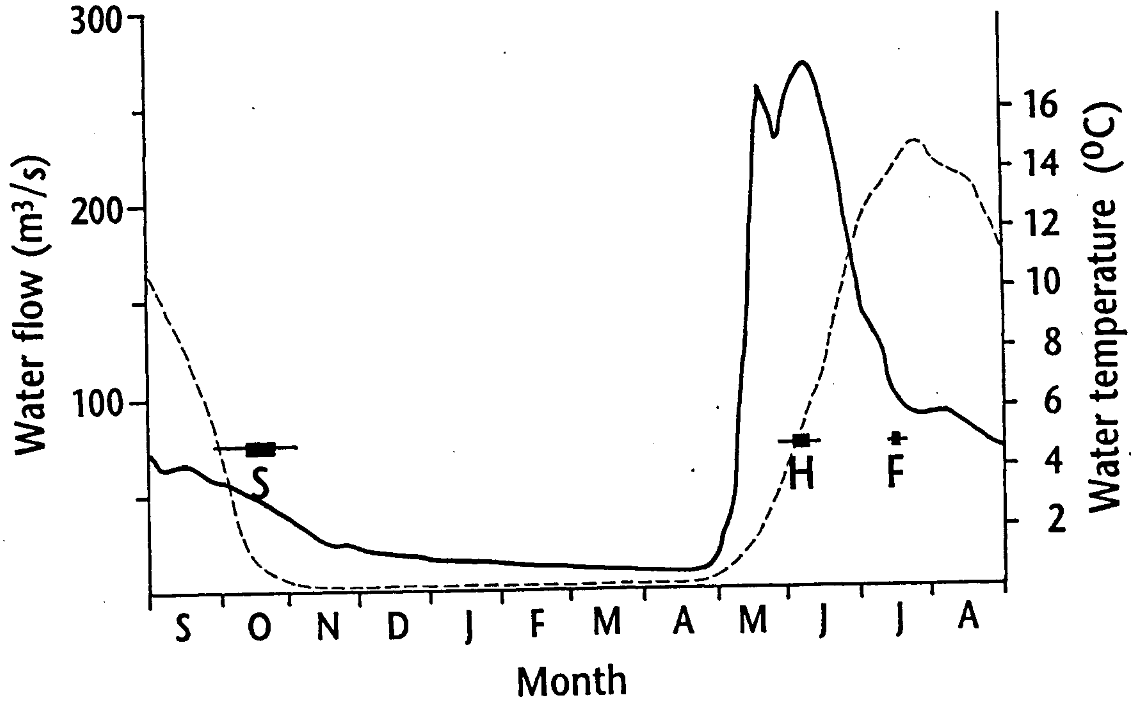

Figure 4. Present water discharge (solid line) and water temperature (stippled line) regimes in the river Altaelva. Spawning time (S), hatching time (H) as well as time for initial feeding of alevins (F) are also given.