

# Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*)

- Implications for distributional patterns in small lotic systems

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## Abstract

Over the years, several salmonid species have been widely spread and successfully introduced all over the world. In Sweden, introduced brook trout (*Salvelinus fontinalis*) has been successful in establishing a substantial number of new populations, a fact that has raised concerns about indigenous brown trout (*Salmo trutta*) populations being outcompeted. The competitive relationships of introduced and native salmonids have received much scientific attention, yet most studies have failed to reveal the specific mechanisms by which species interact. A powerful way of dealing with interspecific competition is measuring of species-specific changes in fitness over environmental and biotic gradients, an approach that requires accurate measurements of life historical metrics. I compared the expression of life history traits in stream resident populations of 1) sympatric brook trout and brown trout, 2) allopatric and sympatric brown trout. This information was complemented by a survey on patterns of distribution and density of the two species on a larger geographical scale, covering various environmental gradients. The comparisons of sympatric and allopatric brown trout indicated that brown trout life history was effected by brook trout presence in terms of lower growth rate, delayed maturation and increased apparent mortality. The life history of brook trout was clearly shorter than that of brown trout, with higher growth rate, earlier maturation, higher fecundity and higher mortality. Data from the Swedish Electrofishing Register indicates that brown trout in many cases can withstand competition from brook trout. It should be remembered that very small streams where brook trout is most likely to be competitively dominant, probably are underrepresented in the database. Still, it seems as though certain stream characteristics are required for competitive exclusion of brown trout to occur. With stream size and productivity as the main features structuring interactions between the two salmonids, combinations of other factors like temperature, level of structural heterogeneity, amount of pools and deeper habitats and possibilities for female migration seem important on a spatially smaller scale. I suggest that behavioral differences in combination with the above factors, might gradually decrease the ability of brown trout to withstand competition from brook trout as stream-size and/or productivity declines.

## Sammanfattning

Genom åren har laxartade fiskarter spridits och etablerats på många håll världen över. I Sverige har bäckröding (*Salvelinus fontinalis*) etablerat ett betydande antal nya populationer, något som framkallat oro över eventuella effekter på inhemska populationer av öring (*Salmo trutta*). Konkurrensförhållanden mellan introducerade och inhemska laxartade fiskarter har erhållit mycket vetenskaplig uppmärksamhet. Trots det har det stora flertalet studier misslyckats med att avslöja de specifika mekanismer genom vilka arterna interagerar. Ett kraftfullt sätt att behandla mellanartskonkurrens är att mäta fitness och dess artspecifika variation över abiotiska och biologiska gradienter, ett tillvägagångssätt som kräver noggranna mått på livshistoriska karaktärer. Jag jämförde livshistoria hos strömstationära populationer av 1) bäckröding och öring i sympatri 2) öring i allopatri och sympatri. Som komplement användes data från det Svenska elfiskeregistret där tätheter och utbredning av de två arterna jämfördes i en rumsligt större skala, över olika abiotiska gradienter. Jämförelsen mellan allopatriska och sympatriska öringpopulationer indikerade att öringens livshistoria påverkades av bäckrödningens närvaro, detta i form av lägre tillväxt, senarelagd könsmognad samt högre mortalitet och/eller vandringsbenägenhet. Bäckrödningens livshistoria var tydligt kortare än öringens, med högre tillväxt, kortare generationstid, högre fekunditet samt högre mortalitet. Data från det nationella elfiskeregistret indikerar att öring i många fall klarar av att utsättas för konkurrens från bäckröding. Det bör påpekas att de mycket små vattendrag där sannolikheten för att bäckröding ska vara konkurrensmässigt dominant är störst, med stor sannolikhet är underrepresenterade i elfiskeregistret. Resultaten indikerar ändå att det krävs vissa specifika habitatkaraktärer för öring ska konkurreras ut av bäckröding. Medan vattendragsstorlek och produktivitet är de huvudfaktorer som strukturerar interaktionen mellan de två arterna, verkar habitatkaraktärer som temperatur, strukturell heterogenitet, tillgång av höljor och djupare områden samt möjligheter till habitatskiftet vara viktiga i den mindre skalan. Jag föreslår att beteendemässiga skillnader i kombination med ovanstående faktorer kan leda till en succesiv försämring av öringens förmåga att klara av konkurrens från bäckröding när vattendragsstorlek och/eller produktivitet minskar.

## Introduction

Over the years, several Salmonid species have been widely spread and successfully introduced all over the world. In Sweden, rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*), three North American salmonid species, have been frequently used for stocking purposes. However, only brook trout has been successful in establishing a substantial number of new populations. In recent years, it has become increasingly evident that the spreading of brook trout continues despite an improved awareness of the risks involved in introducing foreign species. According to Filipsson (1994), there were 41 documented populations of brook trout, mainly in the northern boreal parts of Sweden. Today, estimates of the number of naturally reproducing brook trout populations occurring in Sweden are much higher, a fact that has raised concerns about indigenous brown trout (*Salmo trutta*) populations being outcompeted (Swedish National board of fisheries 2003).

The natural distribution of brown trout ranges over the western parts of the Eurasian continent and the northernmost parts of Africa (Elliott 1994). Brook trout on the other hand is indigenous to eastern North America (McCrimmon and Campbell 1969). Today the two species coexist in both North American and European streams as a consequence of man-made dispersal. Ecologically, brown trout and brook trout have many features in common. Habitat demands and life history characteristics are quit similar for the two species (Cunjak and Power 1987), as well as temperature preferences, ability to withstand high and low temperatures (McCrimmon and Campbell 1969), feeding habits and timing of spawning (Nyman 1970, Cunjak and Power 1987). However, some differences have been suggested. Brook trout generally seems to have a higher growth rate during the first years and earlier attainment of sexual maturity (McFadden and Cooper 1964, Nyman 1970, Jensen 1971). Brown trout is generally considered more piscivorous (Scott and Crossman 1973), has a higher adult growth rate and a larger maximum size (Waters 1983). Since the two species have not evolved together, they are not likely to have developed different ways of exploiting resources. Hence, there are reasons to believe that competition for a limited resource is a strong interaction between the two salmonids, when coexisting in sympatry (Fausch 1988).

Stream dwelling Salmonids compete primarily for positions in a stream as a critical resource which provides access to food and cover (Kalleberg 1958, Chapman 1966, Hearn 1987). This territoriality can limit maximum density of juvenile salmonids in shallow streams (Grant and Kramer 1990). Territory size depends on the balance between benefits and costs of defending an area of a given size (Davies and Houston 1984). In a theoretical model developed by Hixon (1980), benefits and costs associated with feeding territories of different size were analyzed. A large territory provides more potential food but on the other hand more time must be spent defending it. Not surprisingly, Hixon found the optimal territory size to be when time available for foraging was maximized compared to time spent on defending the territory. The model predicts territory size to be negatively correlated with food availability, a pattern that has been confirmed for stream dwelling salmonids (Slaney and Northcote 1974, Dill et al. 1981). Brown trout and brook trout are both territorial species. However, several studies have indicated that brook trout is less rigid in its territorial behavior compared to other salmonids (Newman 1956, Kenleyside 1962). Kenleyside found brook trout to have a varied social behavior with territorial behavior in shallow gravelly rapids, but congregating in large numbers in pools, exhibiting a behavior typical of schooling fish. Fausch and White (1981) found that brown trout excluded brook trout from preferred resting positions in a Michigan stream. This suggests brown trout to be a more aggressive interference competitor which is in line with the findings of other studies on competition among salmonids (Kalleberg 1958,

Nyman 1970, Gibson 1973b, see also Fausch and White 1981 and Waters 1983). There are however indications that this does not apply for fry or juvenile fish where brook trout might be the more aggressive competitor (Kjellberg 1969, Nyman 1970, Fausch and White 1986). Lindberg (2001) found no difference in interference-competitive ability between the two species, but a tendency for brook trout to be less effected by attacks from brown trout, than the other way around.

