VARIATION IN THE YEARLY AND SEASONAL ABUNDANCE OF JUVENILE ATLANTIC SALMON IN A LONG-TERM MONITORING PROGRAMME

Methodology, status of stocks and reference points

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Abstract

The long-term monitoring programme for the River Teno Atlantic salmon (Salmo salar L.) stocks has covered the juvenile densities (25 yr) and the abundance and characteristics of the returning adults (31 yr). The feasibility of the programme was examined by studying the interrelationships between the yearly catches and juvenile salmon densities, performance and reliability of the electrofishing method, and the effects of fishing regulations on the salmon stocks. Finally, juvenile salmon abundances were related to the available fluvial habitat and reference levels were defined by using habitat models.

Extensive seasonal variation in juvenile salmon density was apparent. The densities of fry and parr showed an increase from early summer towards late August and a subsequent decline towards the autumn. Long-term electrofishing monitoring is recommended to be carried out in as standardized a form as possible in order to reduce variations in catchability.

Over the 25-year monitoring period, the abundance of parr (1+) increased in one sampling site cluster out of nine clusters and declined in one cluster. Fry densities increased in seven clusters. Juvenile densities exhibited considerable temporal and spatial variation. Similarly, the salmon catches varied extensively, and the numbers of 1-2SW salmon and previous spawners increased.

The numbers of 1–2SW female salmon in the catches and the subsequent juvenile densities were significantly related, as regression models explained 19–44% of the variation in juvenile abundance. The juvenile monitoring allows evaluation of the relative spawner abundance in preceding years, confirming the information provided by catch statistics.

Juvenile salmon densities explained 23–41% of the variation in subsequent 1–2SW salmon catches. Significant correlations were detected with a lag of one year between the subsequent sea-age groups of salmon in the catches. Thus, these relationships can be used for forecasting future salmon abundances.

Large areas of high habitat quality in the River Teno system fail to meet their expected juvenile densities, and factors others than physical habitat characteristics, such as a lack of spawners, restrict the juvenile abundance. More than 50% of the permanent sampling sites where habitat would predict high densities (≥50 parr per 100 m²) had observed densities in the mid (10–49) or low density category (<10).

It was expected that the densities should increase after regulatory measures implemented in 1989–1990, but results indicate that the reference levels of parr densities have not been attained and the densities have not increased, whereas a general increase in salmon fry densities was detected. Nonetheless, the management measures have succeeded in maintaining the River Teno salmon stocks, which still today enable and support diversified fisheries.

Keywords: density, electrofishing, long-term monitoring, Salmo salar, spatial and temporal variability, trends
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References
1 Introduction

The wild Atlantic salmon (*Salmo salar* L.) still has a special position among fish species as a profitable target for professional fishermen and a desirable objective for recreational fishermen. Wild salmon also have aesthetic significance, being a symbol of undamaged river habitats and of unpolluted water. Healthy wild salmon stocks also offer a source of genetic biodiversity when maintaining and developing the quality of salmon used in aquaculture. Throughout Europe and North America, recreational salmon fishing has developed into an important economy for landowners and tourism entrepreneurs. However, the Atlantic salmon as a species is now extinct, or in a critical condition, in over 27% of the salmon rivers of the world, and endangered or vulnerable in a further 30 rivers (WWF 2001). During recent decades, salmon stocks have widely declined or being extirpated due to overfishing and habitat degradation in the North Atlantic region (Saksgård & Heggerget 1990, Parrish et al. 1998) or due to a lethal parasite, *Gyrodactylus salaris*, in Norway (Jensen & Saksgård 1987). The increasing numbers of escaped farmed salmon within the distribution area of wild salmon, associated with an increase in salmon cage culture, have further affected wild salmon populations and negatively impacted on the conservation of local stocks and their special characteristics (Youngson et al. 1998, McDowell 2002, McGinnity et al. 2003). Escaped salmon comprise from about one-third to more than 80% of the spawning stock of many southern and western Norwegian rivers (Fiske & Lund 1999).

During the last 20 years, salmon fishing has undergone significant changes at sea in the Northeast Atlantic and in rivers flowing into it. In spite of many plans directed at conserving especially multi-sea-winter (MSW) salmon stocks, catches of Atlantic salmon have continued to decline throughout most of the species' range in the North Atlantic (ICES 2002). Concerns relating to the declining salmon abundance and international responsibility for the highly exploited salmon stocks at sea resulted in the establishment of the North Atlantic Salmon Conservation Organization (NASCO) in 1984 (Windsor & Hutchingson 1994). Through this convention, salmon fishing on the high seas has been closed and is only permitted in the Faeroes fishing zone in the Northeast Atlantic according to yearly catch limits. Norway banned drift net fishing in coastal areas in 1989 with the aim of strengthening the weakened salmon stocks (ICES 1990). However, at the same time as salmon fishing at sea was regulated or even closed in the 1980s and 1990s, the
culture of salmon in sea cages increased tremendously. The increased cage culture and low price of farmed salmon has resulted in a low price for wild salmon, which in turn can reduce their exploitation at sea. It is most probable that the commercial fishing effort for salmon at sea will decline during the next decades, coinciding with the expansion of aquaculture. The decline of salmon fishing in the Faeroes since the mid-1990s (ICES 2002) is an example of a fishery at sea becoming unprofitable following the start of salmon cage culture in the Faeroes and the decline in the price of wild salmon.

Increasing salmon cage culture will most likely increase the number of escaped salmon. It is estimated that some two million salmon escape each year in the North Atlantic region, accounting for c. 50% of the total pre-fishery abundance of wild salmon in the area (see McGinnity et al. 2003). Concern has been raised about the potential detrimental genetic and other changes that may take place in wild populations when escaped farmed salmon enter rivers and interact with wild salmon.

The objectives of the monitoring of salmon stocks can be divided into two categories: scientific and management. Scientific objectives focus entirely on learning and developing an understanding of the dynamics of the salmon stocks, and monitoring programmes designed to aid management provide information that is useful in making informed management decisions (Yoccoz et al. 2001). To succeed in the management of wild salmon stocks with the aim of sustaining and enhancing them, it is necessary to obtain thorough long-term data on the stocks to help in understanding the stock dynamics. Typical features of most salmon stocks include yearly fluctuations in the abundance of returning salmon and the relative proportions of different sea-age groups (Gee & Miller 1980). These indicate the effects of environmental changes at sea, which are largely responsible for regulating salmon stock dynamics (Scarnecchia et al. 1989a,b, Dempson 1992, Friedland & Reddin 1993, Friedland et al. 1993, Reddin & Friedland 1993, Antonsson et al. 1996, Friedland 1998, Friedland et al. 1998). Monitoring must therefore be long-term to identify trends in measured variables because salmon stocks are renewed slowly, especially in the northern part of the distribution area. In addition, natural long-term trends in the abundance of salmon stocks and environmental fluctuations can mask the effects of regulatory measures on both catches and juvenile production.

Valuable indicators of salmon stocks include spawning escapement, the age distribution of spawners, the number of smolts migrating to the sea and juvenile abundance. In large rivers, long-term monitoring of the size of salmon stocks is difficult. In most cases, there are no possibilities to accurately estimate the number of ascending salmon or the spawning escapement, and the reported catch is therefore used as an index of abundance and spawning escapement (Chadwick 1985, Saltveit 1996). It is also generally accepted that the catch data describes the fluctuations and development of fisheries (see references in Hansen 1988). Managers would like to know the yearly number of smolts migrating from rivers, indicating the earlier spawning escapement. Smolt estimates would also allow the prediction of trends in subsequent adult catches. In the case of low smolt production, managers have a possibility to regulate the fishery in advance. However, the number of rivers in the North Atlantic in which long-term smolt counting takes place is limited to a small number of index rivers, mainly with 1SW salmon stocks (ICES 2002).

Electrofishing is a widely employed research and monitoring technique used to detect changes in abundance as an outcome of fishery management strategies or in the recruitment of the Atlantic salmon at different spawning levels (Chadwick & Randall 1986), or
to monitor long-term trends in juvenile fish production as an index of changes in natural conditions (Bohlin et al. 1989). A significant positive relationship has been shown between the abundance index of salmon fry and the subsequent smolt production, although the predictive ability decreased as smolt age increased, suggesting the influence of density-independent mortality (Crozier & Kennedy 1995). Thus, juvenile salmon densities can provide a direct measure of juvenile salmon production that can be converted to smolt output estimates if necessary (ICES 2003b).

The monitoring of juvenile salmon densities can include specification of the reference levels, i.e. the target abundance of juvenile salmon, which are based on the available habitat and can be defined by the site, habitat type or river (VI). However, the exact target abundance or the maximum density (reference points) in sites or habitats might be difficult to determine because densities are temporary and fluctuate throughout the summer (IV, Saksgård et al. 1992). Juvenile salmon density estimates allow evaluation of the relative spawner abundance in previous years, and confirmation of the stock status information provided by catch statistics. On the other hand, significant deviations in juvenile abundance from what is predicted by the catch estimate would indicate changes in the exploitation rate in river fisheries.

The large River Teno system in the northernmost distribution area of the Atlantic salmon is at present probably the most productive Atlantic salmon river in the world in terms of the annual run and catches of wild salmon. The river valleys and aquatic habitats are virtually pristine and the only notable human impact affecting the salmon stocks is fishing. In addition, variation in natural mortality causes fluctuation in the salmon stocks (Dempson 1992).

Under a bilateral agreement between Finland and Norway regulating the fishery in the River Teno with the objective of maintaining and enhancing wild salmon stocks, a joint monitoring programme on the status and development of the salmon stocks was initiated at the end of the 1970s. The long term monitoring programme includes annual collection of catch statistics and catch samples and estimation of juvenile salmon abundance by electrofishing. To monitor the annual and long-term variation in densities of juvenile salmon, permanent electrofishing sites have been sampled annually in the main stem of the River Teno and its two major tributaries, Utsjoki and Inarijoki, since 1979. Such a long time series in juvenile salmon monitoring is rare.

In this thesis the results of the long-term monitoring of the juvenile salmon densities in the River Teno system are analysed (I, II) and factors affecting the performance and reliability of the electrofishing method are assessed (III, IV). Moreover, variation in juvenile fish production was expected to reflect changes in salmon fishery management strategies that took place in 1989–1990 (see above; I, II, V). Juvenile salmon abundances are also related to the available fluvial habitat by using habitat models in defining reference levels (VI). As the monitoring programme also includes assessment of the adult salmon returns through catch statistics, the possibility of using the juvenile data to predict subsequent catches, and the use of adult salmon estimates in predicting subsequent juvenile abundance, is studied (V).

