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Stocking of Brown Trout (*Salmo trutta L.*): Factors affecting survival and growth

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Abstract

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In this thesis, a 23-years stocking program of brown trout (*Salmo trutta*) smolts, annually released into the rivers Ume- and Vindelälven is evaluated. The statistics of homing adults caught in a fish ladder as well as individually tagged trout caught in the fishery were evaluated. Stocked anadromous trout migrated only short distances since > 95 % of the recaptured tagged fish was caught <200 km from the home river. A 50 % loss of fish was seen when they were released upriver (and above a dam) compared to released more downstreams. Relative size of survival for smolts (recapture rate) was more important than their absolute size. Few trouts migrated to smaller forest rivers in the vicinity of the larger Umeälven. Upstream migrating trouts counted in a fish-ladder showed that 42.7 % of all passing fish from 1974 to 1997 were of wild origin and that the annual average was 29 individuals per year. It is concluded that the wild anadromous trout in these rivers are near extinction despite the effort with stocking programs.

Growth and survival of stocked 1-year old brown trout were analysed in a field study where the effect of acclimatisation by keeping the fish in enclosures before stocking, increased the number and size of the fish recaptured within the stocked area, two month after the release.

The first period after stocking is of vital importance for the juvenile fish stocked into a natural habitat. Growth of stocked 1-year old brown trout released into artificial stream tanks was strongly effected by individual characteristics, density, prior residents and food level.

Competitive ability, defined as a behavioural profile is an important growth determinants. The two most dominant behavioural profiles differed in profitability depending on density and size of the fish. Large size combined with aggressive behaviour were beneficial at low competitive levels (densities), while large size and non-aggressive behaviour were beneficial at high densities. Prior residence was beneficial at intermediate and high-competitive levels but had no impact at low densities of fish. The mean growth rate of all fish decreased with increasing density.

Both food abundance and behaviour profile of juveniles affected growth. Food abundance had no effect on the number of territorial individuals. Instead, the proportions of the alternative behavioural strategies, i.e. a floating behaviour (individuals that occasionally displayed a territorial behaviour) and a non-territorial (shoaling) behaviour changed with food abundance. In the lowest food regime, more individuals displayed a non-territorial than a floating behaviour.

Keywords: Brown trout, *Salmo trutta*, hatchery reared, Carlin tags, Vie tags, PIT-tags, stocking, recapture, size, acclimatization, resident fish, food level.

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Contents

Appendix

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Lundqvist, H., Jonsson, S. & McKinnell, S.M. Are releases of anadromous brown trout compatible with conservation of wild trout? Manuscript.

II. Jonsson, S., Brännäs, E. & Lundqvist, H. 1999. Stocking of Brown trout *Salmo trutta* L.: effects of acclimatization. Fisheries Management and Ecology 6, 459-473.

III. Jonsson, S., Brännäs, K. & Brännäs, E. Behavioural profile, size and prior residence as determinants to growth in juvenile brown trout at different densities. Manuscript.

IV. Brännäs, E., Jonsson, S. & Lundqvist, H. The effect of food abundance on individual behavioural strategy and growth rate in juvenile brown trout (*Salmo trutta* L.). Submitted ms.

Paper II is reproduced by permission of the journal concerned.

Introduction

Brown trout is my favourite fish! I have devoted a lot of time to this species during my PhD studies. The trout's flexibility, both "distributionvise" as well as "behaviourvise" makes it fascinating. I am not the only one with this fascination! Brown trout attracts millions of fishermen, mostly for recreational purposes and thousands of fish biologist worldwide. Like most natural resources in aquatic environments, the species is threatened due to man made activities. Great effort is put into restoration of habitats and stocking programs of hatchery reared trout. Less effort has, however, been put into the evaluation of these activities. This is not because there is a lack of willingness to do so, more because it is expensive to conduct field studies and difficult to interpret the results.

In this thesis, I evaluate 24 years of annually stocked brown trout smolts that have been released to compensate for hydroelectric damming in the river Umeälven (Paper I). In the late 1990′s, when hundreds of thousands of 1-year parr were stocked in the upper parts of the tributary Vindelälven to improve the wild sea-running brown trout population I examined the effect of acclimatisation of fish when they faced their new habitats (Paper II). While in the field, several questions arouse: Which individuals would be most successful? How does the prey level affect their chances to grow and survive? What chances do they have when competing with prior residents, etc. Looking at the natural river in early June, I knew I would never get answers to all my questions. Instead, I scaled the river habitat down to a stream channel and conduced two behavioural studies (Papers III and IV) under controlled laboratory conditions, just to secure answers to some of my many questions.

