

Conservation of Atlantic salmon by supplementary stocking of juvenile fish

Atso Romakkaniemi

Academic dissertation

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Cover (photo by Atso Romakkaniemi): Tornionjoki smolts stocked as 2-year old smolt (uppermost) and as 1-year old parr (middle), and a wild Tornionjoki smolt (lowermost)

LIST OF ARTICLES INCLUDED

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INDIVIDUAL CONTRIBUTIONS OF AUTHORS OF THE ARTICLES

- I Atso Romakkaniemi had the main responsibility in data gathering and processing, in performing the analysis and in writing the paper. The other authors helped in data gathering and processing and in writing.
- II Atso Romakkaniemi defined the original research problem and provided the biological information and information on the trapping procedure. He also provided the data set for the analysis. Samu Mäntyniemi had the main responsibility in formulating the model structure and in conducting the analysis. The paper was written jointly with Samu Mäntyniemi.
- III Atso Romakkaniemi provided the original idea, and had the main responsibility in conducting the analyses and writing the paper. Samu Mäntyniemi designed the statistical models and wrote the section of the paper dealing with statistical inference. Irmeli Torvi and Ari Haikonen assisted in data gathering and processing.
- IV Atso Romakkaniemi developed the original concept, and had the main responsibility in both performing the analyses and in writing the paper. Samu Mäntyniemi designed the statistical models and wrote the section dealing with statistical inference.
- V Atso Romakkaniemi provided the original idea, and had the main responsibility in data gathering and processing. Catherine Michielsens conducted the analyses. The paper was written jointly with Catherine Michielsens.

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Abstract

Wild salmon stocks in the northern Baltic rivers became endangered in the second half of the 20th century, mainly due to recruitment overfishing. As a result, supplementary stocking was widely practised, and supplementation of the Tornionjoki salmon stock took place over a 25 year period until 2002. The stock has been closely monitored by electrofishing, smolt trapping, mark-recapture studies, catch samples and catch surveys. Background information on hatchery-reared stocked juveniles was also collected for this study. Bayesian statistics was applied to the data as this method offers the possibility of bringing prior information into the analysis and an advanced ability for incorporating uncertainty, and also provides probabilities for a multitude of hypotheses.

Substantial divergences between reared and wild Tornionjoki salmon were identified in both demographic and phenological characteristics. The divergences tended to be larger the longer the duration spent in hatchery and the more favourable the hatchery conditions were for fast growth. Differences in environment likely induced most of the divergences, but selection of brood fish might have resulted in genotypic divergence in maturation age of reared salmon. Survival of stocked 1-year old juveniles to smolt varied from about 10% to about 25%. Stocking on the lower reach of the river seemed to decrease survival, and the negative effect of stocking volume on survival raises the concern of possible similar effects on the extant wild population. Post-smolt survival of wild Tornionjoki smolts was on average two times higher than that of smolts stocked as parr and 2.5 times higher than that of stocked smolts. Smolts of different groups showed synchronous variation and similar long-term survival trends. Both groups of reared salmon were more vulnerable to offshore driftnet and coastal trapnet fishing than wild salmon. Average survival from smolt to spawners of wild salmon was 2.8 times higher than that of salmon stocked as parr and 3.3 times higher than that of salmon stocked as smolts.

Wild salmon and salmon stocked as parr were found to have similar lifetime survival rates, while stocked smolts have a lifetime survival rate over 4 times higher than the two other groups. If eggs are collected from the wild brood fish, stocking parr would therefore not be a sensible option. Stocking smolts instead would create a net benefit in terms of the number of spawners, but this strategy has serious drawbacks and risks associated with the larger phenotypic and demographic divergences from wild salmon.

Supplementation was shown not to be the key factor behind the recovery of the Tornionjoki and other northern Baltic salmon stocks. Instead, a combination of restrictions in the sea fishery and simultaneous occurrence of favourable natural conditions for survival were the main reasons for the revival in the 1990's.

This study questions the effectiveness of supplementation as a conservation management tool. The benefits of supplementation seem at best limited. Relatively high occurrences of reared fish in catches may generate false optimism concerning the effects of supplementation. Supplementation may lead to genetic risks due to problems in brood fish collection and artificial rearing with relaxed natural selection and domestication. Appropriate management of fisheries is the main alternative to supplementation, without which all other efforts for long-term maintenance of a healthy fish resource fail.

1 Introduction

Contemporary management of fish resources represents a struggle between conflicting demands. Fishing fleets equipped with modern technology are capable of and willing to exploit any available yield from commercially valuable fish stocks. Effective utilisation of natural resources ranks amongst the most important priorities for human society. At the same time however, concern is growing over the detrimental effects of overharvesting on global fish resources, the examples of which are not few. Fish stocks have become depleted not only through excessive exploitation but also indirectly, through destruction of habitats that are vital at some stages of the life cycle of a given fish species. Whatever the ultimate cause or combination of causes that have lead to serious decline in fish stocks, some consequences would seem to be irreversible. Accordingly, the long-term maintenance (conservation) of natural resources has been given urgent priority (Rio Convention on Biological Diversity, Council regulation (EC) No 2371/2002).

Apart from regulating fishing and maintaining and restoring essential habitats, stocking hatchery-reared fish into the wild has been applied in the management of fish stocks for more than a century (Welcomme, 1998). Decisions to implement stocking have been based on diverse and case-specific criteria. As a result, it is not surprising that a wide variety of objectives have been invoked to rationalize stocking and that the terminology used has not always been clear (Ritter, 1997; Welcomme, 1998). Stocking for conservation of an endangered species, aiming at strengthening spawning stock and subsequent natural recruitment falls into the category of enhancement stocking (Cowx, 1998) and may be more specifically referred to as supplementation for conservation purposes (Cuenco et al., 1993; Ritter, 1997; Flagg et al., 2000). Hereafter I refer to this activity simply as 'supplementation'. Anadromous salmonid species in particular have been subject to extensive supplementation.

In Finland, the aquaculture section of the Finnish Game and Fisheries Research Institute (FGFRI) has been given the mandate to run hatchery programmes for threatened valuable aquatic species (Westman and Kallio, 1987). The objectives of the hatchery programmes for the threatened valuable fish species were specified as preservation/conservation and enhancement of the species and stocks (Westman and Kallio, 1987, decree No. 764/1988). Thus, in the case of the endangered Baltic salmon stocks, the definition of supplementation is appropriate when describing the FGFRI hatchery programmes as carried out during the past few decades.

The performance and success of the hatchery programmes should be evaluated against the appropriate criteria. However, there have been few, if any

published attempts in Europe to exhaustively articulate these criteria. According to the extensive review of artificial production strategies for Pacific salmon (Flagg et al., 2000), supplementation should be able to maintain or increase the abundance of naturally reproducing fish. At the same time the long-term fitness of the target population should be maintained, and the ecological and genetic impacts on non-target populations should be controlled. Meeting these top-level criteria require fulfilment of many lower-level (practical) criteria. Fleming and Petersson (2001) made a crucial point in relation to the criterion of maintaining or increasing the abundance of naturally reproducing fish; little is known about the factual ability of stocked fish to provide a net long-term benefit to a natural population. The few existing studies mostly indicate failure in this respect. Indeed, although stocked fish have been extensively studied, surprisingly little is known about the ultimate success of supplementation as a management tool.

I have had three main aims in my study. Firstly, I wanted to employ the most recent, comprehensive stock assessment methods to quantify stocked salmon across their lifespan in detail, and to relate these results to the corresponding quantities of their wild conspecifics. Secondly, I wanted to examine how well the stocked salmon fulfill the requirement of mimicking the phenotype of wild salmon. Thirdly, I wanted to construct some hypotheses concerning causes and effects affecting the survival and life history choices of stocked salmon, based on the above analyses.

Bayesian statistics have been widely applied to Baltic environmental and fisheries research (Kuikka, 1998; Uusitalo, 2007) and especially to Baltic salmon research (Michielsens, 2003; Mäntyniemi, 2006; Uusitalo, 2007; Levontin, 2008). My thesis builds upon these earlier works and thus represents a further step in the overall process of methodological development.

The primary focus of my study is supplementation of the River Tornionjoki salmon. Because this river is one of the largest spawning rivers of Atlantic salmon in the world, my findings may somewhat offset the general paucity of information from salmon population dynamics in large rivers.

2 Bayesian induction - probability calculus

Scientific theories by their very nature extend beyond experimental data and therefore they can not be conclusively verified. While absolute certainty can not be reached, an epistemic status for the theories can be found somewhere between being definitely right and totally wrong. These degrees of certainty can be characterized as a spectrum of probabilities. Inductive logic must say which of the alternative postulates is the most reasonable to believe on the

evidence available (Jeffreys, 1961; Howson and Urbach, 1993).

Bayesian induction treats probabilities of theories as a property of our attitude towards them, i.e. as measures of degrees of belief. This is intuitively plausible as the state of nature in itself is not uncertain, but it is our belief as to what is the state of nature that contains uncertainty.

The basic concept of Bayesian induction can perhaps be most easily understood as a learning process. Let us consider a phenomenon we first 'know' nothing about (meaning that we have no prior beliefs whatsoever about the matter, and which hence leads us to consider all possible hypotheses as equally probable). We make our very first observation about the phenomenon. Intuitively we realize that

- a. Before making the first observation, any state of the nature of the phenomenon was equally probable in our minds; and
- b. Given the observation, we then want to consider a certain state or states of the nature with regard to the phenomenon as more likely than the others; and
- c. Based on only one observation we are still very uncertain about the phenomenon.