Regarding North American streams, scientists and fisheries managers do not share Swedish concerns about the well being of brown trout populations. Their general view is that the native brook trout of many northeastern and Midwestern streams has been and is continuously being replaced by exotic species like rainbow trout (Gard and Flittner 1974, Kelly et al. 1980, Larson and Moore 1985, Moore et al. 1983, 1986) and brown trout (Nyman 1970, Fausch and White 1981, Waters 1983). However, a more detailed analysis of the spatial distribution of the two species reveals similar patterns in both European and North American systems.

According to Nilsson (1967) brook trout has been able to establish populations in small Swedish streams, particularly in cold headwater reaches with a relatively high proportion of ground water influx. In North America, introduced or invading brown trout has replaced brook trout in lower and middle reaches of many streams, leaving the same distributional patterns over a stream-size gradient as in Sweden (Vincent and Miller 1969, Gard and Flittner 1974, Fausch and White 1981, Kozel and Hubert 1989). The displacement of brook trout in lowland streams has been described (Waters 1983), but the underlying mechanisms are not fully understood. Suggestions in the literature include displacement of brook trout from preferred resting or feeding areas (Fausch and White 1981), predation on brook trout by brown trout (Johnson 1981) and differences in susceptibility to angling (Marshall and MacCrimmon 1970) and predation (Alexander 1976). Limitations on upstream dispersal of brown trout have been attributed to low water temperatures (Gard and Flittner 1974).

Over the years, interactions between introduced and native salmonid species have been the focus of numerous studies, yet many of them have not been appropriately designed to reveal the mechanisms by which species interact (Fausch 1988). Nevertheless, the large amount of empirical knowledge available provides an excellent basis for further developing of relevant hypotheses that can be tested in a more rigorous way. A powerful way of dealing with interspecific competition is measuring of fitness and its species-specific changes resulting from variation in physical and biotic environment. This approach requires accurate measurements of life historical metrics, something that is not easily achieved for stream dwelling fish. A life history can be defined as an organism's lifetime pattern of growth, differentiation, storage and reproduction. Age and size at maturity, fecundity and size of offspring are life-history traits of which the expression can be varied within constraints imposed by an individuals genotype. The variability of life histories among fish species is substantial. On top of this variation, a considerable amount of variation exists among and within populations. In Atlantic salmon (*Salmo salar*), age at maturity ranges from 1 year for males in several European and North American populations (Hutchings and Jones 1998), to as much as 10 years for anadromous females in northern Quebec (Power 1969). Variation among populations can also be substantial on a very small geographical scale. Brook trout populations, although close geographically on Cape Race, Newfoundland, were found to differ in age at maturation, reproductive effort and survival cost of reproduction (Ferguson, et al. 1991, Hutchings 1993a, 1994, 1996). Even within a single population, individuals responding in different ways to environmental stimuli can cause different life history strategies to prevail simultaneously (Jones 1959, Gross 1991, Hutchings 1993a).

Life-history theory can be used to predict how changes in biotic and abiotic environment influence selection on different life-history strategies. Studying life histories can answer important questions concerning fitness and its relation to physical environment, other organisms and the constraints on life history strategies imposed by physiological and genetical factors. The aim of this study was to collect and compare life history data from stream resident populations of brook trout and allopatric and sympatric brown trout. This information was to be complemented by a survey on patterns of distribution and density of the two species on a larger geographical scale, covering various environmental gradients. Based on available literature, expectations regarding interspecific differences in life history strategies included higher growth rates and earlier maturation for brook trout. Further more, I expected brown trout life history to be effected by brook trout presence. Such effects could include lower growth rate and hence, according to life history theory, delayed maturation and low mortality (Roff 1984). The existence of distributional patterns resembling those found in North America has been reported also for Swedish streams (Nilsson 1967). Using a more detailed analysis of spatial and numerical patterns in the distribution of the two species, I intended to analyze potential effects on competitive abilities caused by different life history strategies under various environmental conditions.

## Materials and methods

This study includes data from seven small boreal streams in the central and eastern parts of the county of Jämtland, central Sweden (Figure 1). This information was complemented with electrofishing data from 938 localities within the Swedish Electrofishing Register (SERS), ranging from Skåne to Västerbotten.

### Study areas

Färsån (63°13'N, 16°06'E) and Gulån (63°18'N, 15°52'E) are both tributaries to Ammerån which in turn empties into the river Indalsälven. Both streams are inhabited by sympatric populations of brown trout and brook trout. In the headwater reaches of Färsån where all sampled localities are located, the two salmonids are the only fish species present. In Gulån, burbot (*Lota lota*) exists in very low densities. Neither of the two streams have lakes within their catchment. Höglundabäcken (63°08'N, 15°51'E) is a tributary of Indalsälven which harbors populations of brown trout, brook trout and minnow (*Phoxinus phoxinus*). Sågbäcken (62°42'N, 14°21'E) empties into lake Hålen in the catchment of river Ljungan. Brown trout and brook trout coexist with populations of minnow and burbot. Both Höglundabäcken and Sågbäcken run through small tarns (3 and 14 ha). Krokdalsbäcken (63°12'N, 15°46'E) is a tributary to Indalsälven, and Stugubäcken (63°08'N, 15°34'E) reaches Indalsälven through Kvarnån. In Krokdalsbäcken, brown trout is the only fish species present, while the fish community in Stugubäcken consists of brown trout, minnow, bullhead (*Cottus gobio*), and brook lamprey (*Lampetra planeri*). No lakes are present within the catchments of the two streams. Slandromsån (63°07'N, 14°38'E) empties into lake Storsjön within the Indalsälven water course. In Slandromsån, brown trout and pike (*Esox lucius*) are present. (Table 1).

These streams run mainly through peat-bog areas and boreal woodland dominated by norwegian spruce (*Picea abies*), scots pine (*Pinus sylvestris*) and birch (*Betula pubescens*). All catchments are dominated by calcium-rich soils and the altitudinal range of sampled areas is between 225 and 415 m. a. s. l. Fish species other than brown trout and brook trout are present in low or very low densities, leaving the salmonids as dominating species in all