The brown trout

Brown trout (*Salmo trutta*) is a native species to Europe – North Africa. The original distribution of this species has been modified both by extension and restriction. During a period from 1852 to 1938 the brown trout was successfully introduced into 24 countries outside its original distribution (Elliott 1994).

Due to its variable morphology and ecology the brown trout was involved in taxonomic considerations by Linnaeus already in 1758. From being classified into several species (up to 50) most people today commonly refer the different types to be interbreeding fractions of one single species, *Salmo trutta* (Elliott 1994, and references therein). Still, for conservation and management of the species, the existences of genetically distinct populations of brown trout are of importance (Carlsson 2000).

Large differences in terms of growth, age/size at maturity, survival and migratory behaviour are to be found over both small and large geographical areas (e.g. L'Abee-Lund *et al.* 1989; Elliott 1994; Jonsson *et al.* 1993).

Except for a few population of lake spawners (Jensen 1963), the brown trout depend on running water habitats for its reproduction and early development. A variety of life-history types exist depending on biotic and environmental components, while genetic differentiation appears to be greater by locality rather than by life-history type (Hindar *et al.* 1991). The population size of brown trout is primarily dependent on abiotic components such as climate, water quality and topography. These components set the frame for the productivity of the habitat (food availability) and the number of co-existing species (cf. Näslund *et al.* 1998). The management of fish stocks in running waters and the investigation of life history requirements of these populations have developed the ecological concept of "carrying capacity" (Nielsen 1993). Within these frames, processes regulating production can be both density-dependent and density-independent mechanisms (Jenkins *et al.* 1999).

According to Elliott (1994), the number of surviving individuals are mainly regulated by density-dependent survival in the early life stages of the fish rather than the number of parents or the female fecundity (Braum 1978). The unique long-term study of brown trout in Black Brows Beck by Elliot (1994) showed that although population density varied considerably between year-classes, the population was kept at an equilibrium governed initially by density-dependent processes. He observed a high density-dependent mortality during the first critical stages of trouts life, i.e. when they emerge from the gravel (Elliott 1990). After the fry stages, predation and environmental conditions becomes more important as population regulation factors (Hearn 1987). Older fish tend to form more complicated partial territories or home ranges where individuals form social hierarchies (Héland 1999; Amstrong *et al.* 1999). Several authors have assigned the individual heterogeneity of a population as the major factor affecting density-dependent regulation of populations (Hassel, 1987; Mountford 1988; Elliott 1994; Nskano 1995). The ability to hold and defend a feeding territory is suggested to be the important link between the mortality and the growth of the fish (Elliott 1994).

However, flexibility is one of the main characteristics of brown trout and the ability to become a territorial holder is just one way to survive and grow. Pucket and Dill (1985) described the occurrence of alternative behavioural strategies in coho salmon (*Onchorhyncus kisutch)* coexisting besides territorial individuals.

Some trout populations spend their whole life in their natal stream while others make feeding and/or wintering migrations to a larger river or lake within the home river, or feeding migrations to the sea, combined with wintering migrations to freshwater (Jonsson 1985) before returning to their natal stream to spawn. Different life forms also exist within the same breeding population (Jonsson 1985). The growth in the freshwater habitat can have an impact on the subsequent life-history and age at migration. Migrations, beside those for spawning purposes, are thought to have evolved to avoid adverse conditions in the habitat or to ensure an increased food supply (Elliott 1994). Generally migrating population are growing larger, having higher reproductive potential but lower survival than resident conspecific (Jonsson & Jonsson 1993). The mechanism behind seaward migration has not yet been fully determined. Seaward migrating trouts are termed smolts (Allan & Ritter 1978) and generally they reach sizes in natural rivers (Torneälven) from 11 to 30 cm (average 19 cm) and stay 2-6 years in the river (average 3.6) (unpublished observations, Swedish National Board of Fisheries, Luleå) before migration.

Besides the natural factors influencing the production of Brown trout, some of them described above, the human impact may, however, be the most important for several trout populations (e.g., Näslund 1992). To maintain or even increase the a catch of Brown trout, stocking of fish is therefore a common way to secure the trout production in waters.