By the above process we update our belief about the phenomenon. This is a very practical version of the Bayes' theorem:

$$P(h | e) = \frac{P(e | h)P(h)}{P(e)}, \quad (1)$$

where $P(e)$ is the so-called normalizing constant, thus

$$P(h | e) \propto P(e | h)P(h). \quad (2)$$

Here, h stands for a certain hypothesis and e stands for evidence (observation). $P(h | e)$ is the probability that the hypothesis is true given the evidence, i.e. the posterior probability. $P(e | h)$ is the probability of data given hypothesis. $P(h)$ is the prior belief, i.e. the prior probability of the hypothesis. Our prior belief is in this case 'uninformative', that is, we set the same probability for this hypothesis to be true as for any other plausible hypothesis.

When we acquired the first observation we could not avoid going through the above process, consciously or unconsciously. The principle of Bayesian conditionalisation (Howson and Urbach, 1993) states that as soon as we have new evidence we update our belief about the hypothesis.

Consider now that after updating our belief with the first observation, we obtain a new observation. Again we intuitively go through the previous steps of induction. This time we realize that we want to update our belief based on the new observation without forgetting the information included in the first observation. As a result, our prior belief must logically be informative. That is, the $P(h)$ corresponds to the belief that we obtained from the first observation. After updating, the resulting posterior belief contains the information included in both observations.

In mathematical statistics, Bayesian inference typically provides probabilities for a multitude of hypotheses. Probabilities can typically be expressed in terms of a probability density function (pdf), which readily allows testing of statements such as ' $X < x$ ' for continuous variables.

The above example of a Bayesian inference is of course rather naive and yet helps us to appreciate that very seldom is there no prior knowledge about the matter we want to examine. Therefore it is clearly reasonable to use informative prior belief in the process instead of trying to ignore it or to pretend that it does not exist. A practical problem arises, however, in specifying and quantifying prior beliefs. Researchers usually have most of their beliefs based on information from published literature, earlier studies, or pilot experiments etc. One way to quantify a prior belief is to carry out a meta-analysis of the existing, documented observations (e.g., Michielsens and McAllister, 2004). If information relevant for quantifying a prior belief is diverse and/or non-commensurate as such, a Bayesian network fed with expert opinions may be utilised (Uusitalo et al., 2005). In this thesis I have used informative prior beliefs about the parameters of interest in cases when extensive literature reviews [IV,V], meta-analyses [V], or formal ways to combine expert opinions [V] have been employed to derive prior beliefs. However, there are also parameters for which it has been too difficult in practice to construct informative prior beliefs, or where uninformative prior beliefs are used purposely to 'ground test' certain key hypotheses [V].

Prior beliefs are also connected to the construction of statistical models. All statistical inferences entail assumptions that connect observations to the phenomenon of interest (i.e. models), thus reflecting the modelers' perceptions (prior beliefs) about the substance under consideration (Mäntyniemi, 2006). The necessity of such a construction is common both to classical (frequentist) and Bayesian approaches. In this thesis I have endeavoured to transfer my real perceptions of how observations are connected to the phenomenon of interest to the statistical models. In particular, Paper II demonstrates well how the Bayesian approach can be applied to common statistical problems and highlights the issue of model construction.

The Bayesian approach to statistical inference often leads to situations

where no analytical solution can be calculated for deriving the joint posterior distribution of the variables in the model. Stochastic simulation methods offer a way to approximate posterior distributions. WinBUGS and OpenBUGS (Spiegelhalter et al., 2004, 2007) are freely available software which facilitate construction of Bayesian models and approximation of the posterior distributions by using a Markov chain Monte Carlo (MCMC) simulation algorithm (Gilks et al., 1995). These software have been utilised in the papers II-V.

3 Tornionjoki salmon and Baltic salmon fisheries

3.1 Distribution and biology

Atlantic salmon living in the Baltic drainage area is genetically and geographically isolated from North Atlantic salmon. Baltic salmon stocks can be divided into northwestern and southeastern phylogeographic lineages (Koljonen et al., 1999). The northwestern (Atlantic) lineage colonised the rivers of Finland and northern Sweden from the west after the last Ice Age. Salmon is known to have been present historically in about one hundred Baltic rivers. However, pollution, damming, overfishing and other human activities have decreased the number of spawning rivers to less than half of that. Native, self-reproducing strains currently exist in less than thirty rivers (IBSFC and HELCOM, 1999).

The River Tornionjoki is the northernmost of the Baltic Sea catchment river basins and flows to the Bothnian Bay along the national border between Finland and Sweden (Figure 1). The Tornionjoki river system is the largest unregulated in the western Europe (Dyssenius and Nilsson, 1994), having a mean discharge of about 400 m³/s, and is closely connected to the adjacent River Kalixlven through a natural bifurcation. It is also one of the world's largest spawning rivers of Atlantic salmon and the largest producer of wild salmon in the Baltic Sea. The catchment covers 40 010 km² of sparsely populated terrain ranging from the southern boreal zone in its lower reaches to the headwater subarctic zone 400 to 500 meters above the sea level. Only minor anthropogenic disturbances are evident in river water quality. Discharge is lowest from December to May, when the river is frozen. During the spring thaw in May-June the discharge rate is commonly 1000-2000 m³/s. The river flows into the northern end of the Bothnian Bay, where the salinity is only 2-4 per mil and where ice-cover extends annually over several months.

Salmon spawn and parr occur in the swiftly flowing sections of the main stream, in the headwaters and in the major tributaries from the lowermost



Figure 1: *The Tornionjoki river system showing the main stem and major tributaries and the current natural distribution of salmon (black river stretches). The river defining the national border between Finland and Sweden is highlighted by a dotted line and the catchment boundary is indicated with a broken line. The location of the Tornionjoki hatcheries in Muonio and the main release areas of stocked parr (bold black river stretches) and stocked smolts (circles) are also marked.*

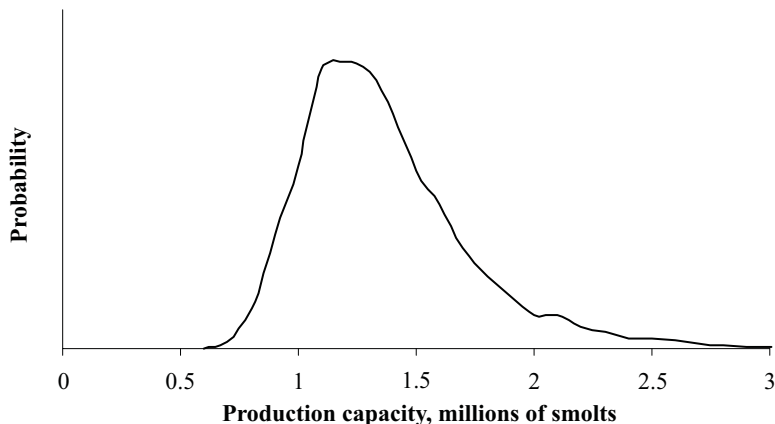


Figure 2: *Posterior distribution of the smolt production capacity estimate for the Tornionjoki river system, based on the most recent assessment of the Baltic salmon stocks (redrawn from ICES (2008)).*

riffles up to 400-500 km from the sea. The approximately 5000 hectares of parr-rearing habitat were first estimated to produce a maximum of 0.5 million salmon smolts (e.g., IBSFC and HELCOM, 1999; ICES, 2001). However, the latest evidence concerning stock-recruitment relationship suggests that the smolt production capacity is most likely on the level of magnitude of 1-1.5 million smolts and it may even exceed this level (Figure 2; ICES, 2008). The spawning stock in Tornionjoki has rapidly increased recently, after a long period of low abundance [I], (Michielsens et al., 2008). This may have resulted in patchy habitat use among spawners and could thus induce local density-dependent effects, which diminish after spawners have gradually dispersed to fully re-establish the natural or most productive structure of habitat use (Walters and Korman, 2001). Therefore, the smolt production capacity estimates based on the recent stock development may be lower than what might be achieved over the longer term.

After 2-6 years as parr in the river [III], wild Tornionjoki salmon migrate, mainly to the southern Baltic Sea, for feeding. Smolts migrate to the sea between mid-May and mid-July and they reach the feeding grounds by the end of the year (Ikonen, 2006). After 1-4 years of feeding, maturing salmon commence their spawning migration northwards along the coast of the Gulf of Bothnia. Multi-sea-winter (MSW) spawners comprise the majority of the spawners and most of them enter the river from June to mid-July. Grilse spawners, a very large majority of which are males, enter the river in July and August (Nordqvist, 1924; Kallio-Nyberg and Romakkaniemi, 1998), [III].

Repeat spawners normally account for 5-10% of the spawners [III], and majority of repeat spawners are females.

3.2 Fisheries and development of stock abundance

The highest historically recorded river catches of Tornionjoki salmon are around 400 tonnes (Fellman, 1906; Virrankoski, 1973, ref. Tuunainen et al., 1984) and were caught 2-4 centuries ago when almost all fishing was confined to the river. Since then salmon fishing spread gradually from the rivers to the Baltic Sea. Offshore fishing targeted at feeding salmon became the dominant form of fishery by the second half of the 20th century (Christensen and Larsson, 1979; Christensen et al., 1994). Coastal fishing also gradually expanded and underwent technological improvements by the late 20th century. Consequently, in recent decades, the majority of Baltic salmon catches have been caught by sea fisheries (Figure 3), and Tornionjoki salmon and other Baltic salmon are harvested by various fisheries along their whole migration route (Figure 4). This system of consecutive fisheries can easily result in overharvesting of a salmon resource, even though none of the fisheries alone would necessary constitute a specific threat for overharvesting (Michielsens et al., 2006).