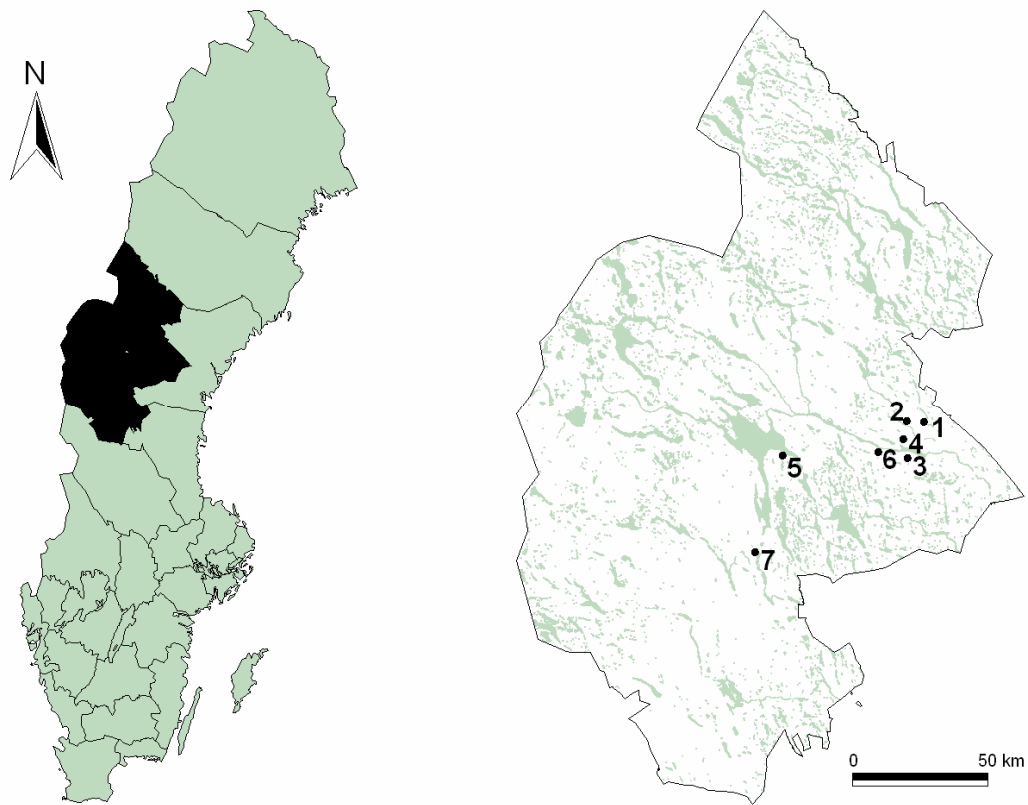


Figure 1. Map with location of the seven streams sampled, where numbers refer to table 1.

Table 1. Environmental data of sampled streams.

No	Stream	Coordinates	Altitude-span of sampled reaches (m.a.s.l.)	Average width on sampling localities (m)	Allopatry/sympatry	Other species
1	Färsån	63°13' N, 16°06' E	340-380	2.26	Sympatry	
2	Gulån	63°18' N, 15°52' E	225-280	2.25	Sympatry	Burbot
3	Höglundabäcken	63°08' N, 15°51' E	225-290	2.35	Sympatry	Minnow
4	Krokdalsbäcken	63°12' N, 15°46' E	270-300	1.82	Allopatry	
5	Slandromsån	63°07' N, 14°38' E	350-405	2.56	Allopatry	Northern pike
6	Stugubäcken	63°08' N, 15°34' E	280-325	3.24	Allopatry	Minnow, brook lamprey, bullhead
7	Sågbäcken	62°42' N, 14°21' E	385-415	3.06	Sympatry	Burbot, minnow

streams. This especially applies for the potential predators burbot and pike, which without exception are very rare. All populations of brown- and brook trout are considered stream resident with the exception of Sågbäcken where migratory behavior possibly is present among the brown trout population.

## Methods

Electrofishing was performed on three locations in each stream except in Sågbäcken where four stations were sampled. All stations, each one about 100 meters in length, were fished in three successive removals. The electrofishing apparatus used were LUGAB 1000S providing a continuous DC of 200-1000 V and BIOWAVE II ver. 2.05 providing a pulsed DC of 400- to 600 V. In Färsån, angling was used as a complementary method for collecting large individuals lacking in the data set. For this purpose, a carbonfiber rod, 0.30 mm nylon filament and a hook baited with earthworms were used. Collected fish were killed using 2-phenoxy ethanol (0.05%). All fish were measured to nearest millimeter (natural length) and weighed to nearest gram. Using length-frequency histograms, catches from each station were separated into proximate age-classes. Scales from brown trout and otholiths from brook trout were collected from fish older than yearlings. Scales and otholiths were subsampled from young-of-year fish. Age was determined using a microscope. All Individuals appearing to be young-of-year fish according to length-frequency histograms were aged as 0+ when all subsampled individuals were 0+. If length-frequency year-classes 0+ and 1+ were not separated, all individuals in the upper part of the 0+ length span were age determined. In one case, where length-frequencies of 1+ and 2+ fish were widely separated, individuals were determined as 1+ based on length frequency distributions (Gulån, data from previous studies). Sex and status of sexual maturation (Dahl 1917) were determined for all fish above the age of 0+, while subsamples were used for yearlings. In sexually mature females, gonads were weighed and fecundity was measured by counting total numbers of eggs.

All samplings were performed between August 28 and October 7 2002. Brown trout populations were considered sympatric/allopatric based solely on the presence or absence of brook trout. Data from previous studies in Gulån (Sundbaum unpublished) and Gulån and Krokdalsbäcken (Hallin 2001) were included in the analyses.

## Data analysis

Mortality was estimated by use of simple catch curves (Ricker 1975, Vetter 1988) where the slope of the linear regression model on  $\ln(N)$  against age gave instant mortality rate for the population. Necessary assumptions for this method of determining mortality are constant recruitment and a constant mortality rate over the age-span of the entire population. Fish of age 0+ were excluded from mortality analyses due to lower catchability and more patchy distributional patterns linked to the location of spawning sites. In Färsån and Krokdalsbäcken, fish of age 1+ were excluded because the catch of 1+ individuals were substantially lower than that of 2+ trout, indicating that recruitment of the 1+ cohort were unusually low. In Gulån, 1+ and 2+ trout had to be excluded due to limitations in the data-set. For the same reason, mortality rates were not estimated for brook trout populations. Age at maturity was estimated by using a logistic regression with mature/immature as a nominal, dependent variable (Trippel and Harvey, 1991). The regression was expressed as a function  $j(x)$ , describing the length-specific probability for a female to be sexually mature. The general expression of this function is  $j = \frac{1}{1 - e^{-k}}$ , where  $k$  is a linear expression of the kind:  $k = (\gamma + \beta_1 N + \dots)$  and  $\gamma$  and  $\beta_1$  are regression coefficients and  $N$  is age or length.



In the analysis of proportion of mature brown trout females in the total catch, results from Gulån and Krokaldsbäcken were based on two or more years of electrofishing data, and status and sex were externally determined.

### **Swedish Electrofishing Register (SERS)**

In the Swedish Electrofishing Register, electrofishing data is provided by various organizations and authorities. Population densities of different species are calculated according to Bohlin et al. (1989) when electrofishing is made in successive removals. If only one removal is made, densities are calculated from the average catch efficiency of the given species and age-class (Degerman and Sers 1999).

Within the total amount of data available in the register, brook trout were present on 469 localities, on 1077 fishing occasions. For each locality with brook trout present, the nearest locality without brook trout was chosen as reference. Each reference locality was always in the same size class and watercourse as, and was not allowed to deviate more than 50 meters in altitude from, the corresponding brook trout locality. Localities used in the analysis ranged from Skåne to Västerbotten and were located in the altitudinal range of 1-648 m.a.s. When data from several fishing occasions were available, the latest occasion was chosen. Localities used as reference did not deviate in altitude from brook trout localities (t-test,  $p > 0,05$ ; mean values 305 and 300 m.a.s. respectively). Given the methodology of selecting reference localities, there was no difference in geographical average position (x and y coordinates) or catchment size. In analyses, data was pooled in two classes; brook trout present and brook trout absent.