Stocking procedures

Several brown trout populations are negatively affected by pollution, acidification, habitat modifications, damming and over-fishing (Laikre 1999). Due to its great commercial value, effort is put into the mitigation of these losses (Cresswell 1989). The measures used are: increased efficiency in sewage treatment, liming (Degerman & Appelberg 1992), restoration of rearing habitats (Näslund 1997), removal of manmade migration barriers, installations of fish-ladders, and restrictions in the fishery. The most used measure, alone or combined with the ones above, is to release hatchery reared trout. The purposes of these releases range from the creation of a put-and-take sport fishery to a supplementation of the natural recruitment or to reintroduce extinct populations (Cowx 1994).

Depending on the purpose of the stocking, different broodstocks are used. Also, the age and size classes, time and place of release vary accordingly (reviewed by Näslund 1992b). In dammed rivers, stocking programs are usually legislated by the government or regulated by court decisions, and are usually the most evaluated stocking events. In these systems the spawning and rearing areas are significantly reduced, resulting in declining wild populations, or even worse, extinction. Besides releases of trouts of different age classes directly into reservoirs and in regulated river areas, downstream releases of smolts below the most coastal dam are common to compensate the loss of previously healthy anadromous trout populations (Karlsson 1994; Saura *et al.* 1999). In Sweden 0.6 million sea trout smolts are released annually to the Baltic Sea, of these are 15,000-25,000 individually tagged to provide an opportunity to examine the recapture rates of stocked fish in a national evaluation program (Karlsson 1994, Carlin 1965). However, stocking of fish into waters with coexisting wild populations is less evaluated and also questioned. There are potential threats of spreading diseases, loss of genetic variability and increased hybridization (Laikre *et al.* 2000). Also, the stocking programs tend to keep fishing effort at a high level. This can contribute to an overexploitation of natural stocks (Bergelin & Karlström 1985) or of reintroduced natural stocks (Jokikokki *et al.* 1999). Generally, it has been seen that stocked fish experience high initial mortality (Berg & Jørgensen 1991) due to both abiotic and biotic factors. Several examples of overstocking exist, both numerically and in terms of size, that induce high mortalities (Kelly-Quinn & Bracken 1989 and references therein). Rearing methodology (Näslund 1992a), stocking practices (Pickering *et al.* 1982) and the origin of the stocked fish (L'Abee-Lund 1995) are other factors affecting the outcome of a stocking procedure.

The evaluation of long-term stocking programs (> 20 years) are important for future sound fishery management, both in terms of reared and wild populations. Although there have been many attempts to evaluate the success of stocking trout and factors affecting the outcome (review by Näslund 1992b; Cresswell 1981) few studies have evaluated the qualities of the released fish in relation to the receiving habitat or how different release methods effect the post stocking performance. The survival of stocked fish is likely to be regulated in a similar manner as for newly emerged fry (Berg & Jørgensen 1991). Thus, the density of the resident population will probably affect the survival of stocked fish both through density-dependent mechanisms and through a prior residence effect. The competitive advantage of prior residency has been demonstrated in several studies on juvenile territorial salmonids (Brännäs 1995; Huntingford & De Leaniz 1997; Chellappa *et al.* 1999; Deverill *et al.* 1999). For example, Atlantic salmon fry that emerge earlier than the rest of the batch have a competitive advantage by being the ones that display territorial behaviour sooner than later emerging fry (Brännäs 1995; Huntingford & De Leaniz 1997). Thus, behavioural characteristics also affect the chances of an individual fish to survive after release.

Aim of the thesis

The aim of this thesis is to evaluate a long-term stocking program, to evaluate the effect of acclimatizing and to examine some specific factors affecting growth just after stocking. The studies were undertaken under controlled experimental conditions as well as in the field.

The main questions raised were as follows:

1. Does behavioural profile, prior residence and body size affect growth in one-year old brown trout, stocked at different densities?
2. Does food abundance in the habitat effect the proportion of individuals displaying territorial versus a non-territorial behaviour, and what are the benefits of either strategy in terms of growth rate?
3. Does release site affect growth, place and rate of recapture in brown trout released as two-year old smolt?
4. Does acclimatization before release improve the poststocking performance in releases of one-year old brown trout?

Material and methods

Field studies

The river system

Umeälven and its major tributary Vindelälven together with the tributary Laisälven are the rivers in focus here. They originate from the mountain region of north-western Sweden, some 450 km from the coast. About 37 km from the coast, the river Vindelälven enters the Umeälven before the entrance into the gulf of Bothnia near 63°50'N, 20°05'E. The river Umeälven is exploited for waterpower and the terminal hydroelectric dam located 7 kilometres downstream the confluence of the two rivers is equipped with a fishladder. The fishladder is open from 20 May to 30 September each year (described by Rivinoja *et al.* 2001). A maximum of 1000 m^3/s goes through the turbine inlet and re-enters the river about 8 km downstream the fish ladder.