The salmon stock was especially weak throughout the entire 1980's [I] and was considered to be at the verge of extinction (Pruuki, 1993). Natural spawning was probably at its lowest level in the early 1980's, and the annual abundance of wild Tornionjoki smolts was no more than 70 000 - 80 000 individuals in the late 1980's (Karlström, 1995),[I]. However, the stock showed rapid recovery during the 1990's [I], as a result of which annual runs of wild smolts have been around 600 000 - 800 000 in recent years (Figure 6). The tentative analysis of smolt trapping data of the year 2008 indicates smolt abundance of over 1 million individuals.

3.3 Hatchery practices and stocking

By the 1970's Swedish and Finnish fish biologists and fisheries managers had become alarmed about the decline in the northern Baltic salmon stocks and a joint Finnish-Swedish hatchery programme of Tornionjoki salmon was established. Annual supplementation started in 1977, when for the first time a larger amount of Tornionjoki salmon was stocked from the Muonio hatchery (Figure 1). Annual stocking volume increased throughout the 1980's and early 1990's and was at its highest level in the middle and late 1990's (Figure 5). Following the recommendations of the Finnish-Swedish expert group, supplementation ceased in 2002, due to the recovery of the stock. Thereafter

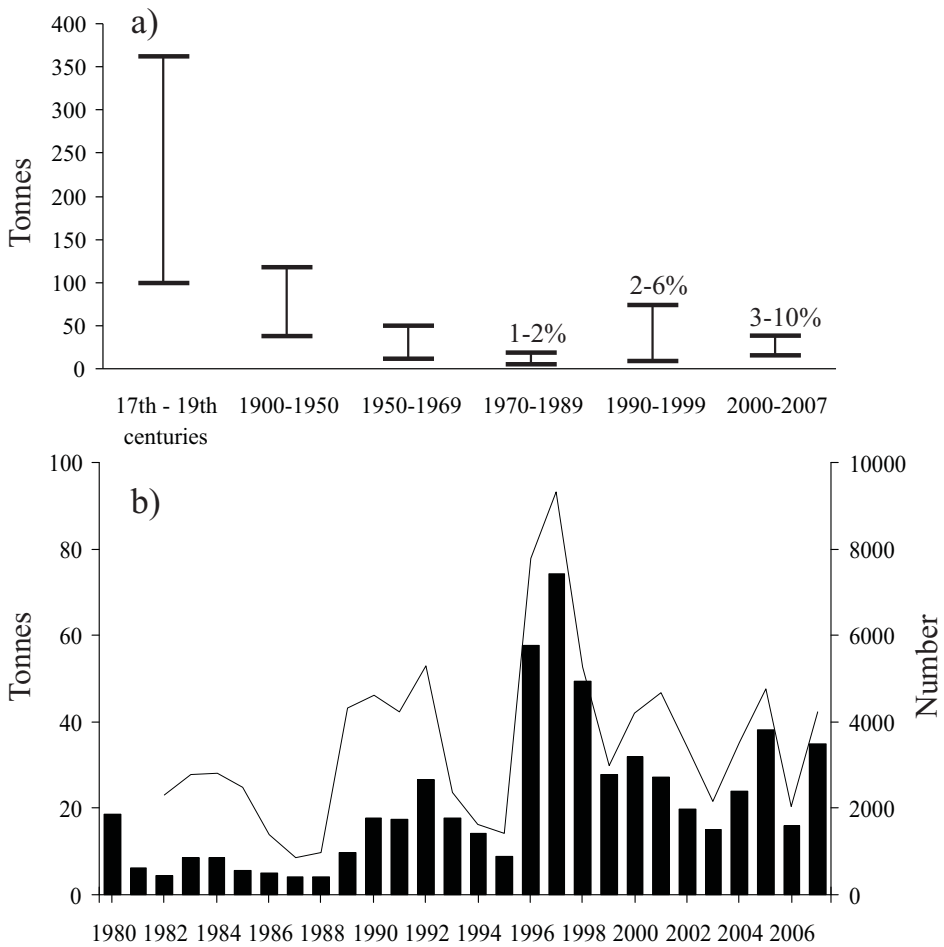


Figure 3: Annual salmon catches in the River Tornionjoki: (a) approximate catch levels over past centuries and decades (modified from Karttunen and Pruuki (1992)), and (b) annual catches in weight (columns) and numbers (line) since 1980. The catches prior to 1980 are based on various sources referred to by Tuunainen et al. (1984) and thereafter they are based on annual surveys of the Finnish Game and Fisheries Research Institute and the Swedish Board of Fisheries. The percentage values above the recent catch levels indicate the proportion of tag recaptures from river fishing.

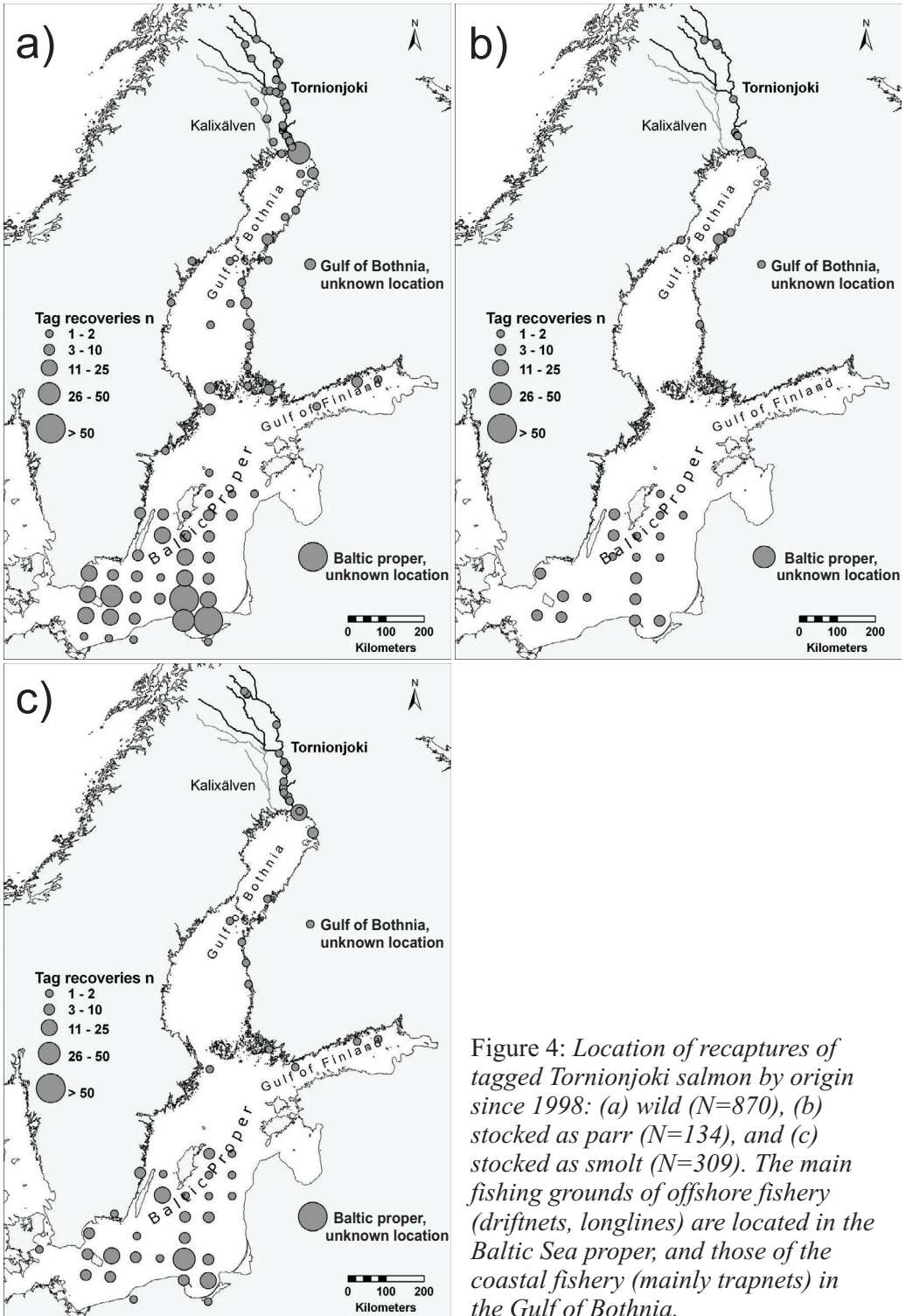


Figure 4: Location of recaptures of tagged Tornionjoki salmon by origin since 1998: (a) wild ($N=870$), (b) stocked as parr ($N=134$), and (c) stocked as smolt ($N=309$). The main fishing grounds of offshore fishery (driftnets, longlines) are located in the Baltic Sea proper, and those of the coastal fishery (mainly trapnets) in the Gulf of Bothnia.