In the comparison of growth of longest under-yearling brown trout in allopatry and sympatry, the relation between allopatric under-yearling growth and Julian date, altitude and proportion of lakes within catchment was defined as follows (based on SERS-data):

*Longest under-yearling (mm)* =  $0.151 * \text{Day-number} - 0.034 * \text{Altitude} + 4,11 * \text{Lake proportion-class} + 29,026$  (Equation 1,  $p < 0.001$ ,  $r^2 = 0.269$ ,  $n = 179$ ).

Equation 1 was used to calculate expected length of longest under-yearling for sympatric brown trout.

## Results

### Life history of allopatric and sympatric brown trout populations

Comparisons were made regarding the expression of life-history traits in three sympatric and three allopatric brown trout populations. Brown trout coexisted with brook trout on all localities sampled in Färsån and Gulån, with a slight numerical dominance of brown trout. In Höglundabäcken, the two species were more segregated and the major part of the brook trout sample originated from the uppermost locality.

### Growth

Age-specific lengths tended to be higher in allopatric populations of brown trout than in sympatric ones. (Figure 2). For each respective age-class, brown trout of ages 0+ to 3+ were significantly smaller (ANOVA, Tukey-Kramer's HSD test  $p < 0.05$ ) in Färsån and Gulån than in all three allopatric populations, with the exceptions of 2+ in Gulån and 3+ in Färsån.

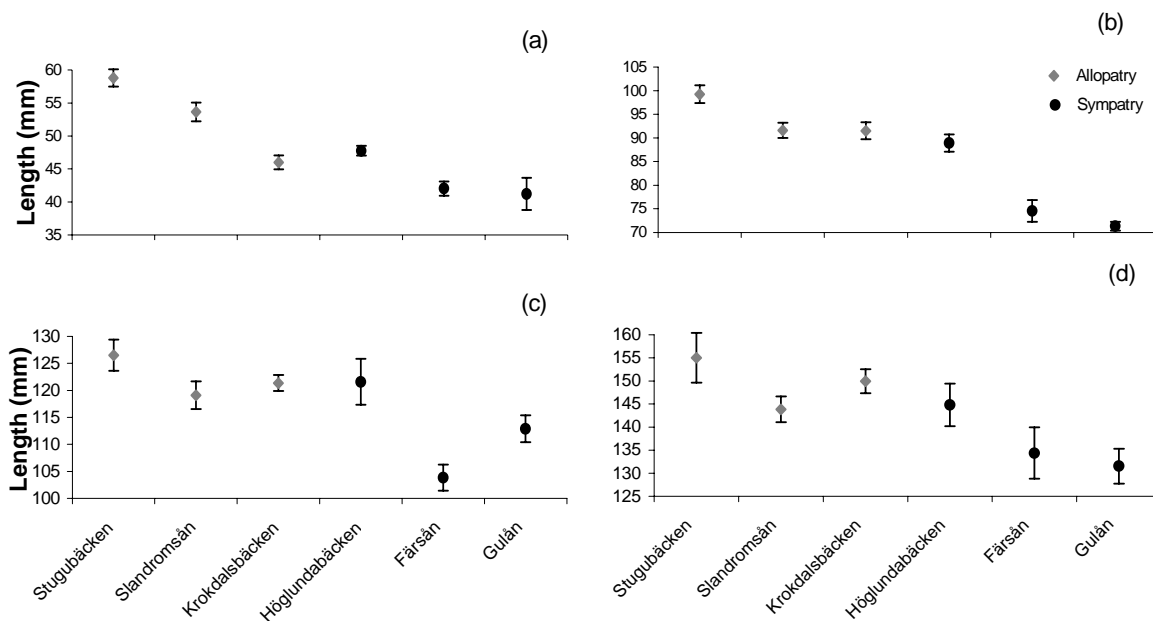


Figure 2. Age specific lengths with 95 % confidence intervals for age-classes (a) 0+, (b) 1+, (c) 2+ and (d) 3+.

Although age in many cases is not determined, the Swedish Electrofishing Register (SERS) provides information on the length of 0+ fish, based on length-frequency distributions. This data revealed no significant deviation of observed brown trout under-yearling growth in sympatric populations, from the growth expected based on equation 1 (one-sample t-test, average difference 0.5 mm,  $p = 0.575$ ,  $n = 177$ ). Hence, in contrast to the above results, growth of 0+ brown trout did not seem to be slower in the presence of brook trout.

### Maturation

Estimates were made for the age when 50% of females would be mature. For all three sympatric populations, these estimates were higher than in two of the allopatric ones, Slandromsån and Stugubäcken (Table 2). The estimate for Krokdalsbäcken was, not consistently with this pattern, higher than the ones for Gulån and Färsån. This difference was however not significant and the mature females caught in Krokdalsbäcken were younger than the ones in Färsån and Gulån (two-sample t-test,  $p < 0.05$ ). Due to data configuration abnormalities, confidence limits could not be calculated for Stugubäcken,

Table 2. Estimated age when 50 % of females have matured, with lower and upper limits of 95 % confidence intervals. Numbers within brackets under n represent mature females.

Sympatry/ allopatry	Stream	Estimated age	Lower limit	Upper limit	n
Sympatry	Färsån	3.57	3.18	3.91	121 (20)
	Gulån	3.70	3.36	4.33	48 (15)
	Höglundabäcken	4.09	3.63	4.96	145 (18)
Allopatry	Krokdalsbäcken	3.95	3.47	6.74	51 (10)
	Slandromsån	2.93	2.72	3.15	174 (43)
	Stugubäcken	2.98	-	-	113 (20)

while Slandromsån was significantly deviating from all three sympatric populations. The frequency with which mature females were caught was compared between localities where standardized electrofishing was performed in each stream respectively. Mature females were more common in allopatry than in sympatry when normalized against the total catch of individuals above the age of 0+ (figure 3). This difference was on the verge of significance (T-test ArcSin-transformed data,  $n=3$ ,  $p=0.056$ ).

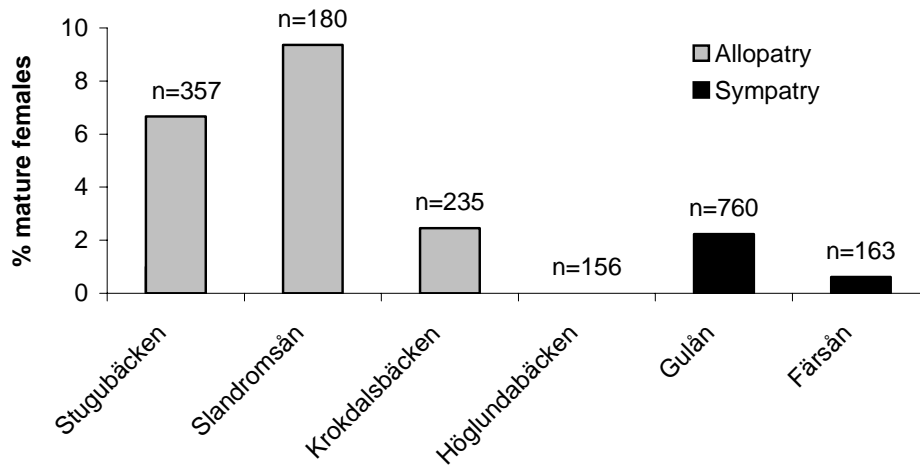


Figure 3. Number of mature females caught as proportion of over-yearling individuals.

## Mortality

Sympatric brown trout appeared to have higher mortality rates than brown trout from allopatric populations (figure 4). This pattern was significant for Färsån (ANCOVA,  $p<0.01$ ), while mortality rates in the other five populations were not significantly separated. Estimates was however higher for the sympatric populations than for all three allopatric ones (table 3).