The extinction of naturally reproduced salmon and sea running brown trout in river Umeälven has since 1963 been compensated for by annual releases of hatchery reared two-year old smolts: 94 000 salmon smolts and 22 000 brown trout smolts. As an attempt to enhance the wild sea trout stock in the river Ume/Vindelälven system the compensatory releases of brown trout were redirected from releases of 22 000 smolt to about 120 000 one-year old trout released in nursing areas in rivers Vindelälven and Laisälven during 1997-2001.

Broodstock and hatchery routines

Initially, most of the reared brood stock originated from other rivers than river Umeälven. From 1959-1969 35 % of the releases were of unknown origin and from 1970-1978 45 % were from river Dalälven in central Sweden. Thereafter, homing trout, have been used as broodstock independent of origin (wild or hatchery). The rearing routines at the Norrfors hatchery was described by Lundqvist *et al.* (1994). Most releases are done with two-year old smolts from the Norrfors hatchery. When fish are released in other areas, they are transported with trucks. Releases of smolts are generally made in early summer, usually the last week of May, when ambient temperature increases to about 8° C.

Evaluation of the stocking program

All returning brown trout caught in the fish ladder are counted, determined by sex and weighed. This catch plus some remaining fish found below the dam build up the trout brood stock. Also, during the years 1971-1997, the adipose fin was removed of all hatchery reared fish, enabling differentiation between hatchery and wild reared fish ascending the ladder.

As a control of the hatchery production and an evaluation of the contribution of hatchery reared brown trout to the fishery, a sub sample of the released smolt is individually tagged each year (Carlin 1955). At catch, those tags are reported and analysed. These data sets will form the basis for evaluating the migration, growth characteristics and fishing mortality of released brown trout smolts (paper I).

A stocking program for one-year old fish in the upper parts of the river system evaluated the effect of acclimatization to the river before fish were released (paper II). More than 16 000 juveniles were used in this study. Eight different groups were created using Alcian blue and VIE-tags. In early June 1997, 50% of the fish were transported 400 km (5 h transportation) to the release locations in Laisälven. In each of four different stocking areas, the fish were placed into small enclosures (1 m^3), at densities of 500 fish, six days before release. Six days later the remaining fish were transported to the four stocking areas. In each stocking area 500 fish /100 m alternating between acclimatised and directly released fish were stocked. The survival, growth and migration of the stocked fish were analysed by electro fishing the release sites two months later.

Experimental studies

The experimental studies were carried out at the Umeå Marine Research Centre (UMF) (63° 35′ N, 19° 50′ E), Sweden, from 1996 until 1998. The fish originated from wild caught brown trout from Vännäå, central Sweden. They were transported to the experimental facilities and were treated according to standardized hatchery procedures.

The studies were done in 2 types of stream tanks. In three smaller stream tanks (2 x 0.5 x 0.6 m) three treatments could run simultaneously (paper III) and in one larger tank (6.5 x 2 m) divided into two parallel compartments (6.5 x 1 m) where two treatments were conducted at the same time. Both types of stream tanks were equipped with 2 PIT-antennas for registrations of PIT-tags (Passive Integrated Transponders) injected into the fish. Thus, the swimming activity of each individual was automatically recorded throughout the observation period.

Ambient temperature, light conditions and feeding level were controlled. Each fish in the two studies was observed at regular and identical time intervals. Individual status was determined stepwise. In paper (III), a number of indicators were noted for each individual; the horizontal as well as their vertical position, a switching behaviour, whether it was shoaling or solitary, attacking or being attacked. These were reduced by factor analysis into hypothetical variables or behavioural profiles. In paper (IV), each individual was classified by observation into three behavioural categories; territorial, floaters and non-territorial. These categories were described by Pucket & Dill (1980) and fitted well to the behavioural profiles extracted by factor analysis in paper (III).

Growth rate, defined as DGC was the measurement for individual performance after stocking. The per day growth coefficient (DGC) was calculated according to: $DGC = 100\ (w_2^{\sqrt{3}} - w_1^{\sqrt{3}})\ t^{-1}$, where w_2 and w_1 are the weights at the end and start of each testing period, respectively, and t is the number of days between measurements (Iwama and Tautz 1981).