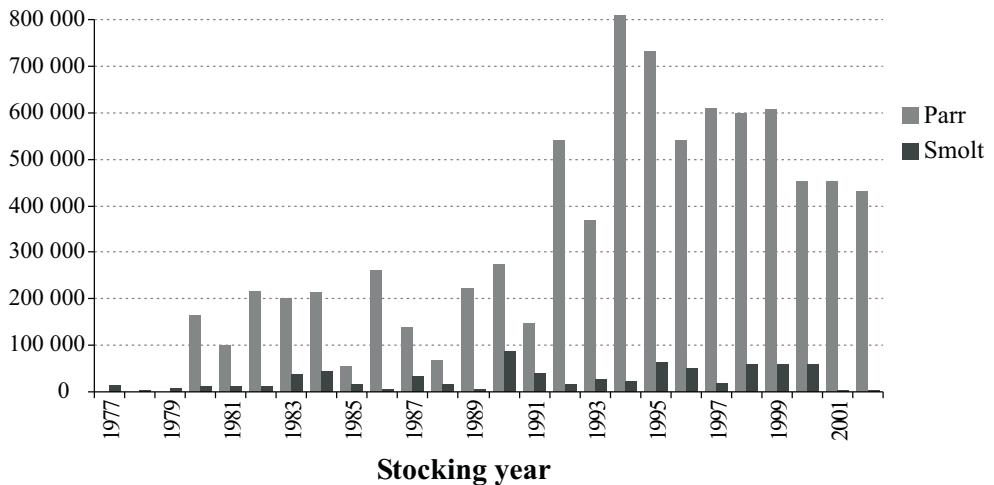


Figure 5: *Statistics of juveniles stocked as parr (92% one-year old and 8% one-summer old) and as smolts (96% 2-year old and 4% 3-year old) in the River Tornionjoki.*

only a few thousand 2-year old smolts have been annually stocked to continue parallel Carlin-tagging and release of wild and reared smolts for research purposes.

1-year and 2-year old juveniles accounted for 93% of the total stocking volume over the years. The rest were mainly of 1-summer and 3-year old juveniles. Eggs, alevins and fry were rarely stocked [I] and they were mainly surplus production dumped into the lowest reaches of the river system, with only limited possibilities to survive. Juveniles that were 1-summer or 1-year old were regarded as parr and will be referred to below as 'stocked as parr' or simply 'stocked parr'. Juveniles that were 2-year old or 3-year old were regarded as smolts and are hereafter called 'stocked as smolts' or simply 'stocked smolts'. Stocked parr were distributed widely throughout typical salmon juvenile biotopes in early summer or in autumn (1-summer old). Stocking densities mostly ranged from 5 to 15 juveniles per 100 m², which together with the extant wild juveniles, theoretically resulted in maximum average densities of 15 one-year old and older juveniles per 100 m². Stocked smolts were released in early summer at few points along the river. The bulk of all juveniles were stocked within the river along the Finnish-Swedish border (Figure 1). About 12% of parr and none of the smolts were stocked in the stretches flowing through the Swedish territory (Swedish Torneälven, Lainioälven), and all stocking ceased there after the year 1994.

The Muonio hatchery with a conventional rearing technique reared salmon until 1988, when a second hatchery with more advanced rearing facilities was established nearby. The new hatchery incubated an annually varying fraction of eggs in artificially warmed water at the end of the incubation period, in order to advance hatching by about two months. These newly hatched fry were kept further in warmed water for their first two months to speed up initial growth. After that they were kept in similar conditions as the rest of the fish. These juveniles were on average over two times heavier than their siblings reared under normal temperature conditions.

Brood fish for the hatcheries were mainly caught by trapnets in the estuary. Determination of sex was uncertain under the conditions of the breeding fishery and small (grilse) spawners were presumably avoided in order to increase the proportion of females and thus the number of eggs. This led to selection favouring large, MSW males as broodfish [III]. Moreover, breeding fishery focused on catching sea-run salmon and mature male parr were used for breeding only once. Egg collection from the wild continued until 1993, when extra mortality caused by M74 syndrome (Koski et al., 1999) extinguished supply of live fry. Captive broodstocks were established from the offspring of wild spawners in the late 1980's and after 1994 they were the only source of eggs for rearing. In spite of periodic renewal of broodstocks from the wild, high production levels could only be maintained by establishing second- and even third-generation captive broodstocks.

Since the early 1980's it has been customary to remove adipose fins from the juveniles reared to the age of one summer or older. This practice was interrupted only in 1995, when most of the cohort hatched in 1994 were not finclipped. During manual removal of the adipose fin, some fish were accidentally left without marks or were poorly marked, which had to be properly taken into account in the data analyses [III-V].

4 Challenges in stock monitoring methods

Quantitative assessment of fish populations is especially challenging in large rivers (Cowx, I. G. (ed.), 1996). Standard fish survey methods are poorly suited to fast flowing, deep and rocky conditions, which may even vary temporally, thus affecting both the success of fishing and the success of fishery-independent surveys.

Therefore, fish stock assessment in large rivers often relies on compiling various indices of abundance and their subsequent interpretation, on the basis of which conclusions are drawn and management decisions made. This procedure has certain drawbacks. Firstly, it is difficult to quantify manage-

ment actions based on index information. Secondly, drawing conclusions from such indices becomes difficult if different indices convey conflicting messages. Thirdly, stock indices are invariably case-specific as conditions between different rivers vary, thus precluding the possibility of making generalizations and extrapolations across rivers. Attempts to attain comparable results via standardization of methods between rivers can only have limited success because standardization can only be applied to plans of action, not to the river-specific circumstances themselves. The third problem is especially problematic because it leads to a lack of commensurate information. Therefore it is important to strive to obtain rigorously quantified information from the large river systems as well.

Traditional electrofishing represents a typical index-producing approach when applied in a large river because sampling is restricted to shallow, wadeable parts of the juvenile habitat preventing representative sampling (Niemelä et al., 2001), and also because of the large uncertainty related to the removal estimates of true population size imposed by unequal (individual) catchability (Mäntyniemi et al., 2005). A Finnish-Swedish monitoring network of almost one hundred electrofishing sites covers the distribution of salmon in the Tornionjoki river system. Parr abundance has been monitored in these sites annually in late summer and autumn [I]. Electrofishing data were utilized as such to describe changes in wild parr abundance [I,V], but most importantly the data were used in conjunction with quantitative smolt mark-recapture estimates to obtain a 20-year long time series of smolt abundance [V].

Trapping of smolts is another survey method world-wide used in salmon rivers. This approach is primarily aimed at obtaining a quantitative abundance estimate, either by total trapping and counting of smolts (small to medium-sized rivers) or by partial trapping with mark-recapture experiments (large rivers) (Mills, 1989). One of the world's largest smolt traps is deployed in the River Tornionjoki and have provided data which are central to the present study. A Swedish smolt trap provided smolt abundance estimates for most of the years 1987-1996 (Karlström and Byström, 1994). A Finnish smolt trap was set up for the first time in 1991 and since 1996 it has been producing quantitative population estimates. Even when population estimates could not be obtained by mark-recapture experiments as described in [II], population samples were collected as described in [III] and they provided information on age, sex and origin of smolts. Trapping has occasionally missed the earliest part of smolt migration or been cancelled because of extreme flood conditions. The partial trapping normally catches only 3-6% of the whole smolt population, which together with a proper account of schooling behavior of smolts and the effect of varying trapping circumstances on the

catchability leads to relatively uncertain estimates of true smolt population size [II]. Formally combining the information included in parr density indices and smolt trapping results decreases the associated uncertainty and even provides population estimates for the years with missing or defective smolt trapping data (ICES, 2004; Mäntyniemi, 2006).

Tag recapture data from fisheries is potentially very informative and valuable for stock assessment if properly modeled (Hilborn and Walters, 1992; Martell and Walters, 2002). A Carlin tag, which is widely and routinely used in studies of Baltic salmon and trout, is attached under the dorsal fin of an anaesthetized smolt (Carlin, 1955). In the River Tornionjoki, wild smolts and smolts stocked as parr were daily tagged at the smolt trap and released back in the river below the smolt trap after a couple of hours of recovery. Older-reared smolts were tagged in the hatcheries several weeks or several months before release. About 37 000 wild smolts, 5000 smolts from releases of younger-reared juveniles, and 59 000 older-reared smolts were tagged in the years from 1987-2006. Respectively, 1080, 141 and 2431 recaptures of 1SW and older older fish were reported from various fisheries by autumn 2007 (Figure 4). The mark-recapture analysis for Baltic salmon developed by Michielsens et al. (2006) was adapted and applied to Tornionjoki salmon enabling parallel estimation of survival, maturation and harvesting of salmon with different background on their feeding and spawning migration [V].

A generalized and river-specific connection exists between river catches and salmon abundance (Crozier and Kennedy, 2001; O’Connel, 2003). Salmon catches in the River Tornionjoki are annually estimated by mail and telephone surveys addressed to a sample of salmon fishers [I]. Routine statistical methods have been applied to infer the total catches from the survey data. Apart from tag recapture data, river catch statistics represents another source of information describing exploitation of spawners and related spawner abundance and such data are accordingly used in this thesis in the modeling network of salmon abundance [V].

Information from catch samples are utilized in almost all routine fish stock assessment methods, such as Virtual Population Analysis (VPA; e.g., Gulland, 1983). Thousands of catch samples were collected, mainly from the lower reach of river along the Finnish-Swedish border, as described in [III]. The samples contain information on the age and sex structure of spawners and relative proportions of spawners with different background. Care must be taken to account for, e.g., different vulnerability to river fishing of spawners ascending the river at different times of the season (Pérez et al., 2005). In the River Tornionjoki, grilse spawner run occurs later in season than the run of MSW spawners, thus, these two spawner groups were treated as separate information sources in the stock assessment. A similar vulnerability to

angling of spawners with different backgrounds was assumed based on the literature (Mills and Piggins, 1983; Jokikokko et al., 2006a) and on the finding that Tornionjoki spawners of different origin have no obvious differences in run timing [III].