The main questions addressed in this study were:

1. Do long-term changes in juvenile salmon abundance take place in the River Teno system and could they be linked with major changes in salmon fishing regulations in the river and at sea?
2. Are the electrofishing methods used in the long-term monitoring reliable?
3. Are the long-term catch and juvenile estimates linked, i.e. is it possible to use juvenile salmon abundance as a predictor of subsequent catches, or catches in predicting subsequent juvenile abundance?
4. Are the juvenile salmon densities in the River Teno system comparable to the estimated production capacity of the available habitat?
2 Material and methods

2.1 Geographical location and natural conditions of the River Teno system

The River Teno system (catchment area 16 386 km²) is located in northern Europe (70ºN, 28ºE) running into the Barents Sea through Tanafjord. The River Teno is the most important and one of the largest salmon rivers in Finland and Norway. The mainstem of the River Teno, and one of the three main headwater rivers, the River Inarijoki, form the border between Finland and Norway (Fig. 1). The total length of the rivers Teno and Inarijoki is 351 km. The largest tributary on the Finnish side of the catchment area is the River Utsjoki (1 665 km², 66 km). The largest areas of rapids and riffles in the system can be found in the middle section of the River Teno mainstem. The River Inarijoki passes through a series of shallow lakes, while the River Utsjoki consists of large number of deep lakes with connecting river stretches.

The River Teno system is located in a subarctic area where winter conditions are extreme: ice covers the rivers for about six months, from late November until late May. The spring flood usually takes place in late May or early June, continuing for 2 to 3 weeks. The mean annual discharge in the middle part of the River Teno between 1979 and 1995 was 156 m³·s⁻¹ measured close to the outlet of the River Utsjoki. The discharge can be as low as 19 m³·s⁻¹ in the middle of April and as high as 2 740 m³·s⁻¹ in the end of May. The water in the rivers is of good quality for juvenile salmon (pH 7.0–7.7, alkalinity 140–450 meq·l⁻¹, conductivity 2.8–6.1 mS·m⁻¹ and total P 9.8–27.1 mg·l⁻¹, Lapland Regional Environment Centre, unpublished data). From 1979 to 1994, the mean water temperature in the River Teno was 1.5 °C in May, 8.6 °C in June, 12.9 °C in July, 11.9 °C in August and 6.9 °C in September. Severe environmental conditions dominate the winter months, as is apparent for the period from October to May when the water temperature is constantly 0.1–0.4 °C. Water temperature normally peaks at the end of July and the beginning of August. The annual maximum temperatures (July or August) in 1992–1995 varied between 13.9 °C and 21.0 °C in the River Teno main stem and between 13.3 °C and 18.3 °C in the River Utsjoki. Under the polar conditions the area is illuminated for 24 hours a day during 2.5 months from mid-May until the end of July.
Juvenile Atlantic salmon coexist with 16 other fish species in the River Teno system (I). The occurrence of other species at electrofishing sites representing the shallow flowing sections of the rivers Teno, Utsjoki and Inarijoki was low and their densities negligible from 1979–1999 (I). A newly introduced species in the River Utsjoki, the bullhead (*Cottus gobio* L.) (Pihlaja *et al.* 1998a), has increased its distribution since the late 1970s and frequently occurs in areas with a low salmon density but is seldom found in areas with a high salmon density. In 2000 the bullhead was recorded for the first time in the main stem of the River Teno some hundreds of metres below the outlet of the River Utsjoki (Niemelä *et al.* 2003).

Fig. 1. Electrofishing sites within the River Teno system and the distribution of Atlantic salmon (grey line above the river).
2.2 The Atlantic salmon

The Atlantic salmon (*Salmo salar* L.) is typically an anadromous fish species that reproduces and spends juvenile phases in freshwater and grows to reach maturity at sea (Jones 1959, Thorpe 1988, Mills 1989, Thorpe 1994). Freshwater residency provides a refuge from potential predators and relatively stable survival conditions for eggs and juveniles (Chaput *et al.* 1998). There are also some non-anadromous populations, land-locked salmon, that have become isolated from the anadromous salmon populations, such as during the period of rapid land-upheaval after the last ice age, and they have adapted to spending their entire life in freshwater (Berg 1985 and references therein). The Atlantic salmon shows remarkable plasticity within and between populations in its reproductive life cycle in terms of the age at sexual maturity, the age at which the juveniles migrate to sea, the years spent at sea, and the ability to recondition to undergo successive reproduction (Saunders & Schom 1985).

In Atlantic salmon, males and females have adopted different life history strategies in terms of the age at sexual maturation. There are certain special characteristics indicating strong adaptation to various environments and the plasticity of life history strategies, e.g., the early maturation of juveniles before seaward migration to form so-called precocious males, which are usually found in all salmon populations (Jones 1959, Thorpe & Morgan 1980, Saunders *et al.* 1982). In the River Teno system, precocious males comprise 5–10% of the population and this phenomenon has been detected in all age groups between 1–6 years (Elo *et al.* 1995, Heinimaa & Erkinaro 2004). Some male parr mature repeatedly, while others mature once or not at all (Saunders & Schom 1985). Precocious females are rare (Bagliniere & Maisse 1985) and are not typically found in northern salmon populations.

The juvenile period lasts 1–8 years before transition to the smolt stage (Power 1981). The freshwater growth rate is lower at higher latitudes (Power 1981, L’Abee-Lund *et al.* 1989, Metcalfe & Thorpe 1990), resulting in a greater seaward migration age (Dahl 1910, Prouzet 1990). In southern distribution areas under optimal growing conditions, juveniles generally migrate to the sea after a one-summer residency in freshwater. For example, the mean smolt age range is between 1 and 1.4 years in some salmon rivers in France (Prouzet 1990), whereas in northern areas juvenile salmon generally reach the migration phase after 3–5 years in the river (Oklund *et al.* 1993, Niemelä *et al.* 2000). Under conditions of extreme cold, juveniles need up to 7–8 years before smoltification, as in Ungava Bay in Northern Canada (Power 1969), glacial rivers in Norway (Jensen & Johnsen 1986), the Russian Kola Peninsula (Kuzmin & Smirnov 1982) and also in some parts of the River Teno (Englund *et al.* 1999, Niemelä *et al.* 2000).

The sea migration takes 1–5 years before salmon reach the age and size of maturity at which homing can take place. Salmon tend to return to their natal river (Hansen & Jonsson 1994) and even to the same spawning sites within a watershed that they occupied as juveniles (Heggberget *et al.* 1986). However, homing is not perfect, and some salmon stray into foreign rivers where they may spawn and produce progeny (e.g., Mills 1989). Salmon usually spawn in the year when homing takes place (Jones 1959), but in some cases so-called late running salmon first overwinter in freshwater and then reproduce after a one and a half year stay in the river, as occurs in the rivers Pono (Whoriskey *et al.* 1996) and Varzuga (Lysenko 1997) in the Kola Peninsula and in some rivers in Scotland.
Such late-running salmon are also common in the River Teno, but their contribution to juvenile production is unknown. Some salmon survive spawning and either return to the sea soon afterwards in the autumn (Jonsson et al. 1991), or spend the entire winter in freshwater and then migrate to sea with the spring flood, as in the rivers Alta (Berg et al. 1988) and Teno (Niemelä et al. 2000). Survival following the first spawning and subsequent repeat spawning enables a particular year class to genetically contribute to the salmon stock over a number of years, as some salmon may spawn as many as six times (Ducharme 1969), and in the River Teno system up to four times.

The total salmon catch in the North Atlantic has markedly declined since the beginning of the 1970s, from 11 000 tonnes to 3000 tonnes in 2002, which was amongst the lowest on record, although catches in several countries were above the 5 year and 10 year averages (ICES 2002). The reduction in catches in recent years has largely resulted from a lower exploitation rate within the high-seas area of fisheries jurisdiction of NASCO (the North Atlantic Salmon Conservation Organization), and can also be accounted for by management plans that have reduced the fishing effort in the home waters of several countries. The pre-fishery abundance of salmon at sea has also markedly declined, indicating drastic changes in marine survival (ICES 2002). However, the pre-fishery abundance of multi-sea-winter salmon, especially in Northern Europe, has slightly increased in recent years (ICES 2002). The growth in salmon aquaculture in the North Atlantic may also have affected the decline in commercial fishing. Fluctuations in salmon catches can be substantial and commonly occur over wide geographical areas (Dempson et al. 1998). This oscillation can follow a longer cycle of 20–30 years (Bielak & Power 1986) or a shorter cycle of between 8 and 9 years, as in the north-eastern rivers Teno and Näätämö-joki.

2.3 The Atlantic salmon stocks in the River Teno system and the fisheries exploiting them

The River Teno salmon show very diverse life history traits, including exceptionally large variation in the freshwater residence time, age at maturity and the extent of ocean migration. There are 28 smolt age (2–8) and sea age (1–5) combinations for virgin salmon and 68 combinations of previous spawning salmon. This variation is among the widest in a single river system in the distribution area of the species, if not the widest. Salmon catches mainly consist of virgin salmon, but repeat spawners contribute a significant supplement to the catch, especially at the beginning of the season and in the spawning escapement (Figs. 4 and 7, Niemelä et al. 2000).

The considerable variability in life history, i.e. individuals from a given year class can spawn during several years and can breed with salmon from other year-classes, is a safeguard against occasional reproductive failure, since nonspawning individuals in the river or at sea could spawn in subsequent years (e.g., Saunders & Schom 1985). This type of life history strategy is ecologically necessary for the survival of salmon, especially in rivers where the exploitation is high, as in the River Teno system, or where extreme environmental drawbacks such as the destruction of spawning grounds by ice blocks during the
spring flood, can cause loss to juvenile production in some years. In addition, the strategy among juveniles of responding to the harsh subarctic ecosystem by growing slowly and smolting at a late age (2–8 years, mainly 3–6 years) safeguards certain age and size groups against losses caused by unfavourable conditions and may improve the stability of the populations. On the other hand, the wide variation in smolt and sea ages and their variation between years (Englund et al. 1999, unpublished data, Finnish Game and Fisheries Research Institute) complicates interpretation or prediction of the relationships between juvenile abundance and expected subsequent run sizes (catches) of various sea-age groups. In the River Teno system, smolt ages differ between sea-ages in that the mean smolt age declines with increasing sea-age (Erkinaro et al. 1997, Niemelä et al. 2000, Fig. 2). This is common in salmon life history strategies and has also been described elsewhere (Meerburg 1986).