Results

Paper I. The post-stocking performance after 23 years of compensatory releases of two-year-old Carlin-tagged smolt was evaluated together with the abundance, size and run-timing of wild contra reared fish returning to the fishladder in Umeälven. The study showed that stocked trouts migrated only short distances, since 95 % of all fish were caught less than all recoveries were taken more 200 km from the home river. Most fish caught in a foreign river were found in the Ångermanälven, while smaller forest rivers close to the home river had few catches. The mean recapture rate of all tagged and released trout at upriver locations was 4.4 %, while the recapture rate for release locations down river in Umeälven (below the dam) was 8.0 %. There was an overall high recapture rate in the in-river fishery in Umeälven. The relative size effect on the survival of released smolts seemed more important than absolute smolt size. Mean body weights of trouts at recapture were 0.4 kg, 0.8 kg, 1.5 kg, 2.8 kg, 4.1 for fish caught at the year of release, two, three, and four year after release, respectively. 42.7 % of all upstream migrating trouts passing the fish ladder during 1974 -1997 were of wild origin and that the annual average was 29 individuals per year . Most of these fish were females (n=16) The average date when 50 % of the wild females had passed the ladder was July 17 over all years but varied between from June 25 to August 17.

Paper II. The effect of acclimatization of fish after transportation (5 h) and prior to release was examined in one-year old hatchery brown trout. (n = 16 520) released in Laisälven at high flow conditions in June. During the electric fishing survey, two month later, a higher number of the acclimated hatchery fish were recaptured than those directly released. The size increase of stocked fish differed significantly between stocking areas and fish from the acclimated group were larger than those directly released. The recapture rate of hatchery fish varied between stocking areas (6.4 % - 17.4 %). Movements of juveniles within and between the stocking areas seemed to be low.

Paper III. The importance of behavioural profile, size and prior residence as determinants to growth in juvenile brown trout at different densities was examined in juvenile Brown trout under experimental conditions. It was found that the behavioural profile of the fish is important for growth. The two most dominant behavioural profiles differed in profitability depending on density and size of the fish. Large size and an aggressive behavioural profile were beneficial at low and intermediate competitive levels, while large size and non-aggressive behaviour were beneficial at high densities. There was also a general positive relationship between initial size and growth. Prior residence was beneficial at intermediate and high-density levels. The relative growth rate of all fish decreased with increasing density. Increased movements were not observed due to increasing densities.

Paper IV. The effect of food abundance on the proportion of individuals displaying a territorial versus a non-territorial behaviour, as well as on the benefits of either strategy in terms of growth was examined in juvenile Brown trout released into an experimental stream. We found no significant relationship between food abundance and the number of territorial individuals. Instead, the proportions of the alternative behavioural strategies, i.e. a floating behaviour (individuals that occasionally displayed a territorial behaviour) and a non-territorial (shoaling) behaviour changed with food abundance. In the lowest food regime, more individuals displayed non-territorial than floating behaviour, but these two strategies were equally represented in the highest food regime. Increasing food abundance was beneficial for all fish irrespectively of behavioural strategy. Both food abundance and behaviour affected growth significantly. The swimming activity between sections in the stream tank was, however, unrelated to territorial rank and highest in the lowest food regime.

Discussion

When juvenile trout are stocked, the probability of an individual fish to grow and survive will depend on a number of factors related to the carrying capacity of the habitat (Näslund 1992b). Growth of hatchery-reared brown trout released into streams are strongly effected by individual characteristics, density of fish, prior residence and food level. It is easy to believe that the first period after stocking in a natural habitat (or in a stream tank) is of vital importance for the survival of the juvenile fish. While in the river, its size, its behavioural response to the release location and its ability to become acclimated are all factors that will determine its future survival. In the following I discuss some parameters that are important for juvenile survival if being a naturally borne fish, a hatchery-reared fish, stocked in the river as juvenile or smolt.

Individual characteristics

Relative size was one of the most important factors for individual performance in papers I, II, III and IV. Size of fish has been related to territorial dominance in a number of salmonid species (Jenkins 1969; Wankowski & Thorpe 1979). The observed behavioural characteristics were reduced into 5 behavioural profiles (Paper III). Two of these (behavioural profile 1 and 2) included characteristics of highly competitive individuals (Pucket and Dill 1985; Abbott *et al.* 1985; Grant 1990; Bachman 1984; Armstrong et al 1999, paper IV).