In the case of the River Tornionjoki, none of the assessment methods can alone provide more than a highly uncertain estimate of the true quantity of fish, as demonstrated by the smolt trapping [II]. Therefore, various information sources were formally combined in a Bayesian framework following the principles discussed in Section 2, in order to obtain the most accurate perception about the parameters of interest.

5 Juvenile stage of the stocked salmon

With an average freshwater survival of 16% [IV], stocking parr mostly resulted in annual numbers of 50 000 -100 000 smolts, with the highest numbers occurring at the end of the 1990's. Together with stocked smolts the total number of smolts of reared origin varied mostly between 50 000 and 100 000 during the late 1980's and early 1990's, and between 100 000 and 150 000 in the late 1990's. The numbers declined rapidly during the first years of the current decade due to the termination of supplementation (Figure 6).

Stocking parr produces phenotypically more natural-like fish than stocking smolts. This is especially the case if juveniles are reared in ambient water temperatures [III]. The size of smolts stocked as parr is on average somewhat smaller than the size of wild smolts, but the size distributions overlap greatly. Stocked parr predominantly smolt at the same ages as wild parr. The sex ratio of smolts stocked as parr also resembles that of wild smolts. These characteristics increase the potential for reared salmon to express survival and life history and behavioral traits similar to those of wild salmon across their lifespan. Annual smolt runs of stocked parr consist of several (3-5) cohorts similar to wild smolts, which stabilizes abundance and increases natural life history complexity of the stock. However, smolts stocked as parr tend to migrate to the sea later in the season than wild smolts [III]. This is potentially a serious behavioral divergence from wild conspecifics and may lead to mismatch with the optimal timing of entering the sea (McCormick et al., 1998) and thereby to reduced initial survival in the sea.

Stocked smolts show notable divergence from wild smolts in almost all respects [III]. Stocked smolts comprise single cohorts, which may lead the population to a more vulnerable and unstable development, one indication of which is the high variation in the later survival [V]. The lifespan and the natural life history complexity of the stock are reduced and there is even

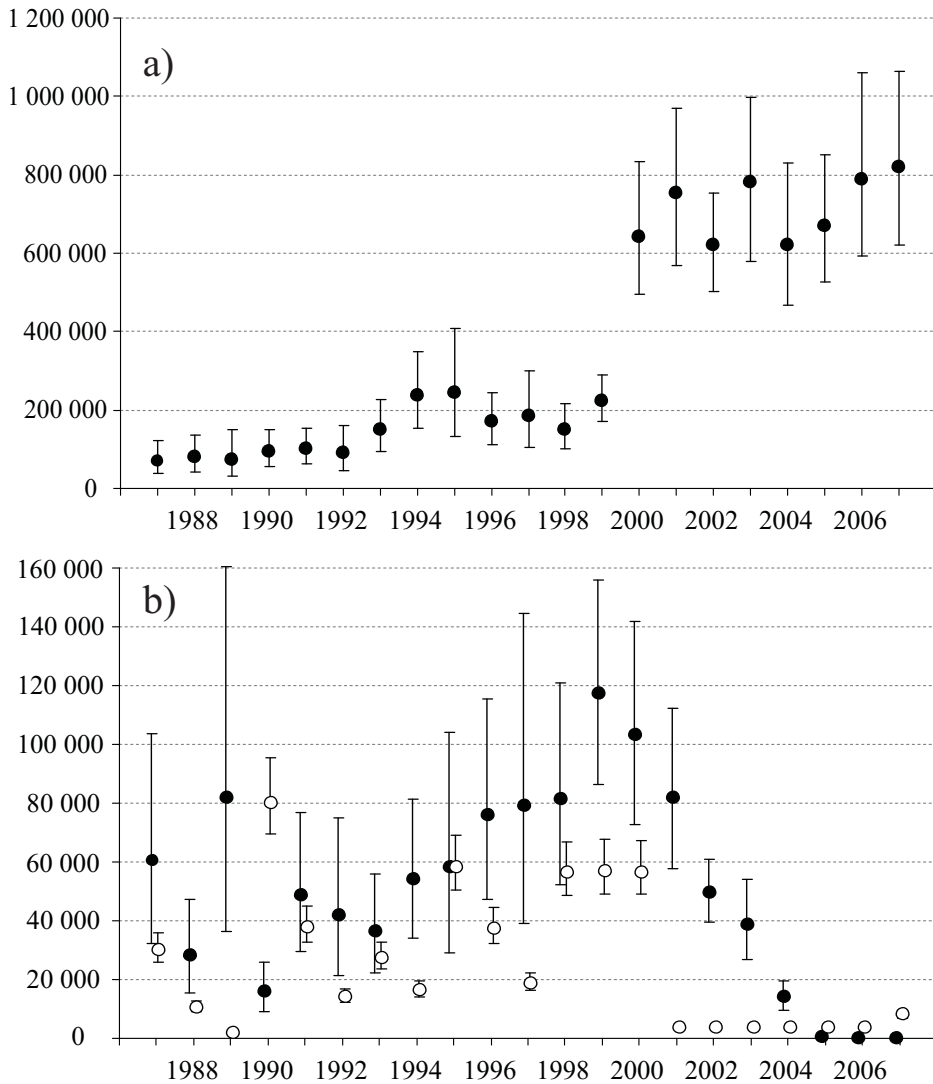


Figure 6: *Expected values and 95% probability intervals of annual smolt abundance in the River Tornionjoki based on the model results of the paper V: (a) wild smolts, and (b) smolts stocked as parr (closed circles) and smolts (open circles). The numbers of stocked smolts closely correspond to the stocking statistics (Figure 5), but include associated uncertainty.*

a possibility of artificial selection for faster-developing fish (Kostow, 2004; Obedzinski and Letcher, 2004). The peak migration of stocked smolts from the River Tornionjoki to the sea usually coincided with the peak migration of wild smolts, which was probably a result of successful timing of stocking, perhaps due to the availability of on-line information about natural migration timing from the smolt trap.

A fraction of warm-water reared juveniles smolt at the age of one year during the spring they are stocked [IV]. One-year old smolts were observed always when warm-water reared juveniles were stocked but never when only juveniles with normal rearing were stocked [III, IV]. The size distributions of juveniles with different rearing temperatures further confirms that 1-year old smolts must have been warm-water reared [IV]. However, hatchery growth varies considerably amongst warm-water reared individuals and some of them smolt as late as 4-5 years old [IV]. Female juveniles were on average longer than males, but they showed a larger individual variation in size.

All juveniles of the cohorts 1999 and 2001 stocked as 1-year old were warm-water reared. Of these juveniles (which survived over the period immediately after stocking), 9% and 21% turned to 1-year old smolts, respectively. As a consequence, tens of percent of smolts were one-year old in these cohorts. At lower levels of occurrence of 1-year old smolts, both sexes seemed to smolt to the same extent (1999 cohort: 8% females vs. 9% males), while at high levels of smolting females smolted to a greater extent than males (2001 cohort: 27% females vs. 14% males). Perhaps the warm-water reared cohorts with the strongest boost in growth resulted in optimal conditions for males to select an early maturation pathway instead of smolting (Berglund, 1995).

Warm-water rearing does not seem to increase overall survival to smolt [IV]. This is a somewhat confusing finding, because a young smolting age should have a decreased accumulation of mortality and large juveniles have been generally found to survive better than small ones (Sogard, 1997). There are two potential explanations for this: (1) fast growing and early smolting juveniles adapt poorly to natural conditions in the river, which increases their mortality; or (2) other factors than size affected survival much more and masked the smaller effects of size among the studied cohorts. Several factors may contribute to the first explanation, including physiological changes due to fast growth (Fleming et al., 2002) that lead to increased demand for food and risk-prone behavior (Gotceitas and Godin, 1991), and other behavioral changes due to artificial rearing (Brown and Laland, 2001), which may become pronounced among fast developing fish.

Sexual maturation reduces survival of male parr (Myers, 1984), and it is the only known sex-specific survival factor in the parr population. The

sex ratio is more skewed among wild than among reared-origin smolts [III] and the annual mortality among reared parr differs only slightly between the sexes [IV]. Thus, either maturation is more frequent among wild than among reared parr, or mature wild parr have higher mortality than mature reared parr. The procedures for broodfish collection [III] and the use of second and third generation captive broodstocks may both reduce maturation of reared parr (Fleming and Einum, 1997; Kallio-Nyberg et al., 2007). Spring-time hatchery conditions or stocking stress with delayed food intake in the wild may further suppress growth and subsequent maturation of the stocked 1-year old parr (Saunders et al., 1982; Berglund, 1995). Consequently, there are several factors which point to a lower parr maturation among stocked than wild parr. Sexual maturation of reared parr seems to occur at the ages of 1 and 2 years [IV]. Maturation of stocked smolts is frequently observed in the hatcheries during the second year of rearing (e.g., 11-14% of males in 1999-2000). The very low hatchery mortality over the second winter (about 1%) obviously means that recovery from maturation is safeguarded well in the hatchery.

Although almost all stocked smolts start their smolt migration within the same spring that they are stocked [III], it is nevertheless questionable if point releases of large amounts of smolts is a sensible practice. Firstly, even a brief residence period by the stocked juveniles at the stocking site would lead them to territorial intercourse with the wild conspecifics. Not all the juveniles are necessarily ready to start migration immediately if the population includes large size variations. A mismatch in timing of stocking and smolt migration would also cause stocked smolts to stay longer at the release point. Secondly, large shoals of newly stocked juveniles attract predators and the wild juveniles are also affected by their attacks (Collis et al., 1995; Kekäläinen et al., 2008). Thirdly, precise homing of spawners may induce high densities of spawners in the release points, potentially leading to unnecessary strong competition of spawning sites and local density-dependent mortality among offspring.