![Graph showing the distribution of 1-4SW salmon smolt ages in Teno, Utsjoki, and Inarijoki from 1997-2003.](image)

Fig. 2. Smolt age distribution of 1–4SW salmon and the mean smolt age (on the top of the bar) in the rivers Teno, Utsjoki and Inarijoki in 1997–2003.
There are 14 main tributaries and numerous smaller tributaries to the mainstem or to the main tributaries, which sustain salmon populations that differ genetically from the rest of the system or even within river stretches (Elo et al. 1994) (Fig. 3). In most of the tributaries, as in the rivers Buolbmátjohka, Lákšjohka, Veahéajohka, and smaller tributaries of the Utsjoki (Fig. 1), salmon consist mainly of 1SW female and male fish and previous spawners, but 2SW female salmon also occur to some extent. In the River Teno mainstem, females are mainly multi-sea-winter (MSW) salmon with previous spawners included, but among males the 1SW salmon outnumber other sea-age groups (Fig. 3). MSW females also form an important component, especially in the uppermost reaches of the watershed, as in the rivers Kárášjohka and Iešjohka and also in the lowermost large tributary of the Teno system, the River Maskejohka.

Fig. 3. Sea-age distribution of salmon in various parts of the River Teno system. Females: left bar; males: right bar.

Sea-age at maturity is founded on a complex of genetic and environmental factors (Saunders et al. 1983, Martin & Mitchell 1985, Saunders 1986, see comprehensive review by Meerburg 1986). Large MSW salmon, which spawn in the mainstem of the River Teno and in some of the largest tributaries, produce offspring where females tend to mature mostly after more than one year at sea (unpublished data, Finnish Game and Fisheries Research Institute). In the River Teno at the spawning sites in August, the catch of virgin females consists mainly (c. 70%) of MSW females, indicating their high significance in juvenile production (Fig. 3). However, salmon stocks have undergone long-term adaptation in each tributary and within the River Teno mainstem, and a suitable composition of ages at maturity has developed for each environment. The ability to return to the river of origin is regarded as the basis of the genetic differentiation of anadromous salmon populations (Quinn & Dittman 1990), and salmon tend to return to the same river (Hansen & Jonsson 1994) and even to the same spawning sites within a watershed that they occupied as juveniles (Heggberget et al. 1986). Elo and coauthors (1994) concluded that the numerous sub-stocks found within the River Teno system have most probably adapted to their rivers of origin.

In addition to the main stem and the spawning tributaries of the River Teno system, juvenile salmon make use of small brooks, where no spawning takes place but the fish
enter from the spawning grounds of the main stems (Erkinaro 1995, Erkinaro et al. 1997). The growth of salmon parr is better in tributaries than the main stems (Erkinaro & Niemelä 1995), and the role of salmon production in these secondary habitats is estimated to be notable (Erkinaro et al. 1997, Erkinaro et al. 1998a). Juvenile salmon are also found in the lakes of some tributaries, especially in the River Utsjoki (Erkinaro et al. 1995, 1998b, Jørgensen et al. 1999).

To date there have been no estimates of the yearly smolt production from the entire watershed, but it is thought vary between 1 and 1.5 million smolts.

The significance of the River Teno system to the entire wild salmon production in the region is exceptional. The total salmon production of the River Teno system, including both sea and river catches and the spawning escapement, is estimated to be up to 600 tonnes (NOU 1999), out of which an average of 139 tonnes has been caught annually (range 93–250 tonnes in 1972–2003). The annual salmon catch in the River Teno system is the highest single river catch within the distribution area of Atlantic salmon, and it has accounted for up to 15% of all riverine Atlantic salmon harvests in Europe from 1995 to 2001 and as much as 22% in 2001 (ICES 2002). The salmon catch of 213 tonnes from the River Teno in 2002 accounted for 33% of the total Atlantic salmon catch in all Norwegian rivers.

Since the closure of the Norwegian marine drift net fishery in 1989, salmon of the River Teno system have still been subjected to marine exploitation with numerous bag nets and bend nets during its feeding and homing migration along the Northern Norwegian coastline, including the Tanafjord just before the fish enter the river. This was clearly indicated by smolt tagging experiments in the River Teno mainstem in the 1970s, when 45% of recaptures of adult salmon were taken from the sea (10% from Tanafjord, 35% mainly in other coastal areas, unpublished data, Finnish Game and Fisheries Research Institute). In Tanafjord there are approximately 300 sites designated for marine salmon fisheries with bag nets and bend nets (Henriksen & Moen 1997). These fisheries target stocks from the River Teno and other rivers, especially those east of the River Teno (Rikstad 1982, Erkinaro et al. 1999).

There has been a steady decline in effort in the Norwegian coastal fisheries. For example, the number of gear units in operation on the northernmost coast in Finnmark has declined by c. 25% over the last decade. In the Tanafjord, there were 219 bag nets and bend nets operating in the salmon fishery in 2003, whereas the annual average in 1994–1996 was 294 sets of gear. At the same time, however, the coastal salmon catches in Finnmark have roughly doubled (Stura Brørs, County Governor in Finnmark, Norway, personal information).

Another characteristic of the Norwegian coastal fishery is its size-selectivity. Smolt tagging in the 1970s indicated that marine salmon fishing at sea outside Tanafjord also mainly targeted 2SW salmon (58%) and to a lesser extent 1SW (23%), 3SW (17%) and 4SW (2%) salmon (unpublished data, Finnish Game and Fisheries Research Institute), which is in accordance with other studies (NOU, 1999). After the drift net fishery was prohibited in 1989 the number of 2SW salmon increased in catches from the River Teno system (Fig. 4). Smolt tagging experiments indicate that coastal fishing in Tanafjord exploited more MSW salmon (2SW 35%, 3SW 20%) than small salmon (1SW 45%), while in the River Teno, 1SW, 2SW and 3SW salmon comprised 65%, 13% and 22% of the catch, respectively. Moreover, recent information collected in 2003 in the Tanafjord
and in the River Teno salmon fisheries indicates that sea fishing in coastal areas harvests relatively more large salmon than fishing in the River Teno. The marine exploitation rates elsewhere in the North Atlantic area also indicate that MSW salmon have especially been subjected to excessive harvesting (NOU 1999, Dempson et al. 2001 and references therein).

Despite the decline in catches within most of the salmon distribution areas, the total salmon catch has increased within the River Teno system during last few years, as in many other rivers in the Barents and White Sea areas, which are the northernmost distribution areas of salmon (ICES 2002). However it is notable that the catch of 1SW salmon has especially increased from very low numbers at the end of the 1970s and beginning of the 1980s to high levels at the beginning and end of the 1990s. By contrast, the catches of 3SW salmon, especially females, declined from the mid-1970s until 2000, but in 2001 it peaked at a level as high as 11500 fish (Fig. 4).

Salmon catches in the River Teno system have fluctuated over periods of 8–9 years from 1972–2003, when statistics have been collected systematically (Figs 4 and 5). A plausible reason for the low catches before the 1970s (Fig. 5) is the lack of precise information describing catches from the entire Teno system. However this historical catch information suggests that salmon populations have always been characterized by considerable fluctuations in abundance. The salmon catch in the River Teno system is believed to be a crude measure of the abundance of salmon stocks and partly used as such in describing the status of stocks (e.g., ICES 2002).
The River Teno salmon stocks are exploited in the river using various fishing methods, including weirs, gill nets, seines, drift nets and hook and line. The net fisheries are practiced by local people, mostly native Sami, and are based on special fishing rights related to land ownership or inherited rights. Within the entire river system, including tributaries, the average proportions of salmon (in weight) captured by different methods in 1980–2003 have been 58% for hook and line, 20% for weirs, 9% for gill nets and 13% for drift nets (Fig. 5). In both Finland and Norway the proportion of salmon caught by hook and line fishing has increased since the 1980s, whereas over the past two decades the proportion of fish captured by gill net fishing in Finland and drift net fishing in Norway has decreased (Fig. 5).

Fluctuations in the salmon catches of recreational fishermen, as in all fisheries, are at least partly dependent on the fishing effort (Fig. 6). Because the number of recreational fishermen is unlimited and no quota or bag limit policies are practiced either in sport fishing or with different net fishing methods used by local fishermen, at least some sub-stocks could be overexploited, especially when the stock abundance is at its lowest. However, there is typically a positive relationship between the salmon stock abundance and the effort of recreational fishermen, even though their fishing effort has generally increased in long-term (Fig. 6).
Fig. 6. The number of recreational fishermen and fishing days used, the salmon catch of recreational fishermen in terms of weight and numbers in the size classes, the salmon catch per unit of effort (kg/fishing day) and the mean size of salmon on the Finnish side of the River Teno.

The fishing effort with various fishing methods can vary annually, which can result in varying size-selective exploitation. An extreme flow in the summer can prevent the use of weir and gill nets. Similarly, a late break-up of the ice followed by high and late spring floods can prevent effective drift net fishing, which is permitted from May 20 until June 15. Nevertheless, there are significant correlations in the catch between fishing methods, indicating that environmental conditions in general are stable enough to allow undisturbed fishing for all fishing methods throughout the summer, and the run size may generally drive the success of all fisheries.
Salmon catch data from 1997–2003 provide the most reliable and comprehensive description of the run timing and the exploitation of salmon of different sea-ages throughout the summer in the River Teno (Fig. 7). This was made possible by a special intensive programme using logbooks and catch sampling throughout the system, including the lowermost part of the river in Norway. The substrate below the lowermost riffle section in Tana Bru (38 km from the sea) is completely dominated by moving sand, with no spawning areas or pools for resting, and hence salmon prefer to move rapidly upstream. Therefore, fishing within the lower section of the mainstem can be used as an indicator of the actual run timing of salmon into the river (Fig. 7).