Aggression and high activity were pronounced ingredients in behavioural profile 1 together with an active, probably foraging, position in the middle of the water column. Behavioural profile 1 was also strongly correlated with size. All these characteristics agree with those of a highly competitive individual (Pucket & Dill 1985; Grant 1990; paper IV). When salmon or trout parr are released into a new environment the largest individuals have the highest exploratory activity (Armstrong *et al.* 1997) and are more commonly found in areas far from the place of release (paper IV). However, the benefits of aggressive behavioural profile was decreasing with increasing density. This result agrees with studies showing that the cost of dominance increases at high densities (Brown *et al.* 1992; Armstrong *et al.* 1999).

Individuals possessing our behavioural profile 2 are typically non-shoaling and non-aggressive solitary individuals that actively switch between the feeding area (close to the feeder) and a resting place at the end of the tank. My results agree well with Bachman (1984) and Armstrong *et al.* (1999), who showed that dominant territorial individuals were free to move between feeding positions without expressing any particular aggressiveness towards conspecifics, who adjust their position according to the most dominant individuals. Behavioural profiles 1 and 2 correspond to territorial solitary individuals, also classified in paper (IV). This behavioural profile was most profitable at high densities and was strongly correlated to size.

Behaviour corresponding to an alternative behavioural profile was found besides a territorial and non-territorial shoaling behaviour (Pucket & Dill, 1985). Some individuals apply a "floating"-strategy and switch between shoaling and territorial behaviour depending on the level of competition (Paper IV). These individuals were of all sizes and had a more successful strategy than a non-territorial fish.

In comparison with the studies on Arctic charr by Brännäs *et al.* (2000), three main "competitive levels" were also identified when they were living in small groups (i.e. 5-15 individuals). One category of fish was aggressively dominant, the second category was made up of subdominant individuals that successfully competed for released food but were not aggressive or successful enough to monopolise the central area of the tank. The third category consisted of suppressed subordinate fish.

The positive effect of size was also demonstrated in Paper (I). A positive effect was found on the rate of recapture after release so that larger individuals within a release group generally had a higher survival rate. However, one important finding is that the relative size at release instead of the absolute size of fish in the stocking population of smolts seemed more important. It is surprising that the increased smolt size in our release experiment (Paper I) did not improve the recapture rates for fish released in the Umeälven. Large sized smolts are at times produced in Swedish hatcheries and are commonly believed to increase the recapture rates of fish after release. Since growth is a regulator of life-history events in salmonids it can be speculated that their timing of seaward migration had been changed, or that good growth opportunities in the hatchery affected post-stocking performance by promoting sexual maturation (Jonsson & Jonsson 1993) and block the seaward migration. However, it can also be an effect of high predation in the river and/or coastal areas after release. At present, I have no good answer to this question.

Effect of density

In paper III, increasing fish density had an overall negative effect on growth for individuals of brown trout. A negative relation between trout density and average body size has previously been demonstrated under natural conditions as well as in controlled semi-natural stream environments (Jenkins *et al.* 1999). Stocking high densities of one-year old brown trout resulted in a negative effect on the population growth (Berg & Jørgensen 1991). The authors' conclusion was that stocking fish at higher densities than the carrying capacity of the stream was more harmful than beneficial. An overall reduced growth rate may thus result in a collapse of the trout population in the stream and survival may turn out lower than that of the carrying capacity of the stream. Nielsen (1983) also found a negative relationship between stocking density and smolt production of brown trout in Danish rivers. A stocking experiment of newly emerged Atlantic salmon fry at high vs. low densities gave similar results (McMenemy 1995). Low stocking densities resulted in equal or greater densities of salmon parr with a much higher survival rate compared to stocking fry at high stocking densities. The implication of these results was that more smolts could be produced by stocking fry at lower densities over wider areas compared to stocking fry at high densities in a few spots. A limited brood stock can then be used in a more efficient way.

These findings contradict the theory that density-dependent regulation of salmonid fry populations in freshwater systems mainly is governed by mortality and that the mean growth rate of the surviving fish is independent of population density (Elliott 1994). In these situations, fry establish a mosaic of territories and the degree of competition is so extreme that only territorial individuals can utilize the available resources. Grant & Kramer (1990) suggested that territory size is independent of population density and would be a predictor for the upper limit of a juvenile salmonid populations. Also, the relationship between the size of the juvenile fish and the size of the defended area is positive, resulting from a self-thinning effect as the fish grow (Grant & Kramer 1990).