Table 3. Estimated mortality rate with standard error.

Sympatry/ allopatry	Stream	Estimated mortality rate $\pm$ S.E	Range	n
Sympatry	Färsån	-1.47 $\pm$ 0.02	2+-5+	104
	Gulån	-1.05 $\pm$ 0.00	3+-5+	84
	Höglundabäcken	-0.85 $\pm$ 0.07	1+-5+	156
Allopatry	Krokdalsbäcken	-0.73 $\pm$ 0.15	2+-5+	305
	Slandromsån	-0.64 $\pm$ 0.09	1+-6+	231
	Stugubäcken	-0.81 $\pm$ 0.12	1+-6+	179

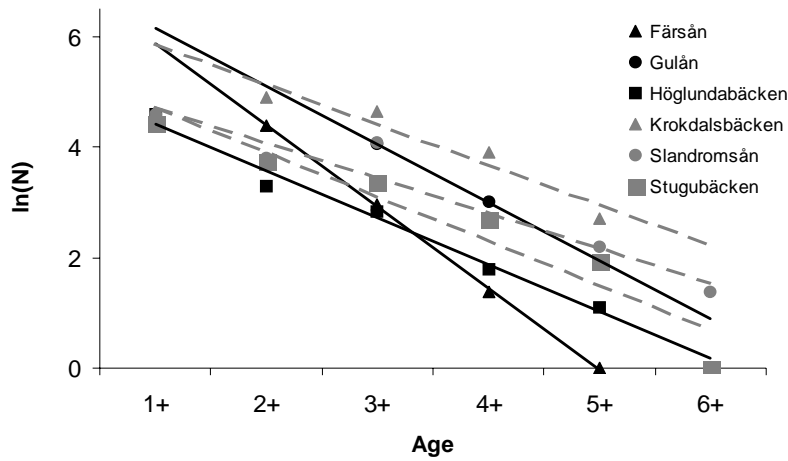


Figure 4. Catch curves with slopes representing instantaneous mortality rates for six brown trout populations. Black solid regression lines indicate sympatry and grey wedged lines allopatry.

### Fecundity

Length-specific fecundity tended to increase faster with length in two of the allopatric populations, Krokaldsbäcken and Slandromsån (figure 5). When pooled in two groups, there was however no difference in length-related rate of increase in fecundity between allopatric and sympatric populations (ANCOVA, log-transformed data,  $p=0.49$ ).

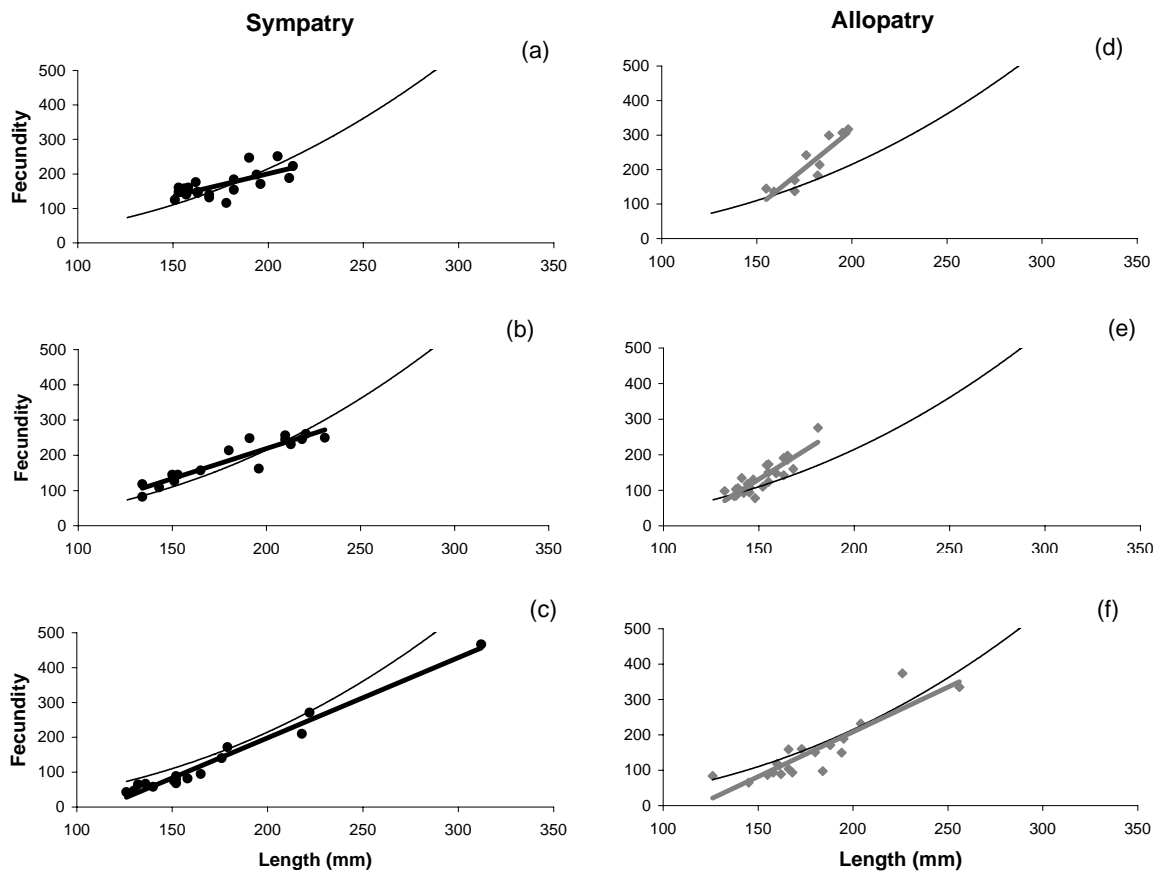


Figure 5. Length-specific fecundity in mature females for six brown trout populations, where (a) = Färsån, (b) = Gulån, (c) = Höglundabäcken, (d) = Krokaldsbäcken, (e) = Slandromsån and (f) = Stugubäcken. Thin regression lines represent average fecundity for all six populations.

## Life history of sympatric brown trout- and brook trout populations

Corresponding comparisons were made regarding interspecific differences in the expression of life historical traits. Data from the fourth sympatric stream, Sågbacken, was included in the growth analysis.

### Growth

Brook trout grew faster than brown trout in Färsån and Gulån (figure 6). In Sågbacken, brook trout tended to have a slightly higher average length in most age-classes but this pattern was not as clear as in the earlier mentioned streams. In Höglundabäcken, brook trout tended to have higher adult growth rate, while juvenile growth was similar or perhaps slightly higher for brown trout.