The run of MSW females and males was followed by a run of 1SW salmon in the lower section (section 1). This temporal pattern could also be observed in the catches in the upper section (section 2, Fig. 7). Although the peak migration of MSW salmon into the River Teno is short and takes place over 4–5 weeks in the lower section, they were exploited during the entire season in the upper section. Fishing in the lower section is in the form of a mixed-stock fishery that continues throughout the season, whereas in the upper section mixed-stock fishing extends until the second half of July (Fig. 7), when stocks from the tributaries have predominantly ascended to their spawning rivers. In the upper section, fishing in August is directed to sub-stocks reproducing mainly in the main stem. Very few spawners ascend the River Teno in September and October, and their contribution to the spawning escapement is unknown. Generally, the timing of the migration in the River Teno follows the typical pattern, where older individuals return earlier in the season than the younger ones (Dunkley 1986, Shearer 1992, see also Niemelä et al. 2000).

Salmon fishing in the River Teno system has been regulated since 1873 by bilateral agreements between Finland and Norway. A general fishery agreement has been concluded between the governments of Finland and Norway, and this agreement primarily regulates the local fisheries and their fishing rights. Tourist angling is regulated by regional authorities in both countries, and these regulations can be amended on a yearly basis. The latest general agreement, concluded in 1990, states that the fishing season commences on 20 May and terminates on 31 August. Net fishing is allowed for three days per week and drift net fishing can take place only from the beginning of the season until 15 June. All fishing is prohibited for one day per week.

The River Teno salmon fishery has also been regulated outside the river by the prohibition of high seas salmon fishing in the North Atlantic since 1984. This was implemented through the NASCO convention with the aim of enhancing and conserving various stocks (Windsor & Hutchinson 1994). Norway has taken further steps to improve salmon stocks by entirely closing the drift net fishery at sea in 1989 (ICES 1990) and by limiting coastal fishing in fjords.
Fig. 7. The timing of the catch of salmon of different sea-ages in Tanafjord in 2003 and in two sections of the River Teno over five-day intervals in 1997–2003. Section one represents an area covering the lowermost 38 km of the river and indicates the timing of the salmon run into the River Teno. Section two represents an area extending over 136 km, between 70 km and 206 km from the estuary, and indicates the timing of the catch at spawning sites in the mainstem. (unpublished data from Finnish Game and Fisheries Research Institute and Sturla Brørs, County Governor in Finnmark, Norway)
Even though the weekly fishing time and the length of the fishing season has been reduced over the years since the first regulations were implemented in 1873, technical development has improved the net fishing methods. The fishing effort in the River Teno on the Finnish side has particularly increased for hook and line fishing due to the increased numbers of recreational fishermen from 200 anglers in 1953 to 10 500 anglers in 2002. Angler fishing days have increased from c. 600 in 1953 to 37 500 in 2002. A similar development has taken place on the Norwegian side, where angler fishing days have increased from 1500 in 1980 to 8300 in 2002. As a result of the overall intensified fishing, the historical distribution area of adult salmon in the River Teno system (c. 1 270 km) has declined and today covers 860 km, indicating excessive exploitation especially in spawning areas in the uppermost tributaries and headwaters. Some stocks adapted to the uppermost distribution areas have probably become extinct. MSW salmon have mainly disappeared from smaller tributaries when compared to their historical distribution, and 1SW salmon currently form the main component in populations.

The economic value of salmon in the 1970s and 1980s and even until early 1990s for people living in the Teno river valleys was extremely high, resulting in great interest in fishing and extensive exploitation, as indicated by salmon tagging experiments (Rikstad 1982, Erkinaro et al. 1999). However, there has been an obvious trend in salmon harvesting in recent years as many local commercial salmon fishermen have shifted to earning their incomes through recreational fishing by renting out fishing boats and fishing camps and by offering rowing services. At the same time, the price of wild salmon has significantly declined and effort in traditional net fishing methods, gill nets and weirs, has decreased accordingly.

2.4 Field methods and collection of samples

Most of the data on juvenile salmon densities used in this work stems from a long-term monitoring programme started in 1979 (I). This programme includes 35 sampling sites in the River Teno mainstem, 12 in the River Utsjoki and 10 in the River Inarijoki (Fig. 1). Each site was fished with standardized methods once a year in a strict rotation, so that the fishing took place on almost the same date in successive years. When choosing the sites, the habitat characteristics, especially the substratum, were taken into account so that the varying water level would have a minimum effect on the habitat, although it may cause the actual shoreline to move. Special attention was paid to selecting the sampling sites so that both ideal sites (loose, coarse substrate, lots of hiding places) and less favourable ones (solid, compact, fine substrate, with few hiding places) were represented.

In 1991–1995 at two sites in the River Teno and at six sites in the River Utsjoki, seasonal variation in the densities of juveniles was studied throughout the open water season between June and October (IV). These sites were chosen to represent homogenous stretches of favourable habitat in terms of depth, water velocity and size and shape of the substratum.

Data on juvenile salmon densities and habitat characteristics comprise 49 permanent sites of the River Teno, Inarijoki and Utsjoki juvenile salmon long-term monitoring programme, 12 additional sampling sites in 1997 from the River Utsjoki, 31 additional sites
in 1999 from the River Teno and 21 sites from the monitoring programme of the River Näätämöjoki (Niemelä et al. 2001), the neighbouring river system south-east of the Teno (VI). The new sites in the River Utsjoki and the River Teno and the sites in the River Näätämöjoki have been selected to represent favourable, shallow shoreline habitats representing primary salmon parr habitat (VI). The physical characteristics were described along four equidistant transects on each electrofishing site, including measurements or estimates of depth, surface flow velocity, substrate and aquatic vegetation. All the sites were rectangular in shape and aligned with the shoreline, and were of a maximum depth of 70 cm.

Electrofishing (900V, 0.2A pulsed DC current) in the long-term monitoring programme started around 20 July each year, when the spring flood was over, and the newly emerged fry were evenly distributed over their nursery area (I,II). When studying seasonal variation in densities, fishing started in late June and continued in two-week intervals until the middle of October (IV). Surround nets were used at all the sites until 1986, when they were found unnecessary (III), a conclusion also reached by Bohlin et al. (1989) and Julkunen & Niemelä (1997). When studying the seasonal variation in densities, surround nets were not in use (IV).

The same standardized removal fishing method was used (Bohlin et al. 1989) and the number of successive passes was usually between one and three, with a duration of 20 to 30 minutes. A given site was fished only once if the number of salmon was 5 or less (15 or less since 1996), but if the number was greater than 5 (>15 since 1996) the site was usually fished three times with a 30-minute pause between passes. Sites with low numbers of fish were left without further removals due to problems in calculating estimates and/or large error connected with low densities (III, Julkunen & Niemelä 1997).

The electrofishing team consisted of three experienced crew members with one using the anode and the other two using dipnets to capture the fish. The sites were fished in an upstream direction, each site being combed carefully with two-metre anode strokes in a downstream direction, after which 50 cm sideways steps were taken (I–VI).

All the fish were measured (total length to the nearest 1 mm) following capture and a scale sample was taken from the area between the lateral line and the adipose fin from all fish greater than 45 mm in length so that they could be classified as fry or parr. Salmon less than 55 mm in length were classified as fry if scale analysis was impossible. The fish were not anaesthetized and were returned to the river alive after sampling.

Scale samples for age determination were collected from adult salmon catches of net and angling fisheries throughout the fishing season in the rivers Teno, Utsjoki and Inarijoki in 1972–2003. The weight of yearly salmon catches was estimated based on postal questionnaires sent to local fishermen and tourist anglers. Weight was converted into numbers of fish using the sea-age distribution of yearly catch samples.

All fish were aged by scale reading using a microfiche reader (30x magnification) for juveniles, or a semi-automatic scale reading equipment for adult salmon (Kuusela 1996).
2.5 Mathematical methods

A three-pass removal method and the Moran–Zippin maximum likelihood calculation were used to estimate the density of fry (0+), 1+ parr and ≥1+ parr (Moran 1951, Zippin 1956, Seber 1982). In the later application of this method (see Bohlin et al. 1989) the catchability of successive electric fishings is estimated by iterative calculation from successive catches. The population size at a given sampling site was calculated from the equation $N = \frac{\text{total catch}}{1 - (1-p)^k}$, where $k$ is the number of successive fishings and catchability $p$ is the probability of capture of an individual (Seber 1982). Finally, the number of fish at a given electrofished site was estimated as juvenile density (ind. 100 m$^{-2}$). The total catch was used as a minimum estimate if only one sampling took place, or in the case of two or three fishings, if $1.96 \times \text{S.E.}$ of the estimate was greater than the estimate itself. Natural log ($\ln$) transformations of densities were used in the analyses to provide a better fit to the normal distribution and additivity assumptions applying to the statistical methods (Stewart-Oaten et al. 1992).

Cluster analysis was used to identify sites with similar densities (II). The cluster analysis was carried out separately for fry and parr in the three rivers, the clusters being divided into high (cluster 1), intermediate (cluster 2) and low (cluster 3) density ones on the basis of the mean density. Initially, the data were arranged in an $n \times p$ matrix with sites in the rows and ln transformed densities as variables in the columns, so that each column represented one year (1979–1994). Similar sites were combined in stages, using simple Euclidean distance as the distance measure, to form resemblance matrices. The resulting cluster tree (SYSTAT 1996) designates the location of individual sites based on fish density and its variation. In general, cluster analysis assigned the sampling sites in decreasing density order, but there were some cases where the yearly variation at a site was more similar to that found in another cluster than in the one which the site seemed to belong based on its density (II).

The differences in mean catchabilities in electrofishing between the periods 1979–1987 and 1988–1996 were assessed in order to compare years when surround nets were used (1979–1987) and those when they were not (1988–1996). Regression analysis was used to study the existence of linear changes in catchability over time. Regression analysis was used also to study the relationship between catchability and density (III).

A general pattern in the seasonal variation of juvenile salmon abundance was analysed by combining the sampling sites and years for the rivers Teno and Utsjoki (IV). When comparing the densities between mid-summer and the beginning of autumn, which is most frequently the preferred period for electrofishing, the sampling times were presented in four periods, two periods per month (late July, early August, late August, early September), and separate years. In this more detailed approach, an analysis of variance for repeated measures (rANOVA) was employed. The rANOVA model included as trial factors the year (1991 and 1993–1995) and period. A significant interaction for the terms year and period indicates differences in the seasonal profiles of annual densities. If the interaction of year and period was significant in the univariate test, single degree-of-freedom polynomial tests with one to six orders were carried out to reveal different seasonality between years in details (SYSTAT 1996).