The freshwater life histories and survival of wild and the two types of reared juveniles can be approximated at a low abundance level of wild juveniles, i.e. in a typical situation of supplementation (Figure 7). The amount of 10 000 eggs corresponds closely to the average fecundity of a middle-sized (85-90 cm) maiden female spawner [III]. Stocking 1-year old juveniles increases egg-to-smolt survival by a factor of about 2.5 compared to the corresponding survival in the wild. Stocking smolts in turn increases the survival by a factor of almost 15. These survival differences have a remarkable role in the evaluation of efficiency of supplementation - especially in a situation when eggs for rearing are collected from the wild. The comparison is less meaningful

when captive broodstocks produce eggs.

Survival of stocked parr decreases when stocking volume and abundance of oldest wild conspecifics increases, both of which result in higher combined parr densities in the nursery areas [IV]. Density-dependent mortality is suggested to occur mainly at an early life stage of salmon juvenile, but it may also occur within natural or artificial population bottlenecks at older age (Elliott, 2001). Stocking at high densities serves as an example of such an artificial bottleneck. The negative effect of stocking volume on the subsequent survival of reared parr raises the issue of similar negative effect on the survival of wild conspecifics. The oldest wild parr may not suffer from this extra mortality due their superior competitive ability (Wańkowski and Thorpe, 1979; Metcalfe et al., 2003). However, younger and therefore much smaller wild parr may become recessive in competition with large and aggressive stocked parr and thus their survival may become negatively influenced by stocking (Berg and Jorgensen, 1991; Weber and Fausch, 2003). Aggressive interactions between large stocked and small wild parr may especially occur in critical seasons such as winter-time when suitable parr habitat may be insufficient, leading to strong spatial overlap of parr of different size (age) categories (Mäki-Petäys et al., 2004). Any negative effect of supplementation to the extant wild conspecifics should naturally be carefully avoided in supplementation. Stocking of small (young) parr at low densities and careful selection of stocking areas, including collection of prior information about the densities of extant wild population are among the methods used to avoid these negative effects.

The biotic and/or abiotic conditions on the lower reach of the River Tornionjoki are somehow disadvantageous for survival of the stocked parr [IV]. The parr occupying this area grow faster and apparently smolt younger than parr on the upper reaches of the river, as indicated by their larger size-by-age and the smaller proportion of ages 3 or older (Romakkaniemi, unpublished information). The more southerly location and hence the longer annual growth period and higher productivity should increase survival possibilities and smolt production in the area. However, the average densities of wild parr on the lower reach have been lower than on the middle reach of the river system for several decades (Karlström, 1995; Vähä et al., 2007). Factors responsible for low densities of wild parr are not necessarily the same as those which decrease survival of stocked parr; for instance, wild reproduction might be limited by a lack of spawning grounds, which should not directly affect at all the survival of stocked parr. Perhaps the most likely factors contributing to the lower survival may be a high occurrence of predators and the pronounced occurrence of seasonal critical periods on the lower reach: periods of ice formation, low discharge in late winter and ice break-up.

6 Feeding migration of the stocked salmon

Reared fish are more vulnerable to predators, as reviewed by Olla et al. (1985) and Brown and Laland (2001). Domestication seems to increase susceptibility of fish to fishing (Dwyer, 1990). It should therefore not be surprising to find that 'predation by humans', i.e. fishing, catches reared fish more successfully than wild fish [V]. After the post-smolt stage this phenomenon has far-reaching effects on the population dynamics of reared salmon, but also on the use of fishing-related data to compare wild and reared salmon, as is demonstrated later. Divergences between wild and reared salmon in vulnerability to fishing seem to be attributable to gear type, driftnets being the most selective. Different factors may contribute to the vulnerability of salmon in different fisheries. Apart from the potential effects of foraging, migration, schooling and orientation differences between the wild and reared salmon (reviewed by Brown and Laland, 2001; Jonsson and Jonsson, 2006), faster growth of reared salmon (Kallio-Nyberg et al., 2007), [III] may make them especially vulnerable to net fishing during their second winter at sea. Timing of the spawning run and orientation of migration, in turn, may contribute more to the observed differences associated with coastal fishing.

The first weeks and months in the sea are believed to be the most critical periods of sea life for salmon, such that survival rates during this largely determine the abundance and productivity of a salmon stock (Salminen et al., 1995; Hansen and Quinn, 1998; Crozier et al., 2003). Survival through this post-smolt phase is affected by the physiological status of smolts (Virtanen et al., 1991), stocking time (stocked smolts, McKinnell and Lundqvist, 2000), smolt size (Salminen et al., 1995; Saloniemi et al., 2004), predation (Larsen, 1985), availability of suitable food (Salminen et al., 2001) and ambient physical conditions such as seawater temperature (Friedland et al., 2003). The lower rates of sea survival of stocked smolt compared to wild smolt has been widely documented (Jonsson et al., 1991; Crozier and Kennedy, 1993; Jokikokko et al., 2006b) and has generally been attributed to the survival difference over the post-smolt phase.

The post-smolt survival of wild Tornionjoki smolts was on average two times higher than that of smolts stocked as parr and 2.5 times higher than that of stocked smolts [V]. In general, wild smolts are suggested to have a survival rate about two times higher than stocked smolts (Jonsson et al., 1991; Jokikokko et al., 2006b). A direct comparison of tag recapture rates indeed indicates such a difference in survival rate also in the data from the Tornionjoki salmon. This demonstrates how the higher vulnerability of reared salmon to fishing easily leads to overestimation of their survival unless these factors are properly taken into account in the analysis [V].

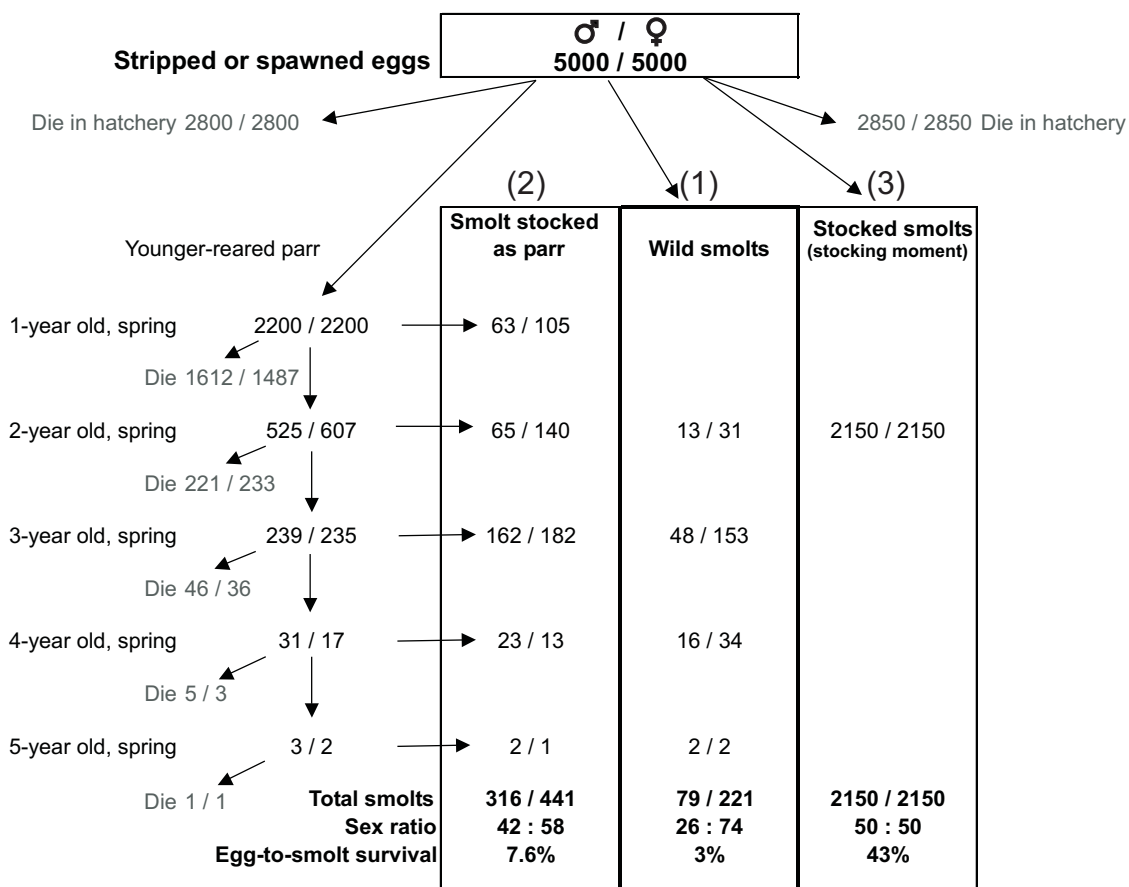


Figure 7: *Expected numbers surviving to smolt stage by sex (males / females) from 10 000 Tornionjoki salmon eggs, following three alternative pathways: (1) natural spawning, (2) hatchery rearing and stocking as 1-year old juveniles, or (3) hatchery rearing and stocking as 2-year old juveniles. The diagram represents conditions prevailing at low abundance of wild juveniles. (1) is based on the Tornionjoki stock-recruit function of Michielsens et al. (2008) and Paper III (period 2 added with cohorts 1995-1996). (2) is based on the follow-up of hatchery mortality in Muonio in the 1990's (Kari Pulkkinen and Ari Savikko, written comm.) and the modelled population dynamics [IV] of the hatchery cohorts 1995-1996 after stocking. (3) is based on the follow-up of hatchery mortality in Muonio in the 1990's. Stocked smolts likely suffer from in-river mortality and their sex ratio may also change before they reach the river mouth [III], which is not taken into account in this presentation. No M74 mortality is assumed to occur.*