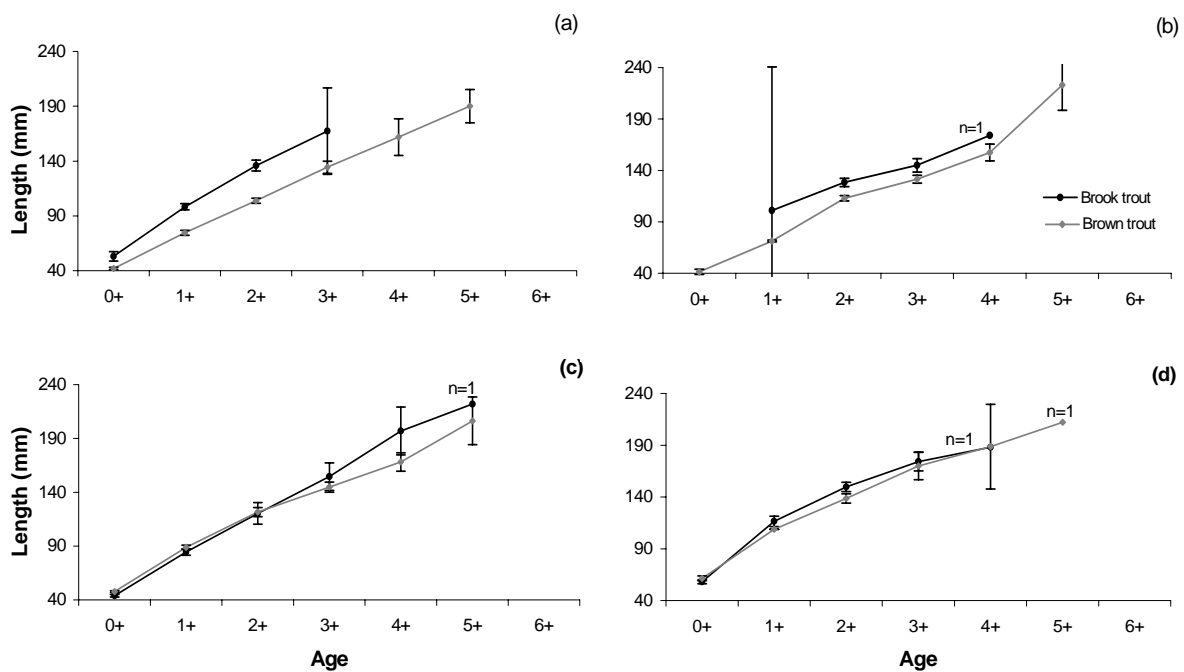


Figure 6. Growth curves for brook trout and brown trout in (a) Färsån, (b) Gulån, (c) Höglundabäcken and (d) Sågbacken.

The SERS-data provided support for the above findings of high brook trout growth rates. Brook trout yearlings were generally longer than brown trout yearlings at a given time (figure 7). From July to October, the average daily length-increase was 0.256 mm for brook trout and 0.177 mm for brown trout.

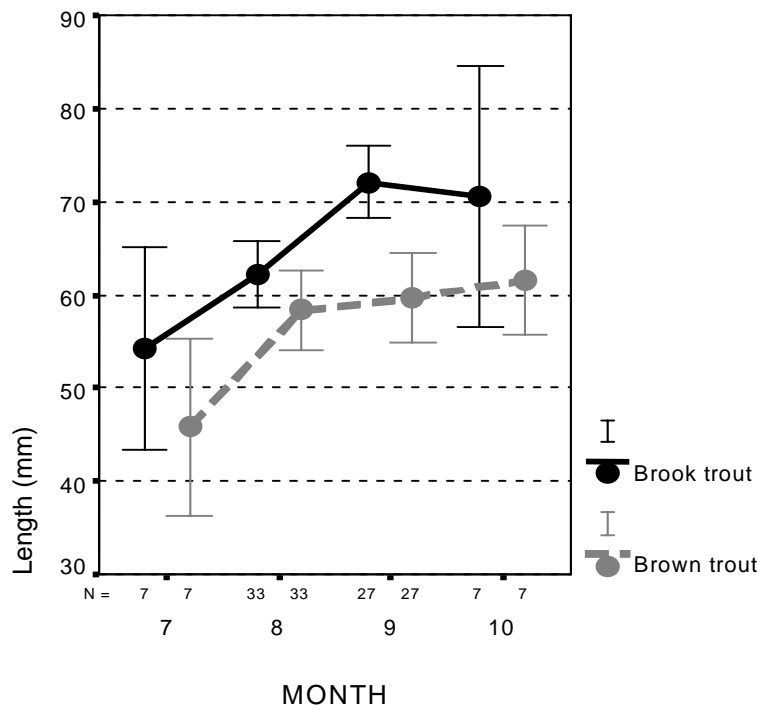


Figure 7. Length (mm) of longest underyearling (0+) of brown trout (wedged line) and brook trout (solid thin line) during July-October.

## Maturation

Estimates of the age when 50% of females have matured were lower for brook trout in all three cases (Table 4). Due to small brook trout sample sizes, confidence intervals were only estimated for Höglundabäcken, where brook trout females matured significantly earlier than all three brown trout populations. Comparing age of the mature females caught, revealed that mature brook trout females were significantly younger than brown trout females in all three streams (two-sample t-test,  $p < 0.05$ ). Mature brook trout females were smaller than mature females of brown trout in Färsån and Gulån (ANOVA, log-transformed data,  $p < 0.05$ ). In Höglundabäcken, sizes of mature females were not significantly separated.

Table 4. Estimated age when 50 % of females have matured, with lower and upper limits of 95 % confidence intervals. Numbers within brackets under n represent mature females.

Stream	Species	Estimated age	Lower limit	Upper limit	n
Färsån	Brown trout	3.57	3.18	3.91	121 (20)
	Brook trout	1.94	-	-	42 (13)
Gulån	Brown trout	3.70	3.36	4.33	48 (15)
	Brook trout	1.71	-	-	31 (27)
Höglundabäcken	Brown trout	4.09	3.63	4.96	145 (18)
	Brook trout	2.19	1.87	2.54	85 (27)

Mature brook trout females were more frequently caught than mature brown trout females, when normalized against the total catch of individuals above the age of 0+ (T-test ArcSin-transformed data,  $n=3$ ,  $p=0.024$ ) (figure 8).

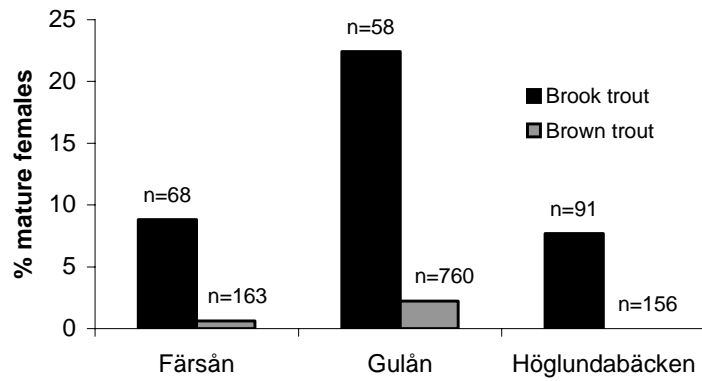


Figure 8. Number of mature females caught as proportion of over-yearling individuals.

### Fecundity

Brook trout females had a higher length-related rate of increase of fecundity than brown trout females in Färsån and Gulån (ANCOVA, log-transformed data,  $p < 0.005$  (figure 9)). In Höglundabäcken, this rate of increase did not differ between females of the two species, but brook trout fecundity was on average higher than the fecundity of brown trout (ANCOVA, log-transformed data,  $p = 0.0005$ ).