Estimated yearly adult salmon catches in numbers were related to the yearly mean densities of fry (n+1 year) and of 1+ parr (n+2 years) by regression analysis (V) Likewise,
the annual densities of fry and 1+ parr were related to the subsequent numbers of 1SW, 2SW and 3SW salmon belonging to the same year classes in the salmon catches (V). The densities were either averages over all sites combined or those of the three clusters in the rivers Teno, Utsjoki and Inarijoki. Examination of potential temporal trends in the abundance of adult and juvenile salmon (\(\log_{10}(x+1)\) transformed) was carried out by regression analyses. Cross-correlation analysis was used to identify the concurrence of abundance (catches) between consecutive sea age groups.

Two methods were used to assess the predictability of the relationship between habitat and juvenile salmon abundance (VI). Firstly, discriminant analysis was used to build a model describing the relationship between juvenile salmon densities and habitat characteristics of the electrofishing sites with varying habitat types. An independent test data set consisting of a subjectively chosen favourable salmon habitat was used to assess the performance of the model. Secondly, earlier established microhabitat preference curves (Mäki-Petäys et al. 2002) were used to assess the habitat-parr density-relationship in the test data set. Habitat models were used for crude classification of monitoring sites into expected density categories and assessing the attainment of these reference levels (VI).
3 Results and discussion

3.1 Monitoring juvenile abundance with electrofishing in the River Teno system in assessing the status of salmon stocks

Long-term monitoring is important to understand ecological phenomena driven by slow processes, rare or episodic events and highly variable, subtle or complex processes (Franklin 1989, Elliott 1990). In addition, the spatial extent of sampling should be selected to enable inference for generalization to the entire area of interest (Yoccoz et al. 2001).

To succeed in the management of wild salmon stocks with the aim of sustaining and enhancing them, it is necessary to obtain thorough long-term data on the stocks to understand the long-term stock dynamics. Assessment of the status of the Atlantic salmon populations in the River Teno system is based on a 25-year monitoring programme for juvenile salmon abundance employing electrofishing, and on more than 30 years of monitoring of the estimated yearly numbers of captured salmon (V). The long-term monitoring of the River Teno salmon stocks has aimed at developing an understanding of the dynamics of these exceptionally diverse salmon stocks representing the most variable sea and river age combinations within the distribution area of the species, and one of the few remaining abundant large wild salmon stock complexes. Sufficient long-term data can facilitate the making of appropriate management decisions in a river system, where the slow regeneration of salmon stocks highlights the importance of long-term monitoring in distinguishing and interpreting the considerable annual variation in catch estimates and juvenile abundances and their relationships (cf., Hilborn & Walters 1992).

In the River Teno system, juvenile salmon densities have been used as an indicator of the size of the prior spawning escapement (I, II, V), and they have also been used to predict the subsequent salmon catches (V). Although electrofishing is an important and widely used method in assessing juvenile salmonid abundance in running waters (see references in Cowx 1990), there are several uncertainty factors that can affect the reliability of the electrofishing method (III, Jensen & Johnsen 1988, Bohlin et al. 1989).

When analysing changes in juvenile salmon densities in large rivers like the Teno, Utsjoki and Inarjoki, it is vital to consider the fact that the sampling sites have been restricted to shallow areas close to the river banks, and thus only a small proportion of the
biotope inhabited by the juveniles has been studied (I, II, see also Saksgård et al. 1992). In spite of the wide range of smolt ages in the River Teno system (see above, chapter 2.3), relatively few older (age ≥3+) salmon parr have typically been captured in the juvenile monitoring programme (I, II, V, Erkinaro 1995). One explanation for the small proportion of older parr could be that the deeper habitats of the large parr were probably not represented. The monitoring programme in the River Teno system, however, covers habitats with depths down to 0.7 m, and it has been shown that large fluvial salmon parr also prefer depths of 0.2–0.5 m in the summer (Heggenes et al. 1991), while habitats deeper than 0.7 m are little used (e.g., Heggenes 1996). A proportion of the older juveniles in the rivers Teno, Utsjoki and Inarjoki migrate from their natal rivers to small brooks (Erkinaro 1995, Erkinaro & Niemelä 1995, Erkinaro et al. 1998a) or lakes (Erkinaro et al. 1998b), or some individuals have already migrated to the sea as smolts (Niemelä et al. 2000). For instance, in the River Teno, c. 20% of parr smoltify at the age of 3 years (Fig. 2, Niemelä et al. 2000).

In the River Teno there are 35 electrofishing areas representing habitats over an 80 km stretch of the main stem and covering 0.02% of the total area suitable for juvenile production. The corresponding figures for the tributary rivers Utsjoki and Inarjoki are 0.19% and 0.01%, respectively. In the rivers Utsjoki and Inarjoki the numbers of electrofishing areas are 12 and 10, respectively, covering habitats over a 50 km and 60 km stretch of the rivers. Although the spatial coverage is low in terms of site numbers in relation to the lengths of the rivers, it should be noted that an increase in the number of sites from the present might increase the temporal changes in densities (IV) and thus reduce comparability between years. In similar programmes in some other large rivers in Northern Europe, the number of electrofishing sites in relation to river length has been 14 sites over 46 km in the River Alta (Norway) (Saksgård et al. 1992), 27 sites over 70 km in the River Näätämöjoki (the boundary river between Finland and Norway) (Niemelä et al. 2001), and 60 sites over 500 km in the most important Baltic wild salmon river, the Tornionjoki (boundary river between Finland and Sweden) (Haikonen et al. 2003).

In a large river system like the River Teno with distinct salmon stocks in dozens of tributaries and in different parts of the main stem, it is important to monitor the salmon stocks in individual stock components (Elo et al. 1994, see also Heggerberget et al. 1986). The limited movements of younger juveniles (Saunders & Gee 1964, Crisp 1995) suggest that their abundance at a site or group of sites reflects the size of the local spawning population in different parts of the river system (V, VI). If an electrofishing survey is concentrated on the smaller tributaries where electrofishing is easier to complete, and the large main stem is omitted, the most important component of the MSW salmon of the River Teno system would also be excluded from the monitoring programme (Fig. 3).

Electrofishing is the only satisfactory method for obtaining a quick, comprehensive picture of the status of the juvenile salmon population and hence of the spawning stock escapement within different fluvial habitats. One of the most difficult questions in planning an electrofishing programme is whether to devote the limited resources to more sampling sites, or to more frequent sampling of a limited number of sites (Bohlin et al. 1989). Juvenile abundance data provides detailed information on fish stocks at specific sites for one point in time and are important when precise numerical information is required. Since it is impossible to sample streams along their entire length, it is necessary to sample discrete sites, which requires an extrapolation of the site results to the rest of the stream, i.e.
the number and location of sites must allow an extrapolation to be made on a statistical basis (Winstone 1993). In most studies where juvenile abundance has been monitored to estimate subsequent smolt production (Crozier & Kennedy 1995), or to examine the relationship between fry and parr numbers (Bagliniere & Champigneulle 1986) or between spawning escapement and fry abundance (Chadwick 1985), electrofishing has been carried out only once each summer. In the River Teno system the short period for field work combined with the restricted manpower for electrofishing has only allowed the assessment of juvenile salmon abundance once a summer. The annual sampling starts after the emergence of fry at the end of July and is typically completed at the end of August (I, II).

Juvenile salmon abundances in the River Teno system are normally expressed in two ways: as the annual mean density of fish within the river combining all electrofishing sites (I) or as the mean annual density for areas grouped into density classes (II, V). Clustering sites with similar annual densities into site groups allows a reduction of the spatial variability in order to analyse temporal variability by statistical methods. The adequacy of the method appeared to be good enough in the high-density (cluster 1) and intermediate-density (cluster 2) classes, as their mean densities were above the level that Bohlin and coauthors (1989) deemed necessary for achieving sufficient precision of monitoring by means of electrofishing by the removal method. The low-density clusters (cluster 3) create a problem in monitoring in that their density estimates are not accurate enough and excessive variation hampers the detection of possible trends (see also Bohlin et al. 1989).

Combining the densities of all sites in a river is the most frequently used method, which gives abundance estimates for the general comparison of juvenile production between rivers. However, the calculation of mean density does not allow the detection of finer scale spatial changes in densities, and possible patterns in subpopulations are not accounted for when using this method. One possible approach to monitoring fish densities in a river would be to compare mean values for stream sections representing similar habitats. This method has drawbacks with respect to long-term monitoring in a northern river because the habitat properties of a site can be altered by floods and ice erosion, which thereby influence juvenile salmon densities through habitat changes. Local events may cause serial correlation between yearly densities at a given site and may invalidate the statistical analysis of the influence of the actual impact of interest (Stewart-Oaten et al. 1992), such as the measures taken to regulate fishing. Bohlin and coauthors (1989) has proposed the selection of sampling sites annually on a random basis, but this had been found to lead to twice the spatial standard deviation in parr densities in the River Utsjoki relative to permanent monitoring sites (II).

In a long-term programme monitoring juvenile abundance, at least some methodological changes are almost inevitable. To be able to detect changes in the variables being monitored, it is of great importance to assess the impact of the methodological changes over time. In the River Teno system, where a quantitative three-pass removal method has been used in electrofishing and Moran–Zippin maximum likelihood calculations in estimating the population size, the use of surround nets was discontinued as the same time as the transformer was changed. As a result of these changes, the mean catchability for fry and parr declined (III). Several environmental variables such as water temperature, depth, conductivity and habitat type affect the efficiency (catchability) of electrofishing (e.g. Randall 1990, Zalewski & Cowx 1990, Borgstrom & Skaala 1993). Nevertheless, there is good evidence that the estimation method compensates for variation and bias in catchabil-
ity and density estimation if the basic criteria and assumptions (i.e. constant capture prob-
ability for all individuals, constant catchability within removals and sufficient number of
fish) are fulfilled to a sufficient extent (Seber 1982, Bohlin et al. 1989). The use of sur-
round nets in electrofishing has not been considered a necessity in large river systems
such as the River Teno, where sampling sites are restricted to the near-shore zone and as
such can represent only a small proportion of the river’s entire cross-section (Bohlin et al.
1989).