	Stocked as parr	Wild	Stocked smolts
Smolts	757	300	4300
Post-smolt mortality	656 87%	214 71%	3844 89%
Survivors to feeding	101	86	456
Catches by all fisheries & natural mortality	62	43	270
Spawners	40	43	185
Sex ratio (male:female)	43:57	34:66	39:61
Smolt-to-spawner survival	5.3%	14.4%	4.3%
Egg-to-spawner survival	0.4%	0.4%	1.9%

Figure 8: *Expected numbers of smolts, survivors from post-smolt mortality, and spawners of different origin through sea migration, using as a starting point the number of smolts produced from 10 000 Tornionjoki salmon eggs (Figure 7). Values are based on modelled population dynamics [V] of the smolt cohorts 1997-1999, and the estimated sex ratio among spawners [III, period 2].*

The typically later migration time of smolts stocked as parr when compared with wild smolts [III] could potentially explain their low post-smolt survival, if the sea conditions changed rapidly so as to become unfavourable for late migrating smolts. However, migration times of wild smolts and smolts stocked as parr greatly overlap, which makes it difficult to believe that this factor could alone explain the survival difference. The divergence of salmon stocked as parr in maturation rates and their vulnerability to fishing during their later sea migration point to existence of some more fundamental divergence than run timing from wild salmon. Jokikokko et al. (2006b) found that smolts stocked as parr survived the post-smolt phase as well as wild smolts. However, their analysis was flawed because the study ignored the differences in vulnerability to fishing of wild and reared salmon [V].

The large interannual variation observed especially among stocked smolts [V] has remained largely unexplained (McKinnell and Lundqvist, 2000). Survival rates show some synchronous variation between the groups [V], which is an indication that some survival factors in the abiotic/biotic sea environment are common to all smolt groups. In addition to the shared factors, each smolt group seemed to be affected by some group-specific factors, or the groups responded somewhat differently to the common survival factors. As a result of this changes in survival were not fully synchronous. Investigation of reasons behind the interannual variation in survival is beyond the scope of my study.

Based on tag recaptures, stocked smolts in the Baltic Sea are suggested to show higher rates of grilising than wild salmon (Jutila et al., 2003b). Rearing increases growth and faster growing individuals mature at a younger age than slower growing individuals (Ritter et al., 1986; Gross, 1991; Salminen, 1997). Grilising is also more common among reared than wild Tornionjoki salmon [V], but the actual differences in the grilising rate are minor [V] and can be entirely explained by the higher proportion of males among reared salmon [III]. When sexes are combined, both groups of stocked salmon show more bipolar maturation patterns than wild salmon, maturing either as grilse or after three or four winters at sea and to a lesser extent after the second winter at sea [V].

The age structure of spawners is the end result of both maturation rates and vulnerability of salmon of different ages to fishing, both of which seem to vary depending on the origin of the salmon [V]. Reared grilse are effectively harvested on the coast, as a result of which high proportions of reared grilse are observed in the fishery, whilst the number of grilse surviving to reach the river is markedly reduced. In turn, the reared individuals which mature when very old presumably migrate very early along the coast. As a result few of them are reported in coastal catches but they are relatively abundant among spawners in the river.

The old age structure of reared spawners was only due to the old age structure of males [III]. Heritability of maturation age has been demonstrated among Atlantic salmon males (Thorpe et al., 1983; Naevdal, 1983) even beyond smolting (Duston et al., 2005). Selection against early matured broodfish [III] may have led to a genetic impact on the age of maturation, which became visible among offspring reared in favourable environments (warm-water rearing, rearing to smolt stage) (Qvarnström, 1999). Unfortunately, sexes could not be separated in the analysis of feeding migration which prevented sex-specific tracking of life history choices in the sea. Therefore, the hypothesis of divergence in the maturation among males remains unconfirmed.

7 Spawning stock and reproduction

Quantitative effects on reproduction (amount of spawners, eggs spawned and viable progeny in comparison with the amount that would have been expected without supplementation) are among the ultimate measures of supplementation success (Fleming and Petersson, 2001; Waples et al., 2007). In spite of its seemingly simplicity, this is in fact complicated to study. The complexity is mainly related to three problems. Firstly, although the number of reared spawners that have survived from stocking can often be estimated, it is not known if they represent a real surplus in the spawning stock, rather than replacement of their wild conspecifics via competitive or other interactions at earlier life stages (Hilborn and Eggers, 2000; Fleming and Petersson, 2001),[IV]. Secondly, reared spawners may be inferior in producing viable progeny in comparison to wild spawners (Chilcote et al., 1986; Jonsson et al., 1990; Fleming et al., 1997), especially if they are the progeny of one or more generations of reared parents and thus subject to domestication (Hansen et al., 2001; Araki et al., 2007). Thirdly, the short and longer term effects of supplementation may differ. For instance, a surplus of spawners gained in the short term may increase reproduction temporarily, but the associated fitness reduction may reduce long-term viability of progeny and thus extinguish the net benefits (Reisenbichler and Rubin, 1999; Waples et al., 2007). Here I have only been able to examine the first of the above points and even that indirectly by demonstrating a probable density-dependent interaction between wild and reared parr [IV], which in turn indicates that replacement may occur at some level.

Population status and development is always uniquely linked to space and time and it is clearly impossible to return backwards through time to see what would have happened with/without supplementation. The absence of this

'perfect reference' leaves considerable scope for speculations for and against supplementation. Using many adjacent populations with/without supplementation to carry out a meta-analysis on effects of supplementation is one way of approaching this problem (e.g., Chilcote, 2003; Nickelson, 2003), [I]. However, this approach must be applied with caution, mainly because one can rarely assume that there is no connection between a population's inherent viability and the decision as to whether the population is supplemented or not.

The survival of Tornionjoki salmon of differing origin can be approximated through their sea migration (Figure 8). Average survival from smolt to spawners of wild salmon was 2.8 times higher than that of salmon stocked as parr and 3.3 times higher than that of salmon stocked as smolts [V]. Earlier studies which have been robust to fallacies due to differences in vulnerability to fishing have also indicated several times higher survival of wild than reared salmon over the sea migration period (Crozier and Kennedy, 1993; Jutila et al., 2003a; Siira et al., 2006).

Using the numbers of smolts in Figure 7 as a starting point of the Figure 8 enables estimation of lifetime survival. The values are based on the results of the stock assessment model applied to the River Tornionjoki [V], by calculating the average survival estimates of the smolt cohorts 1997-1999 (i.e., the main smolting years of the hatchery cohorts 1995-1996, see Figure 7). It must be noted that M74 mortality is assumed here to be negligible, and the model proposes a relatively high post-smolt survival and a relatively low (40-60%) total harvest rate. Therefore, the diagram represents a situation in which the spawning stock is low (low density-dependent mortality in the river), but conditions are favourable for quick recovery of the stock, the adult-to-adult replacement rate (Waples et al., 2007) being as high as 1:20 or more.

Wild salmon and salmon stocked as parr have similar average lifetime (egg-to-spawner) survival rates, while stocked smolts have a lifetime survival rate over 4 times higher than the two other groups (Figure 8). If eggs are collected from the wild brood fish, rearing and stocking parr would not produce any more spawners than allowing brood fish to spawn naturally in these conditions. This indicates that stocking parr would not be a sensible operation, whereas stocking smolts instead would create a net benefit in terms of the number of spawners. However, the strategy of stocking smolts has distinctly more serious drawbacks and risks associated with large phenotypic and demographic divergences from wild salmon, as discussed earlier. If eggs for rearing are produced by captive broodstocks and if M74 mortality is notable, conditions become more favourable for supplementation than presented here. Captive broodstocks, on the other hand, pose more genetic and reproductive

concerns than wild broodfish (Araki et al., 2007; Palm et al., 2003).

In the 1987-1999 Tornionjoki smolt cohorts, stocked salmon accounted for 23-57% of the smolts, 7-38% of the young salmon in the sea after the first winter, and finally 5-28% of the returned spawners (Figure 9)[V]. In addition, there were some stocked salmon which had smolted as 1-year old and which had survived less successfully to spawner stage than stocked salmon with older smolt ages [III]. The proportion of males is mostly 5-9% percent higher among reared than wild spawners, which somewhat decreases the egg production per reared spawners in comparison to wild spawners. The age structures of females of different origin, on the other hand, resemble each other. This feature, together with fast growth (and therefore large size-at-age) of reared salmon means that the number of eggs per reared female spawner is probably as high or higher than that of wild female spawner.

The tag recaptures from river fishing indicate that stocked salmon return to the same river section that they are released to (Figure 4). Therefore, the lower reaches (0-130 km from the sea, Finnish-Swedish Tornionjoki) and the upper reaches (300-450 km from the sea, Muonionjoki and Könkämäeno) of river stretch along the national border (Figure 1) should have benefited most from supplementation, by an increased number of spawners and their offspring. Conversely, supplementation should have only little effect on the population development in the river stretches flowing through Swedish territory (Swedish Torneälven, Lainioälven). Results of Swedish electrofishing monitoring covering all the main rivers of the river system (Ingemar Perä and Stefan Stridsman, Swedish Board of Fisheries, Sweden, unpublished) indicate that parr densities in the river stretch along the national border have remained on the same level and also developed similar to parr densities in the Lainioälven (Figure 10). Parr densities in the Swedish Torneälven have been higher than elsewhere and have even increased recently, in contrast to the other parts of the river system. Thus, on the basis of this evidence, no positive effects of supplementation on wild reproduction can be demonstrated.