In our study, the density of trout could not be regulated by emigration. No evidence of an increased swimming activity at higher densities was found, which is expected if increased competition make some individuals search for new habitats. When juvenile brown trout were stocked in small batches throughout a long river stretch, 96 % of the recaptured fish were found in the area of their release, which suggests that their search activity was low (paper II).

Effect of prior residence

Individual trout benefit from prior residence in terms of growth at medium and high densities. When there were only 4 residents, the intruders' growth rates were as high as the residents. We have previously found that juvenile brown trout (paper IV) became territorial within a few days. A pronounced effect of prior residence has been demonstrated in several studies on fish (Brännäs 1995; Huntingford & De Leaniz 1997; Chellappa *et al.* 1999; Deverill *et al.* 1999). In territorial animals, the residents commonly win interactions between resident territory holders and intruders. In the case of stocking practices the residents may be a wild population or in an empty area stocked individuals that quickly migrate downstream from the release area and establish new feeding areas.

There are mainly two categories of hypotheses behind the prior residence effect. First, the most competitive individuals that become territorial in the first place possess such behavioural and physical attributes that they are likely to win over most intruders. This hypothesis is dealing with the resource holding power (RHP, Maynard Smith & Parker 1976) and has received support from most experimental studies (Johnsson *et al.* 1999). In the wild, the RHP-hypothesis appears valid for, e.g., emerging salmonid fry of which only 1-2 % survive and these individuals are likely to possess exceptional competitive abilities. The second hypothesis behind the positive effect of prior residence is that the value and familiarity of the achieved territorial space increases over time and the motivation for an individual to defend a territory therefore increases with time. This is the "payoff asymmetry hypothesis" (Krebs 1982). The result in our study agrees more with the second hypothesis as the size structure, and probably the physical attributes of the intruders were similar to those of the residents. The result is supported by Johnsson *et al.* (1999), who found that ownership rather than fighting ability was a strong predictor for winning fights over territories. They put forward an alternative explanation for the negative effect of being an intruder in short term experiments; there are difficulties for introduced fish to cope with learning a new environment and to cope with territory defenders.

Food level

Field observations suggest that territory size is inversely related to food abundance in juvenile stream dwelling salmonids (Dill *et al.*, 1981). Accordingly, the number of territorial individuals should increase with increasing food abundance within a given area and density of fish. There was, however, no significant increase in the number of individuals displaying a territorial behaviour with increasing food regime (paper IV). Our observation that a maximum of 4 territorial individuals could be found in the stream tank of 5 m^2 fits well to available data (Grant & Kramer, 1990), a 12 cm fish would defend territories with a mean area of 1 m^2 and larger while a 20 cm fish would need at least 4 m^2.

The ratio of the two alternative behavioural strategies, described by Pucket & Dill (1985), and used to classify individual fish in the present study, changed with increasing food abundance. In the two highest food regimes, the number of individuals that adopted any of the three behavioural tactics was equal, whereas the non-territorial was the most frequently adopted strategy in the two lowest food regimes. Thus, more individuals displayed a non-territorial behaviour at low food abundance. Also, in accordance with our results, Symons (1971) found that food abundance had no effect on the number of visible territorial fry of Atlantic salmon while the number of "dominant fry showing hiding behaviour increased when food became superabundant". It is likely that these hiding dominant fry correspond to the definition of a floating behaviour by Pucket & Dill (1985) and used in the present study.

Paper IV confirms that all behavioural categories benefit from increasing food abundance. The territorial fish had the highest growth rate regardless of food regime. However, in the highest food regime, non-territorial fish and floaters were growing nearly as fast as the territorial individuals. Thus, alternative behavioural strategies besides a territorial spacing behaviour are beneficial under conditions of high abundance. Ruzzante & Doyle (1993) found similar results when testing the effect of food regime on aggression in cichlids (*Oryzias latipes*). They showed that the non-aggressive individuals grew even faster than the aggressive ones in cases where there was a superabundance of food. In our study, the territorial individuals only displayed a pronounced aggressive behaviour the first day and had to spend little energy on territorial defence after that.