The age and size of the fish has been found to affect catchability in the River Teno sys-
tem, where the catchability of fry was less than that of parr (III). A larger size usually
leads to increased catchability in fish (Borgstrøm & Skaala 1993), although Crozier and
Kennedy (1994a) conclude that the higher mobility of parr leads to a lower catching effi-
ciency and larger parr are often transported outside the electrical field in strong currents
before they can be caught. It has been indicated on several occasions that density esti-
mates are most often negatively biased due to a decline in catch efficiency with succes-
sive sampling (Schnute 1983, Peterson & Cederholm 1984, Bohlin et al. 1989, Bohlin
1990, Bohlin & Cowx 1990, Riley et al. 1993). This may happen because fish that have
been frightened or shocked may become less catchable in subsequent passes, or because
the assumption of equal capture probability among individuals has not been met. It is pos-
sible that actual capture probabilities decreased with each pass in the River Teno system
after surround net use was discontinued. This potential bias is, however, negative and the
 corresponding abundance estimates therefore conservative and “safer” in providing
advice for management.

A relationship was detected between the density and catchability of parr, in that catch-
ability decreased with density, but the predictability was weak (III). During successive
removals the number of fish becomes rather small in the second and third catch if catcha-
bility is high and the population size is small. An essential prerequisite in electrofishing is
that the total population size in the sampling area should be more than 50 (see also Bohlin
et al. 1989) and catchability should be at least 0.2 for the removal method to be valid, and
greater than 0.4 for consistently reliable results (Seber 1982). The catchabilities in the
River Teno watershed for both age groups fulfilled Seber’s criteria (III). The electrofish-
ing results from the River Teno system indicate that for monitoring purposes, the assump-
tion of equal catchability in three removals leads to density estimates in which the bias is
sufficiently small.

Based on the experience of the present work, electrofishing in long-term monitoring is
recommended to be carried out in as standardized a form as possible: at permanent sites,
on the same dates each year, within the shortest possible time span, and maintaining the
same sampling schedule every year, in order to reduce variations in catchability that stem
from non-standardised sampling.

### 3.2 Abundance of juvenile salmon

The abundance of juvenile salmon displays considerable temporal and spatial variation
among river stretches and sites within the River Teno system (I, II). In the rivers Teno,
Utsjoki and Inarjoki the average fry densities in 1979–2003 were 26, 39 and 28 fish per
100 m$^2$ and parr densities were 18, 31 and 23 fish per 100 m$^2$, respectively (Table I). When comparing these results with juvenile salmon densities in some other northern salmon rivers, the present figures fall within the general range. In the River Alta (Northern Norway) in 1981–1991, parr densities were 12, 24 and 37 fish per 100 m$^2$ in the lower, in the middle and in the upper part of the main stem, respectively (Saksgård et al. 1992), but higher densities have been found in later years as the general range varied for the entire river between 32 and 61 fish per 100 m$^2$ in 1993 and 1995 (Jensen et al. 1997). The River Ponoi (Kola Peninsula, Russia) has yielded large catches of salmon annually, despite mean parr densities as low as 1.5 fish per 100 m$^2$ and fry densities of only 2.2 fish per 100 m$^2$ in the main stem (Whoriskey et al. 1996). However, Whoriskey (1998) reported increasing juvenile salmon densities in recent years after the closure of the commercial fishery in the river mouth. In the rivers Kola and Varzuga (Kola Peninsula, Russia), where commercial or brood stock fisheries still exist, the mean densities have been similar to those of the River Teno, where net fishing methods are permitted in addition to hook and line fishing.

In some cases even the northernmost salmon rivers are able to produce considerable densities of juvenile salmon. In the lower part of the River Näätämöjoki (Northern Norway), where gill net fishing is prohibited, the average density of parr between 1990 and 1998 has been as high as 80 fish per 100 m$^2$ and even 110–120 fish per 100 m$^2$ at certain sites (Niemelä et al. 2001). The high densities of juvenile salmon in some areas in the River Teno system, especially in the lower part of the River Utsjoki (60–70 parr per 100 m$^2$, I, V), point to an exceptionally strong local spawning stock. In the lower Utsjoki, 2–3SW female salmon ascend to the spawning grounds from the River Teno late in September after the fishing season thus avoiding part of the fishing pressure (Kylmäaho et al. 1996). Juvenile densities in the lower part of the River Utsjoki offer a good example of permanently high production and could be used as reference levels for certain habitat types. Similar types of site are included in the long-term monitoring programme elsewhere in the River Teno system, but in most cases their densities have been much lower, indicating permanently low local spawning escapement (V, VI).

There was a distinct decline in parr densities in the middle part of the River Utsjoki in the early phase of the monitoring (II). This development could not, however, be attributed to the introduction and subsequent dispersal of the non-indigenous bullhead, Cottus gobio L., into the River Utsjoki in the 1970s (Pihlaja et al. 1998b), but rather to the high exploitation and low stock abundance of salmon. Bullhead in the River Utsjoki mainly occupy riffle sections not far from the lakes and short rapids between lakes, but they were absent from the principal habitats of salmon parr (Jørgensen et al. 1999). However, parr densities have recently increased in the middle of the River Utsjoki, which might be a reflection of increased spawning escapement (V, Table I).

When long-term trends in juvenile salmon densities were analysed up to 1995 (II), it was shown that parr (1+) densities decreased significantly in one cluster containing 45% of the sites studied in the river Utsjoki, whereas the densities increased significantly in one cluster in the river Teno and in one cluster in the river Inarijoki containing 38% of the sites in these rivers. Fry densities increased significantly in two clusters containing 16% of all the sites studied in all three rivers. When the time interval was extended to 2003, comprising 25 years of monitoring (V), there was still the one declining trend in the River Utsjoki, but only one increasing trend, that of the highest density cluster in the
River Inarijoki, in the case of parr. However, there was a major difference in fry density trends between the periods in that fry densities increased significantly in all clusters in the River Inarijoki and in two clusters both in the River Utsjoki and in the River Teno between 1979–2003 (V).

The increasing trend in fry densities was mainly driven by the strong increase in three last years (2001–2003) and the generally low densities at the beginning of the monitoring period. However, parr densities did not increase in most cases, probably because the high fry densities in recent years have not yet induced an increasing trend in parr densities or probably because fry densities did not show correlations with parr densities in the subsequent year at individual sites (II). In addition, the mean fry densities (all sites combined) increased significantly in the rivers Teno, Utsjoki and Inarijoki and 1+ parr densities (all sites combined) increased significantly in the rivers Teno and Inarijoki between 1979–2003 (V).

### 3.3 Seasonal variation in the abundance of juvenile salmon

Extensive seasonal variation in the density and age distribution of juvenile salmon was apparent in the rivers Teno and Utsjoki. The densities of fry and parr showed an increase from early summer towards late August and a subsequent decline towards the autumn (IV). The stream dwelling juveniles of Atlantic salmon have traditionally been considered typical resident fluvial salmonids that exhibit only restricted movements during their freshwater period (e.g., Keenleyside & Yamamoto 1962, Saunders & Gee 1964). However, many recent studies have revealed extensive movements among juvenile Atlantic salmon before their oceanic migration, often induced by factors such as the obtaining of better food resources and growth possibilities and the avoidance of unfavourable environmental conditions (Erkinaro 1997 and references therein). Seasonal changes in habitat use should therefore be taken into consideration when interpreting juvenile salmon density data between and within rivers.

Fluctuations in water levels and differences in the timing of the summer season have been found to have an impact on juvenile salmon densities (Jensen & Johnsen 1988). Accordingly, Bohlin and coauthors (1989) suggested that quantitative electrofishing should be carried out yearly under similar environmental conditions, especially at a similar water level. The same practice was suggested by Saksgård and Heggberget (1990), who detected a significant negative correlation between juvenile salmon abundance and water flow. In the rivers Teno and Utsjoki the water level varied between years during the same sampling times. However, normal summer time variation in water level (extreme high water levels excluded) did not explain the variation in catchability and juvenile salmon abundance, although a seasonal pattern in juvenile salmon abundance was detected (IV). Seasonal variation in densities of juvenile salmon has also been recorded in the River Alta (Saksgård et al. 1992). However, Saunders and Gee (1964) suggested that juvenile salmon normally follow the water course during water-level fluctuations, when their territories are destroyed/disturbed which could decrease the effect of fluctuating water level on the habitat use.
The seasonal pattern of parr density was more distinct than that of fry between late July and early September (IV). This reflects a difference in their population dynamics, in that fry do not emerge until mid-July and gradually disperse from the spawning areas after that, whereas the habitat selection of parr may be more stable during this period. Within individual sites in different years, density peaked in different weeks from the middle of June to the beginning of September for parr and from the last week of July to the middle of September for fry. To avoid overestimated and misleading fry densities, sampling times should be chosen in such a way that juvenile salmon of all age-groups are evenly distributed in their respective biotopes.

At a few sites in the River Teno system, high fry densities resulted in high parr densities during the following year, but usually the association between these age groups was weak (I). This might indicate age-dependent selection of different habitats, where the properties of microhabitats are important parameters dictating the spatial distribution of juvenile salmon (Morantz et al. 1987). However, the significant variation in the frequency of parr age groups (ages 1+, 2+ and ≥3+), combined with the considerable fluctuation in parr densities between samplings throughout the season in the rivers Teno and Utsjoki (IV), indicated that habitat preference was changing within short time intervals and juveniles were not stationary or keeping their territories for a long time.

In a long-term monitoring programme, the best way to minimise the effect of seasonal variation in density is, as indicated above, to standardize the sampling protocol and dates as strictly as possible.

### 3.4 Relationships between catches and juvenile densities and status of salmon stocks

The 25-year monitoring programme in the River Teno revealed positive relationships between salmon catches and subsequent juvenile abundance, and vice versa (V). The variation in the numbers of 2SW female salmon explained 28–38% of the variation in subsequent fry abundance and 26–34% of the variation in parr abundance (V). These relationships between the catches and juvenile abundance were most obvious for fry at all electrofishing sites combined and at sites with medium (cluster 2) and low (cluster 3) fry densities, and for 1+ parr at all electrofishing sites combined and at sites with high (cluster 1) and medium (cluster 2) parr densities. Regression models did not explain the relationships between the numbers of 1SW and 3SW female salmon and fry and 1+ parr densities in the River Teno. In the tributary river Inarijoki, the number of 2SW female salmon in the catch also had a significant relationship with the subsequent fry and 1+ parr densities of all electrofishing sites combined and at areas with high (cluster 1) and medium (cluster 2) densities, where the regression model explained 19–44% of the variation in juvenile abundance. In the River Inarijoki, regression models also explained significant relationships between the number of 1SW female salmon and the subsequent 1+ parr density of all sites combined and of sites with high densities (clusters 1) and low densities (cluster 3) ($r^2 = 0.26–0.30$) (V).
Similar relationships between the salmon catch and abundance of juveniles have also been found in other rivers (Saltveit 1996, Chadwick 1985). In the absence of true stock-recruitment data, which is the case in most salmon rivers of the world, the reported catch or some similar data have been used as an index of abundance (V, Chadwick 1985). The estimated numbers of salmon caught yearly is believed to indicate realistic variations in abundance between years, as no catch quotas have been set for either the net fisheries or the rod fishery. In this study the juvenile abundance has been used as an index of recruitment. To understand how juvenile abundance responds at different levels of spawning stock size, the stock must be observed over a sufficient range with enough observations near the extremes of the ranges to overcome the time-series bias effects (Hilborn & Walters 1992).