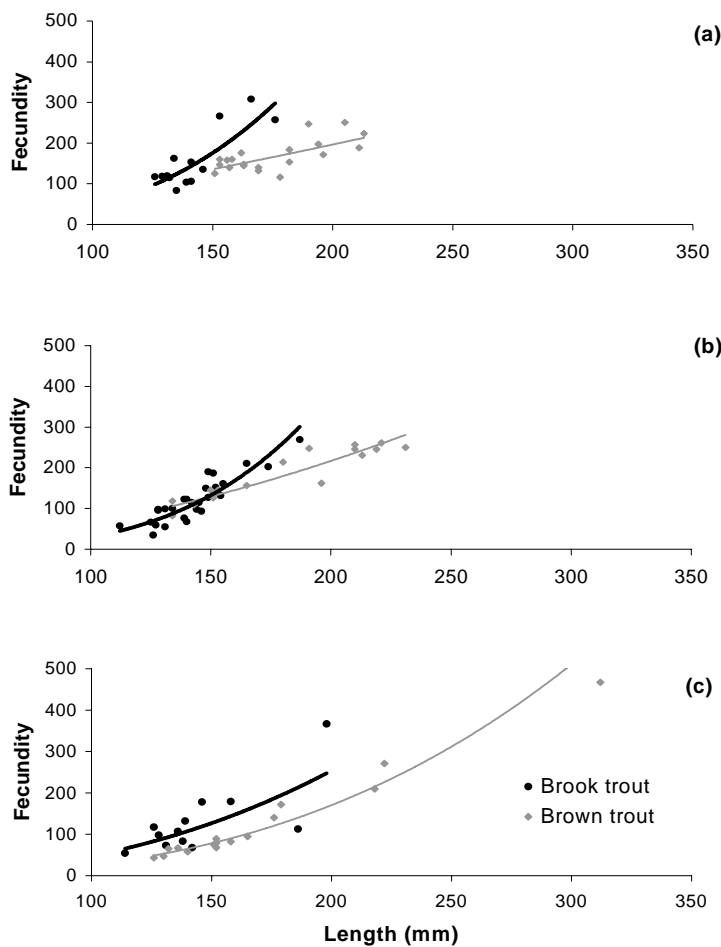


Figure 9. Length-specific fecundity for brook trout and brown trout in (a) Färsån, (b) Gulån and (c) Höglundabäcken.

## Spatial and numerical patterns of brown- and brook trout distribution

### Stream characteristics

The frequency with which brook trout has been encountered on electrofishing occasions within the Swedish Electrofishing Register, is negatively correlated to catchment area size (figure 10). Brook trout was found on 5 % of fishing occasions in streams of the smallest catchment size-class, a percentage that declined as catchment size increased. Frequency of brown trout occurrence also had a weak negative correlation with catchment size. This correlation was however much less obvious than the one for brook trout, and brown trout was less common in catchments smaller than 10 km<sup>2</sup> than in catchments between 10 and 100 km<sup>2</sup>.

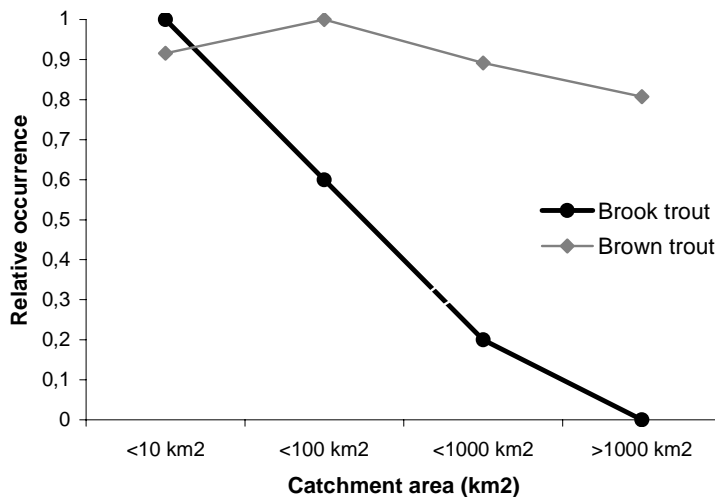


Figure 10. Relative proportion of electrofishing occasions (n=26235) where brook trout and brown trout were present. Percentage of occasions where the species was found in each catchment size-class has been divided with the maximum percentage of occurrence.

Two of the streams sampled in this study, Höglundabäcken and Sångbäcken, had small lakes within their catchments. On downstream localities, brook trout were very rare close to the lakes. On the uppermost downstream localities, brook trout were absent in both streams (figure 11). These localities were totally dominated by brown trout, of which numerical dominance over brook trout seemed to be positively correlated to level of lake impact.

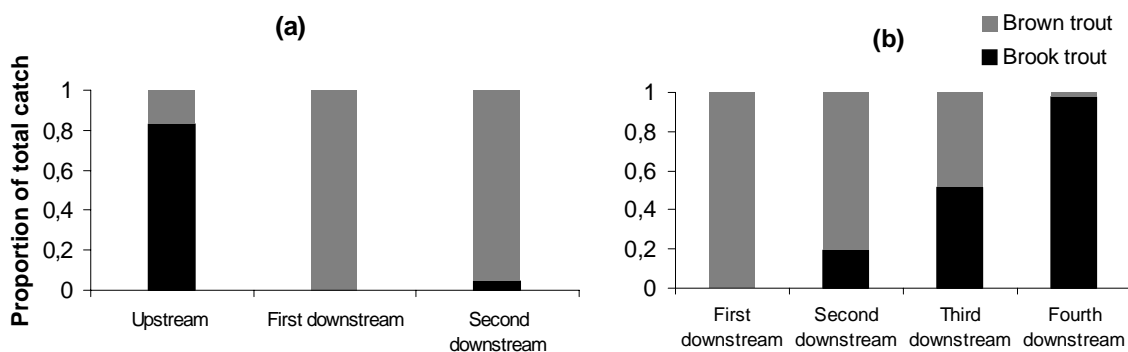


Figure 11. Relative densities of brown- and brook trout on localities situated around lakes in (a) Höglundabäcken and (b) Sångbäcken.



This pattern was confirmed when comparisons were made between habitat parameters and stream characteristics on brook trout- and reference localities in the Swedish Electrofishing Register. Brook trout localities were situated further away from lakes in both upstream and downstream direction (ANOVA,  $p < 0.001$  and  $p < 0.01$  respectively). Localities with brook trout present also had significantly (ANOVA,  $p < 0.001$ ) lower proportions of lakes within their catchments than reference localities (table 5). In contrast to the earlier mentioned results, there was no difference in average stream width. This fact however, is probably related to the means by which localities were chosen. There was a tendency for brook trout presence to be correlated to low structural heterogeneity. Average depth did not differ but maximum depth was significantly higher (ANOVA,  $p < 0.05$ ) and bottom topography more varied (ANOVA,  $p < 0.05$ ) on localities without brook trout. Brook trout localities also seemed to be dominated by finer substrate fractions (ANOVA,  $p < 0.05$ ) than reference localities. Subjectively, brook trout localities were estimated to be a bit less appropriate as habitats for juvenile salmonids. This difference was however not significant.

Despite of the fact that brook trout- and reference localities did not differ in date of sampling, altitude or geographical position, brook trout localities were on average lower in water temperature (ANOVA,  $p < 0.001$ ). This could indicate a higher degree of ground water influx. An increase in the proportion of ground water should lead to a decrease in the relative importance of air temperature in determining water temperature. To test this, correlation between air- and water temperatures on brook trout- and reference localities were compared (figure 12). Water temperature on brook trout localities showed a slightly lower rate of air-temperature related increase than did water temperature on reference localities. Differences between air and water temperatures were higher on brook trout localities than on reference localities (Mann-Whitney U-test,  $p = 0.011$ ,  $n = 564 + 776$ ). Brook trout localities also generally seemed to have lower maximum temperatures when compared to reference localities.