Release procedure and release location

Other factors affecting growth and survival in newly released hatchery reared fish might be related to the rearing background (White et al 1995). Hatchery reared fish have been found to forage less efficiently (Bachman 1984) and are more risk prone than wild conspecifics (Johnsson and Abrahams 1991). Elevated stress levels due to transportation and handling will also effect the behaviour of released fish and its ability to establish in the new environment. In routine stockings, fish from the hatchery are transported in tanks to the release site, where they are released directly into the water. Due to these procedures the fish arrive into the new environment in an already stressed condition (Strange, Schreck & Ewing 1978), causing the fish to be extra vulnerable to changes in environmental factors. This would be one possible explanation for the high post-stocking mortality seen in several stocking projects (e.g. Ersbak & Haase 1983). One suggested method for increasing the survival of stocked fish is to acclimatise them in enclosures before release (Paper II). The positive effect of acclimatising fish in enclosures prior to release was also seen in our study. The fish had established themselves in the area of release to a higher degree than those directly released. They were also larger and had a higher condition factor.

The area of release was also found to be of importance for the subsequent life-history of brown trout released as two year old smolt (Paper I). At release location in upriver areas the fish was recaptured at lower rates. Some individuals appeared to remain in the river. Fish released closer to the coastal area where found to undertake seaward migration to a larger extent. Successful fish that migrate to feeding areas along the coast (Svärdsson and Fagerström 1960, Paper I) have a growth advantage compared to fish that have decided to stay as residents in the stream (Paper I).

How can my findings be applied in fisheries?

When applying my results to a stocking situation and fish are released into a habitat at the level of carrying capacity, I realise that large non-aggressive individuals would have the best chances for growth and survival. Although resident fish would have an advantage, the low dispersal rates (Papers II, III, and IV) may incur local density-dependent survival sensu Elliott (1994), or at least incur a lowered growth rate for subdominant prior resident individuals (Paper IV). When stocking of fish take place into habitats regulated by density-dependent processes, the stocking event will usually have a short-lived effect and may induce negative effects for the resident population (e.g., Näslund 1992b). Berg & Jørgensen (1991) concluded that stocking fish at higher densities than the carrying capacity of the stream is more harmful than beneficial. An overall reduced growth rate due to a high number of fish may thus result in a collapse of the resident trout population in the stream, and survival may turn out lower than carrying capacity of the stream.

My results also indicate that under these circumstances stocked fish may interfere with wild conspecifics given a relative size advantage in combination with a non-aggressive behaviour profile. However, in a complex natural environment the potential impact from other age/size classes and potential predators may alter the benefits of either behaviour (cf. Greenberg *et al.* 1997).

The factors behind the low number of wild (and reared) sea trout ascending the fish-ladder each year would be the high fishing mortality of trouts both in the river and in the coastal areas at all ages. It is not easily explained why so few wild fish enter the ladder yearly: one reason would be the high fishing pressure in both coastal areas and the river. In addition, since the mid 80'ies the recaptures in the river have exceeded those in the coastal areas. Possible reasons are two major changes in the fishing legislation for the estuary and coastal areas in 1982 and 1993 respectively, while restrictions in the river, at least for sportfishing are less pronounced. Future protection of the wild brown trouts, combined with a ban (partial or total) of the fishery in these areas, would help coming generations to enjoy this fantastic fish species, the anadromous brown trout.

All studies have been approved by an ethical board

Conclusions

1. Do the behavioural profile, prior residence and body size affect growth in one-year old brown trout, stocked at different densities?

YES, their behavioural profile was found to be important for the growth and prior residence was beneficial for growth at intermediate and high densities. Size of fish was important for individual growth rate and large and aggressive fish achieved high growth rates at low and intermediate densities, while large but non-aggressive fish was favoured in high density population.

2. Does food abundance in the habitat effect the proportion of individuals displaying territorial versus a non-territorial behaviour, and what are the benefits of either strategy in terms of growth rate?

YES, the proportion of individual trout expressing non-territorial and floating behaviour were affected by increasing food level, while the proportion of fish displaying a territorial behaviour did not change with increasing food abundance. In the lowest food regime, non-territorial individuals were more common than floaters, while these two strategies were equally represented in the highest food regime. In terms of growth, increasing food abundance was beneficial for all fish irrespective of behavioural strategy.

3. Does release site affect growth, place and rate of recapture in brown trout released as two-year old smolts?

YES, trout smolts released in upriver areas had lower recapture rates, lower tendency to migrate to the sea and consequently achieved a lower growth rate compared to smolts released closer to the estuary.

4. Does acclimatisation prior to release improve the post stocking performance in releases of one-year old brown trout?

YES, trout juveniles acclimated to the release environment after transportation, prior to release were recaptured in higher numbers and at larger sizes than directly released conspecifics.

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