Female salmon abundance showed a significant relationship with subsequent juvenile abundance at sites of high and medium density, and this relationship was almost linear, at least within most of the ranges experienced during the 25-year monitoring period (V). This suggests that the best habitats have not yet reached the production capacity (VI) and their parr density closely follows the abundance of the spawning population. Based on the stock (catch) recruitment (parr density) curves, Chadwick and Randall (1986) also concluded that juvenile abundance was low and below the inflexion point.

The annual juvenile density surveys in the River Teno system allow evaluation of the spawner abundance one and two years earlier, and they also confirm the stock status information provided by earlier catch statistics. On the other hand, significant deviations in juvenile abundance from what is predicted by the catch estimates would indicate changes in the exploitation rate in river fisheries. These observed relationships between the catch components and subsequent juvenile abundance suggest that the monitoring programme included feasible and biologically relevant variables and proper methodologies.

In the River Teno, juvenile densities were positively related to the subsequent catches of salmon of the same year classes (V). Significant relationships were detected between fry densities of all sites combined and of those sites with a high density (cluster 1), and the numbers of 1SW salmon in the River Teno ($r^2 = 0.31, 0.41$). The same was true between fry densities (sites combined, clusters 1 and 2) and the numbers of 2SW salmon in the subsequent catch ($r^2 = 0.20–0.24$). Similarly, parr densities (sites combined, clusters 1 and 2) were significantly related to the numbers of 1SW and 2SW salmon in the subsequent catches (1SW: $r^2 = 0.24–0.38$, 2SW: $r^2 = 0.26–0.28$). In the River Inarjoki, regression models explained 24–39% of the relationships between the densities of 1+ parr and the numbers of 1SW salmon in the subsequent catch. These regression models explained 24–41% of the variation in the River Teno salmon catches in relation to the preceding parr abundances, and the predictive power is reasonably high when bearing in mind that catches of 1SW and 2SW salmon included smolt ages of 2–6 years, i.e., one year class produced catches over five consecutive years. Combined with variable sea ages (1–5) and repeated spawning runs, the effects of changes in juvenile abundance are slowly reflected in the subsequent salmon catches. Similar documented relationships between salmon fry or parr and subsequent adult salmon abundance are rarely available from other large salmon rivers, whereas other relationships, including those between fry and parr abundance (Bagliniere & Champigneulle 1986), fry abundance and the number of smolts (Crozier & Kennedy 1995) and the relationships between the numbers of smolts and ascend-
ing salmon (Paloheimo & Elson 1974, Chadwick et al. 1978, Jonsson et al. 1998) indicate clear positive relationships in all the above studies. In the River Teno system, where no annual smolt production estimates are available to predict the subsequent number of ascending salmon, the positive relationships between the abundance of juveniles and the subsequent numbers of salmon in the catch offer a reasonable tool to predict the catches of especially 1SW and 2SW salmon, as these comprise an average of 70% of the total catch in numbers.

Positive and significant cross-correlations were found between the numbers of 1SW and 2SW, 2SW and 3SW, and 3SW and 4SW salmon in the catches in the River Teno system, especially with a 1-year lag (V). This indicates that the survival of post smolts during the first summer and winter is crucial in dictating the abundances of all later sea age classes (see also Scarneccchia 1984b). Such relationships have been used successfully elsewhere as a basis for forecasting the yield and escapement of 2SW salmon from the yield and escapement of 1SW salmon in the preceding year (Power 1981, Scarneccchia 1984b, Bielak & Power 1986, Jonsson et al. 1998).

The 25-year monitoring programme in the River Teno has covered four generations of 1SW and 2SW salmon. The slow regeneration of the northern salmon stocks highlights the importance of long-term monitoring in distinguishing and interpreting the considerable annual variation in juvenile abundance and in catch estimates and their relationships (cf., Hilborn & Walters 1992). These predictive relationships have statistical power only if sufficient time series data are available, because short-term data usually lack the statistical power to detect responses in long-term processes, as the variance can be large compared with the magnitude of the trend (Elliot 1994).

Salmon catches and juvenile densities showed considerable annual variation over the monitoring period in the River Teno system (I, II, V). The mean annual salmon catch in the River Teno system in 1972–2002 was 139 t (SD 48), with a maximum of 250 t in 1975 and 2001 and a minimum of 74 t in 1979 (V, see chapter 2.3, Fig. 5). A significant increasing trend in the estimated numbers of salmon in the catch in 1977–2002 was detected for both sexes of 1SW and 2SW salmon and for previous spawners (see chapter 2.3, Fig. 4). The only significant declining trend detected was in the numbers of 4SW females, and there was no trend in the numbers of 3SW fish (V).

The general declining trends in catches of salmon have been found during 1980s and 1990s throughout its whole distribution area, being most pronounced in multi-sea-winter salmon (ICES 2002). Specific reasons for the continued decline are often unclear, but multiple factors, including overfishing, altered oceanic conditions and freshwater habitat degradation, are probably responsible (e.g., Dempson et al. 1998, Parrish et al. 1998, Hutchinson et al. 2002). High rates of exploitation in ocean fisheries have been associated with many stock declines, but the abundance of many stocks nevertheless continues to fall, despite great reductions in marine salmon fisheries during the past couple of decades (Windsor & Hutchinson 1994, Parrish et al. 1998, Dempson et al. 2001, ICES 2002). Marine exploitation rates have been estimated in the range of 70 to 90% for multi-sea-winter (MSW) components, while 1SW stocks have been commonly harvested at 40 to 60% (e.g., Hansen 1988, Dempson et al. 2001). The decline of multi-sea-winter salmon stocks in North Atlantic has been a general phenomenon and marine exploitation rates illustrate that elsewhere in North Atlantic these fishes have predominantly also been subject area to exceedingly high rates of harvesting (NOU 1999, Dempson et al. 2001 and
references therein). In the River Teno the exploitation rate of the river fisheries can also approach 70% (Erkinaro et al. 1999), having a significant influence on juvenile densities at least in years with low stock abundance. However, some stocks, such as those in the rivers Teno, Näätämöjoki and Kola in the Northeastern Atlantic, fluctuate in a cyclic manner with no general declining trend (Niemelä et al. submitted). The prohibition of the drift net fishing since 1989 along the Norwegian coastline has been reported to increase ISW salmon catches or escapement in rivers in Northern Norway (Jenssen et al. 1999), which is one reason for the increased catches of 1SW and 2SW salmon in the River Teno system, too. In recent years the improved pre-fishery abundance of the northern stocks (ICES 2003a) combined with the new management measures introduced in 1990 in the River Teno system have also allowed stocks to increase in the tributaries of the River Teno. However natural long-term trends in the abundance of salmon stocks and environmental fluctuations can mask the effects of regulatory measures of both catches and juvenile salmon production.

The increased juvenile abundances suggest that the management measures introduced at sea and in the River Teno system have played an important role, together with favourable circumstances in the marine environment, in increasing the catch of 1SW and 2SW salmon in the River Teno system. However, the size and variation of the run is highly dependent on the preceding smolt output (Paloheimo & Elson 1974, Chadwick et al. 1978, Jonsson et al. 1998), fluctuations in natural mortality during the marine phase (Dempson 1992, Friedland 1998, Friedland et al. 1993) and marine fishing mortality (Crozier & Kennedy 1994b, 1999). Fluctuations in the abundance of salmon are apparently strongly affected by annually varying environmental conditions at sea (Scarnecchia 1984a, Scarnecchia et al. 1989a,b, Reddin & Friedland 1993, Antonsson et al. 1996, Friedland et al. 1998), especially in areas where marine salmon fisheries have been greatly reduced or are now prohibited (Friedland & Reddin 1993, Parrish et al. 1998, Walters & Ward 1998, Dempson et al. 2001). Oscillations in abundance can follow a long period of between 20 and 30 years of high catches (Bielak & Power 1986) or a shorter period of eight or nine years, as in the River Teno system (see chapter 2.3, Fig. 4), and can also commonly occur over wide geographical areas (Dempson et al. 1998).

Hansen and Jonsson (1989) and McCormick and coauthors (1998) have concluded that a late smolt migration can cause a low return rate of adults. In general, the first months and first winter following migration to the sea are critical periods that influence the subsequent growth, survival and ultimately the abundance of salmon (Hansen & Quinn 1998, Friedland et al. 2003). An exceptionally late smolt run (peak in August) in Northern Norway in 1962 resulted in high post smolt mortality and thereafter in a low return of 1SW, 2SW and 3SW salmon in subsequent years (Abrahamsen 1968). This is in accordance with the anecdotal reports of poor salmon catches in the mid 1960s in the River Teno system (see chapter 2.3, Fig. 5). The timing of the smolt run, or smolt “window”, is considered to be crucial for the survival of salmon (Hansen 1987). In the tributaries of the River Teno system the timing of the smolt run has varied considerably between years, for instance from early June to mid July in 1989–1996 (Kylmääho & Niemelä 1996). This variation is caused by the timing of the ice break-up (Niemelä et al. 2000) and variable, unpredictable water temperature regimes afterwards. If the smolt migration is delayed, outmigrating smolts can meet an unfavourable sea environment and suffer increased mor-
tality, and thereby the predictability of future salmon catches can be poor even if juvenile abundance had been high in the river in preceding years.