Wild salmon production in the River Tornionjoki increased stepwise around the year 1990 and again in 1996-1997; these increases can be correlated with the presence of spawners originating mainly from the smolts of 1988 and 1994, respectively [I]. The proportions of reared salmon were lower than average in these smolt cohorts (Figure 9). This further confirms the conclusion, that supplementation was not the key factor behind the recovery of the Tornionjoki salmon stock. Instead, the main reasons for their revival were a combination of restrictions in the sea fishery, delayed opening of the coastal fisheries and simultaneous occurrence of favourable natural conditions for survival and decrease in M74-induced mortality [I].

Jutila et al. (2003b) and Jokikokko (2006) argued that the intensive sup-

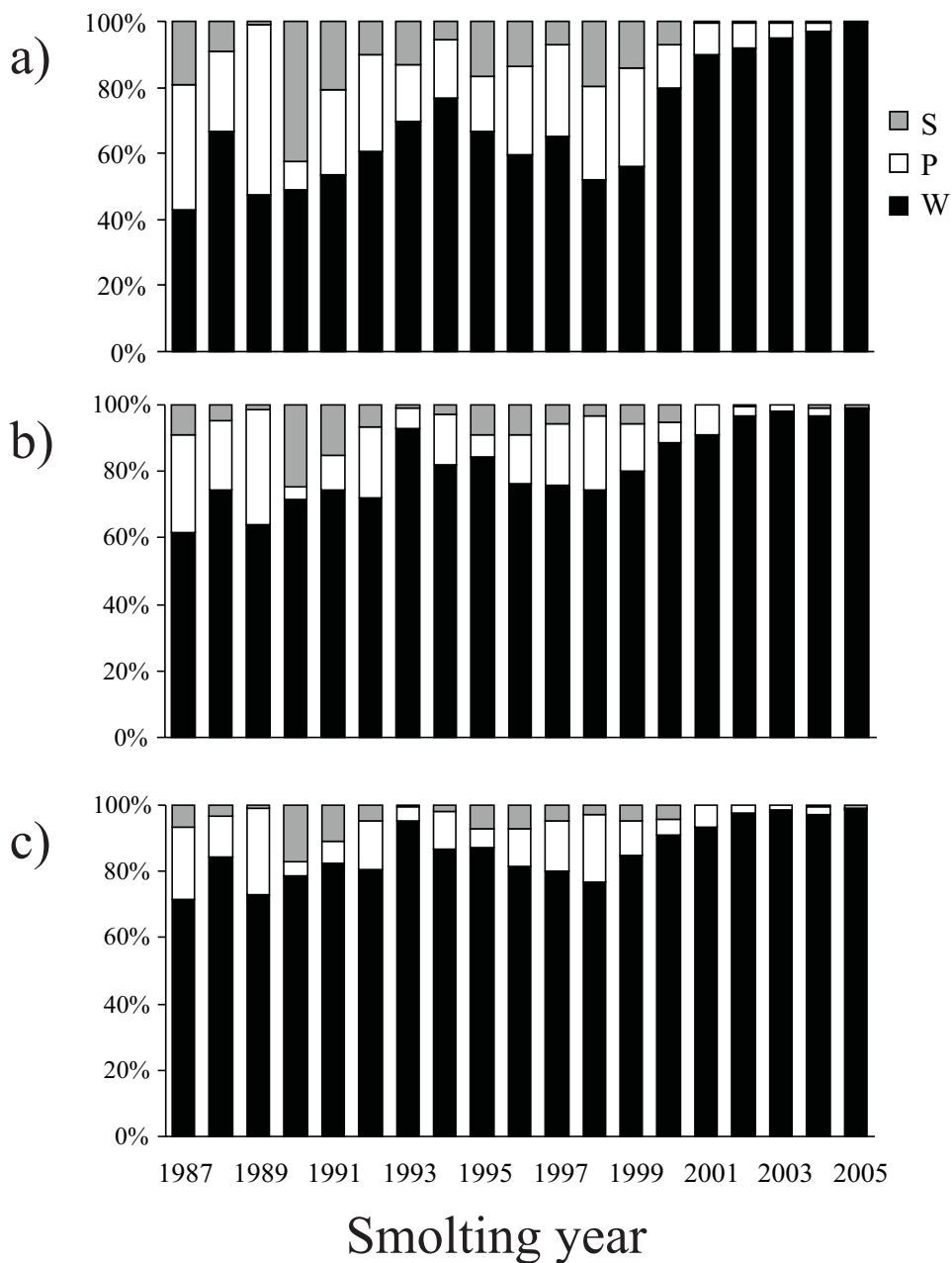


Figure 9: *Expected proportions of salmon of different origin (a) at smolt stage; (b) after post-smolt stage but before maturation/recruitment to fishery; and (c) as spawners (W=wild, P=stocked as parr, S=stocked as smolts). Salmon are grouped according to their smolting year.*

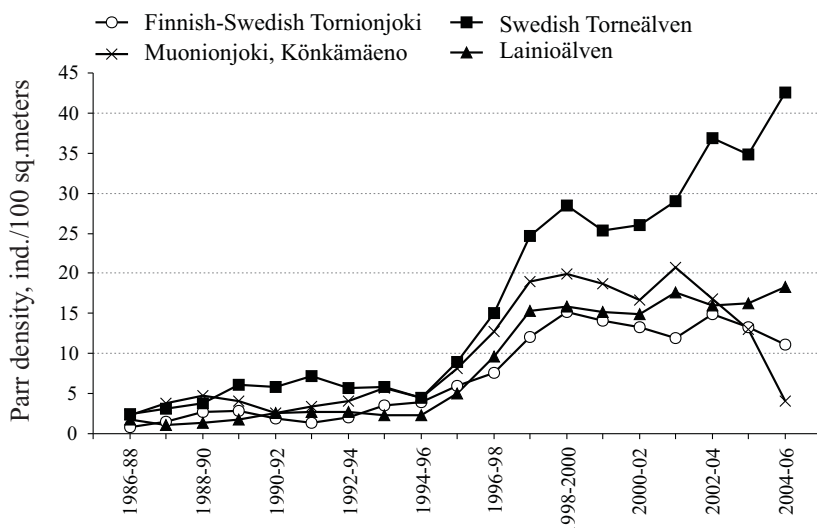


Figure 10: *Three-year moving average of densities of wild parr (ages combined) on the Swedish monitoring sites of different river sections of the Tornionjoki river system (Ingemar Perä and Stefan Stridsman, Swedish Board of Fisheries, Sweden, unpublished).*

plementation in the Baltic River Simojoki increased the number of ascending spawners and thus has likely been an important factor in enhancing the native Simojoki salmon. However, these authors were not able to address the three problematic issues presented in the beginning of this section, which have a critical effect on the ultimate success of supplementation. Hence there are still no examples unequivocally demonstrating the success of supplementation. Instead, wild salmon stocks of northern Baltic rivers (including the Tornionjoki and the Simojoki) have shown similar overall development regardless of them having being supplemented or not [1]. In the light of this evidence and the results of the more elaborate analyses of supplementation of the Tornionjoki salmon, positive effects of supplementation on the conservation of the stocks seem difficult to find.

8 Management implications

My study questions the effectiveness of supplementation as a conservation management tool. The benefits of supplementation in terms of increased number of spawners and progeny seem at best limited, and fishing is more

likely to benefit from stocking than the stock itself. Relatively high occurrences of reared fish in catches may generate false optimism concerning the effects of supplementation. This in turn may even increase harvest pressure and thereby accelerate decline of the stock. Costs of supplementation are also high due to large investments in special facilities such as hatcheries. Moreover, supplementation may lead to genetic risks due to problems in brood fish collection [III] and artificial rearing with relaxed natural selection and domestication (Waples, 1991; Busack and Currens, 1995; Reisenbichler and Rubin, 1999).

If a decision to start supplementation has been made, then my findings stress the need for careful planning of the programme, including paying special attention to representative collection of broodfish. Although not studied in my thesis, mating protocols possibly mimicking natural mate choices should be considered (Fleming and Petersson, 2001). In spite of the lower lifetime survival of stocked parr compared to stocked smolts, stocking youngest (alevin, fry, young parr) stages is preferable, in order to ensure that the stocked salmon phenotype is as natural as possible. Rearing practices such as warm-water rearing, which artificially speed up individual development, should not be used. Reared juveniles should only be stocked in the river sections with very low densities of wild conspecifics and the stocking densities should be kept low. Close monitoring of population development and the effects of supplementation are essential; this also necessitates marking of all stocked fish. Finally, supplementation should be sensitive to the findings of the follow-up studies in order to represent a dynamic management tool for conservation of the best of the stock.

Sometimes the risk of extinction may be so great that a hatchery programme is needed to artificially secure the genetic resource (*ex situ* preservation) before it disappears from the wild. The prolonged overexploitation of wild Baltic salmon stocks together with a sudden increase of M74 mortality in the late 20th century lead to such a situation, in which risk of extinction was real [I]. Thus, collection of genetic material into hatcheries from the most threatened stocks was clearly justified.

Appropriate management of fisheries to ensure survival through to spawning at high enough levels is the main alternative to supplementation in cases where higher number of spawners suffice to correct situation. Maintaining fishing pressure at a sustainable level is a necessity, because without it all other efforts for long-term maintenance of a healthy fish resource would fail.

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