3.5 Reference levels for juvenile Atlantic salmon abundance

It is essential for efficient management of salmon stocks to understand the effects of physical, chemical and biological factors in the rearing environment on juvenile abundance. Therefore, habitat models have been developed for juvenile salmonids to explain the spatial variation in fish abundance. In the present work, habitat models were used to develop methods for defining reference levels of juvenile salmon densities using the annual data from the long-term electrofishing monitoring in the River Teno system (VI). Discriminant analysis was used to build a model describing the relationship between juvenile salmon densities and habitat characteristics of electrofishing sites with varying habitat types. The permanent electrofishing sites were classified into expected density classes (VI). This method allows a yearly inspection of whether the observed parr densities attain the reference levels. This evaluation implies that more than half of the sampling sites where habitat characteristics would predict fish densities in the highest category (50 parr per 100 m²) showed observed densities in the mid (10–49 parr per 100 m²) or low density category (<10 parr per 100 m²). In addition, earlier established microhabitat preference curves (Mäki-Petäys et al. 2002) were used to assess the habitat–parr density relationship in the test data set (HPC method). Similarly, this method also pointed out certain areas with high-quality habitats that failed to attain the predicted density levels (VI).

The data from these analyses covered the years 1988–1999, a period after the prohibition of the drift net fishery in the coastal area of Norway (since 1989) and after the new fishing regulatory measures introduced in the River Teno system (since 1990). It was expected (II) that the densities would increase as a result of the major new regulatory measures, but the results indicate that neither have the reference levels of parr densities been attained nor the parr densities increased (V). The density levels recorded suggest that large areas of high quality habitat in the River Teno system fail to meet the expected densities of juvenile salmon, and factors other than physical habitat characteristics, such as a lack of female spawners, restrict the juvenile salmon abundance (VI).

Even though some habitat models have succeeded in explaining up to 70–90% of the variation in juvenile salmonid population densities, many models tend to ignore temporal variation (e.g., Armstrong et al. 2003). Extensive temporal variation in the densities of juvenile salmon at individual sites occurred between years and throughout the summer due to variation in the spawning escapement in preceding years (V) and due to diurnal, seasonal and ontogenetic habitat shifts within the same stretch of a river (Gibson 1966, Rimmer et al. 1983, Bremset & Berg 1997, Erkinaro et al. 1997). In the River Teno system, parr densities in different years have been found to peak at individual sites in different weeks from the middle of June to the beginning of September, and large variation has also been found in the frequency different parr age groups between sampling periods throughout the typical electrofishing season (IV). In general, parr densities increased from early summer towards late August (IV). In spite of these changes in densities observed at
individual sites in the River Teno, the predictive ability of the habitat models applied was generally moderate, although the modelling data comprised long-term mean densities from more than 10 years (VI). When habitat models have been transferred to other river systems or stream types, their applicability and predictive power typically decreases (Shirvell, 1989, but see Mäki-Petäys et al. 2002). Here, the habitat preference criteria developed by Mäki-Petäys and coauthors (2002) for the River Teno salmon and the HPC method based on this were successfully transferred to the neighbouring River Näätämöjoki system (VI). In the case of the River Näätämöjoki, the removal of a subset of data (upper Finnish territory) significantly improved the predictive power of the habitat model. This implies that in certain areas of the river system, high quality juvenile salmon habitat is occupied by parr at very low densities (VI).

Other methods have also been used in assessing the freshwater habitat characteristics determining the juvenile salmon production capacity. Amiro (1993) used the stream gradient as a predictor and Grant and Kramer (1990) calculated the percent habitat saturation (PHS) as the sum of the predicted territory areas of individual fish in a river. Both these methods require detailed information on the habitats, and the electrofishing sampling design in the PHS method differs from that used in the annual juvenile monitoring in the River Teno system.
4 Management implications and research recommendations

A large amount of information and knowledge is required to manage salmon stocks successfully, including the number of salmon that can be produced in each river, the number of spawners required for this production, the movements of salmon at sea and their survival rates. It is equally important to know when and where each stock is harvested, how many fish are caught and how much effort is required to catch these fish. The monitoring programme for the River Teno salmon stocks covers both the juvenile phase in the river and the abundance and characteristics of the returning adult salmon. In addition to the long-term monitoring programme of the River Teno, a new index river monitoring programme has been started in recent years in the River Utsjoki, the largest tributary of the River Teno in Finland. Here, the numbers of ascending salmon and descending smolts are being estimated with the aid of video cameras. This study aims at creating a long-term data set to assess the stock-recruitment relationship in the subarctic river, information that is badly needed especially for healthy northern salmon populations. In addition, the electrofishing monitoring programme could be expanded to further facilitate defining reference points and to cover some additional important tributaries.

The management measures that have been implemented in the past have succeeded in maintaining the River Teno salmon stocks, which still today enable and support diversified fisheries, including coastal net fisheries and combined net and rod fisheries in the river. The bilateral agreement covering the River Teno fishery in 1979 made the monitoring of salmon stocks obligatory for Finland and Norway with the aim to produce scientific data on the status of the salmon stocks, including catch statistics, in order to maintain and enhance them by appropriate fishing regulations.

Two highly important fishery regulations affecting the stocks in the River Teno system took place almost simultaneously: the prohibition of drift net fishing in the coastal area of Norway since 1989 and new regulatory measures introduced in the River Teno fisheries in 1990. When analysing the long term time series in two periods, 1977–1988 and 1989–2003, the estimated mean annual numbers of 1SW and 2SW salmon and previous spawners in the catches were significantly higher after the new measures were implemented (Table I). In addition, the numbers of 1SW and 2SW salmon and previous spawners have increased over the entire period from 1977–2003, but the number of 4SW salmon has declined (Table I). Although the numbers of 1SW salmon indicated a signifi-
cant increasing trend in the period before the prohibition of drift net fishing, no trend was detected during the later period.

When the abundance of salmon parr (1+ year old) was analysed during the same periods, only one sampling site cluster (in the River Inarijoki) showed higher densities after the introduction of the regulatory measures (Table II). The mean fry abundance was significantly higher during the later period in two out of nine clusters. During the later period, after the prohibition of drift net fishing at sea, parr densities declined significantly in three and increased in one out of nine clusters, and fry densities increased in three out of nine clusters (Table II). The major regulatory measures in 1989–1990 appear to have resulted in higher densities of fry, although corresponding trends have been more problematic to detect in parr.

A high juvenile abundance leads to stable and high smolt production, which is essential for healthy, self-sustaining salmon stocks (Jonsson et al. 1998). To increase the smolt production and thus the number of salmon returning to the River Teno, spawning escapement could still be improved in general and especially in certain areas of the river system (VI). As a single sea age group, 3SW females are the most important individuals for reproduction, accounting for more than 40% of the spawning population (V), and their contribution to egg deposition is even greater due to their high fecundity (Erkinaro et al. 1997). There are certain management measures that could be used to improve the MSW female component in the River Teno salmon stock complex. One of the key elements is the fishing pressure early in the summer, when a large majority of the early run consists of MSW females (Chapter 2.3, Fig. 7). A reduction in the drift net fishing season or other limitations on the drift net effort should be considered to ensure sufficient egg deposition. Similar regulations for the early season coastal net fisheries in Northern Norway would have similar effects as a considerable number of multi-sea-winter salmon originating from the River Teno system are caught there. For instance, the start of the coastal net fisheries in Troms County, west of Finnmark, has recently been postponed to the mid-June to allow more MSW spawners to enter the rivers (K. Kristoffersen, personal information). One possibility to reduce the fishing mortality of large MSW females is to close the fishing season in August earlier than today. A large proportion (c. 20%) of catches in August consist of MSW females (V). At this time just prior to the spawning season, their economic value is very low whereas their reproductive value is at its highest level during the fishing season.

Wild salmon stocks need to be abundant and genetically diverse to buffer the negative effects of escaped farmed salmon (e.g., McGinnity et al. 2003). The current juvenile monitoring programme does not distinguish whether the juveniles are progeny of wild or farmed salmon. To avoid misleading interpretation concerning the relationships between the number of wild salmon in the catch and subsequent juvenile abundance or variations in juvenile abundance, genetic studies should be started to screen the genetic background of juvenile salmon throughout the River Teno system. In addition, studies prior to the spawning period (August and September) should be intensified to assess the numbers or proportions of escaped salmon in spawning populations.

Rod fishing in tributaries on the Finnish side of the River Teno system has intensified in recent years, and there are currently no up-to-date data indicating the status of many tributary stocks. All fishing in the River Teno system takes place without catch quotas and in addition there are practically no limitations on the licences issued or the numbers of
tourist fishermen. In many other salmon rivers in the world the numbers of fishermen and salmon catches are limited in order to maintain and enhance the salmon stocks.

Although the regulatory measures introduced have succeeded in maintaining the salmon stocks in the River Teno, the effective fishery in the rivers and in coastal areas can still potentially overexploit small sub-stocks, especially in years of low stock abundance. Increased tourist angling and local drift net fishing in recent years in the River Teno could result in overexploitation of multi-sea-winter salmon stocks and keep the juvenile abundance low. Thus, the River Teno salmon stocks need protection. Catch reporting should be developed from a voluntary to an obligatory basis using log books, because accurate information would help in understanding the real value of the salmon stocks in the River Teno system.

As shown in the present work, juvenile abundance can predict subsequent catches, and the numbers of 1SW salmon in the catch have been good predictors of the number of 2SW salmon in the following year. Despite this, novel methods and analyses are needed to predict stock dynamics for the future management of the River Teno salmon. Reliable forecasts could help managers to regulate the fishery in advance and allow time to react, such as in the case of declining stock abundance. Regulatory measures aim to conserve and enhance salmon stocks, which could then be exploited in a sustainable way. This is especially important and beneficial to the people living in the valleys of the subarctic River Teno system.

Table 1. Statistics characterizing the salmon catches of 1–4SW and previous spawners in terms of numbers in the River Teno system. Period of the years 1977–1988 demonstrates catches before the drift net prohibition at sea and period 1989–2002 catches after the regulations. Difference in the mean catches between the periods is expressed ** (p<0.01) and *** (p<0.001) (t-test). Direction of significant regression slope; rising (+), descending (–).

<table>
<thead>
<tr>
<th>Sea-age</th>
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<th>Regression coefficients</th>
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<td></td>
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Table 2. Statistics characterizing densities of fry and parr (≥1+ year old) in the clusters and in all sites combined in the rivers Teno, Utsjoki and Inarijoki. Period 1979–1989 (1) demonstrates years before the drift net prohibition at sea and regulations in the River Teno and period 1990–2003 (2) years after the regulations and 1979–2003 (3) the entire electrofishing period. Difference in the mean densities between the periods before and after is expressed * (p<0.05), ** (p<0.01) and *** (p<0.001) (t-test). Direction of significant regression slope; rising (+), descending (–).

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References


Dahl K (1910) Age and growth of salmon and trout in Norway as shown by their scales. Salmon Trout Assoc. IX. London.