*Table 5. Mean value of habitat parameters and timing of sampling for localities with and without brook trout (n=469+469). Comparisons have been made using one-way analysis of variance (ANOVA).*

Parameter	Comment	Brook trout absent	Brook trout present	ANOVA
Proportion of lakes within catchment	%, classed 1-4	1,90	1,58	$p < 0.001$
Distance to lake upstream	km	4,75	6,31	$p < 0.001$
Distance to lake downstream	km	4,41	5,13	$p < 0.01$
Average stream width	m	4,00	4,26	n.s.
Maximum depth of locality	m	0,57	0,53	$p < 0.05$
Average depth of locality	m	0,22	0,21	n.s.
Streambed topography	Classed 1-3	2,15	2,03	$p < 0.05$
Water temperature	°C	11,90	10,80	$p < 0.001$
Sampling date	Julian date	232	232	n.s.
Estimated habitat value for juvenile salmonids	Classed 0-2	1,36	1,33	n.s.
Pieces of wood within water column	/ locality	5,03	4,70	n.s.
Pieces of wood within water column	/ 100 m <sup>2</sup>	3,23	3,01	n.s.
Dominating substrate	Classed 1-5	3,76	3,59	$p < 0.05$
Semidominating substrate	Classed 1-5	3,91	3,82	n.s.
Estimated water velocity	Classed 1-3	1,93	1,91	n.s.
Amount of overwater vegetation	Classed 1-3	1,19	1,14	n.s.
Amount of underwater vegetation	Classed 1-3	1,91	1,86	n.s.
Dominating type of underwater vegetation	Classed 1-3	1,60	1,51	$p < 0.05$

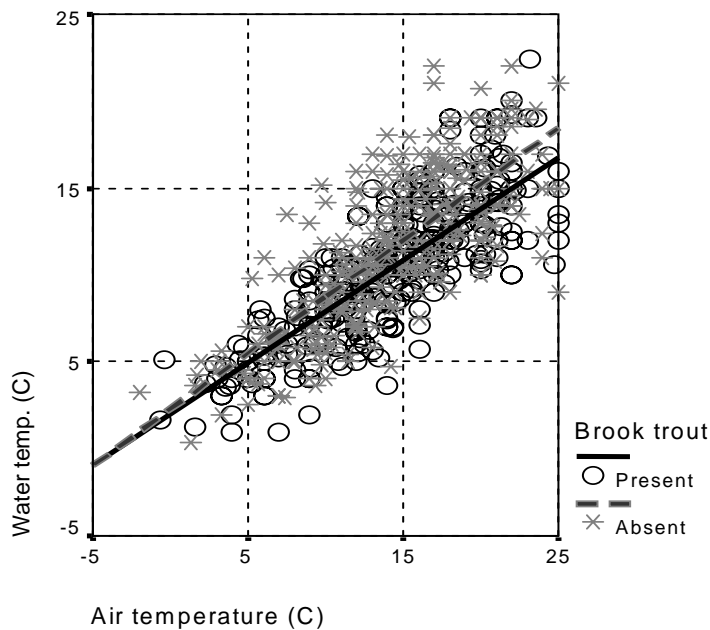


Figure 12. Measured air and water temperature on fishing occasions at localities with and without brook trout.

### Distribution and densities

Brown trout densities were significantly lower where brook trout was present (ANOVA,  $p < 0.001$ ). However, this does not necessarily mean that brook trout limits brown trout density. To distinguish between the relative importance of different factors effecting brown trout density, a GLM-ANOVA was performed. Water temperature, stream width and altitude was accounted for as covariates, while proportion of lakes within catchment, as well as presence of brook trout, was set as fixed factors. This analysis indicated that differences in brown trout density was related to altitude, stream width, and proportion of lakes (ANOVA,  $p < 0.001$ ,  $p < 0.001$  and  $p < 0.05$  respectively), rather than brook trout presence (ANOVA,  $p = 0.749$ ). There were no major differences in results when brown trout densities were divided into the age classes 0+ and >0 (Table 6).

Table 6. GLM-ANOVA on brown trout density, with water temperature, stream width and altitude as covariates and proportion of lakes and brook trout occurrence as fixed factors. Explained variation  $r^2 = 0.185$ .

Source	Type III SS	df	Mean Squ.	F	p
Corrected model	30,189	10	3,019	12,670	<0.001
Intercept	56,292	1	56,292	236,249	<0.001
Altitude	3,216	1	3,216	13,497	<0.001
Stream width	12,896	1	12,896	54,122	<0.001
Water temperature	0,505	1	0,505	2,118	0.146
Brook trout occurrence	0,024	1	0,024	0,103	0.749
Proportion of lakes	3,320	3	1,107	4,645	0.003
Brook trout * Prop.of lak.	1,095	3	0,365	1,531	0.205
Error	120,328	505	0,238		
Total	671,153	516			
Corrected total	150,517	515			

SERS-data revealed no significant difference between brown trout- and brook trout densities in small allopatric systems, while brown trout densities were higher in larger streams (figure 13a). In sympatry, brown trout densities were higher also in small streams with catchment areas smaller than 10 km<sup>2</sup> (figure 13b). However, a more detailed analysis based on the effects of wetted stream width showed that the average density of sympatric brook trout was, although not significantly, higher in the smallest streams (wetted stream width < 1 m, figure 14). Allopatric brown trout densities were significantly lower (independent t-test on log-transformed data,  $p < 0.001$ ) than total sympatric brown- and brook trout densities in small streams (catchments < 10 km<sup>2</sup>). In larger streams, no such difference was found (table 7).

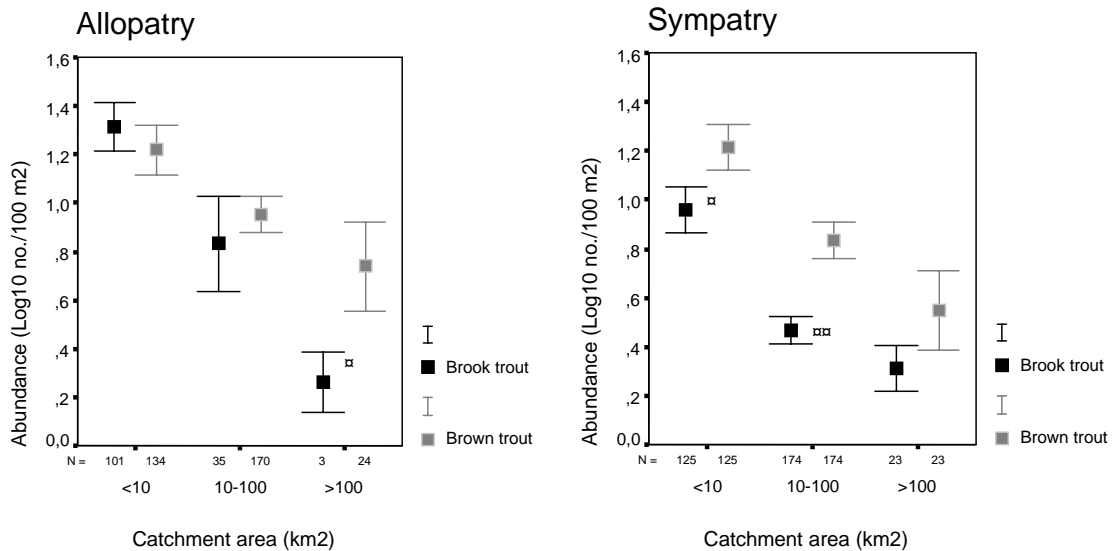


Figure 13a, b. Densities (log-transformed data) of brown trout and brook trout with 95% confidence limits, at different stream (catchment area) sizes in allopatry and sympatry. Significant differences (independent t-test) marked with \* and \*\* respectively.

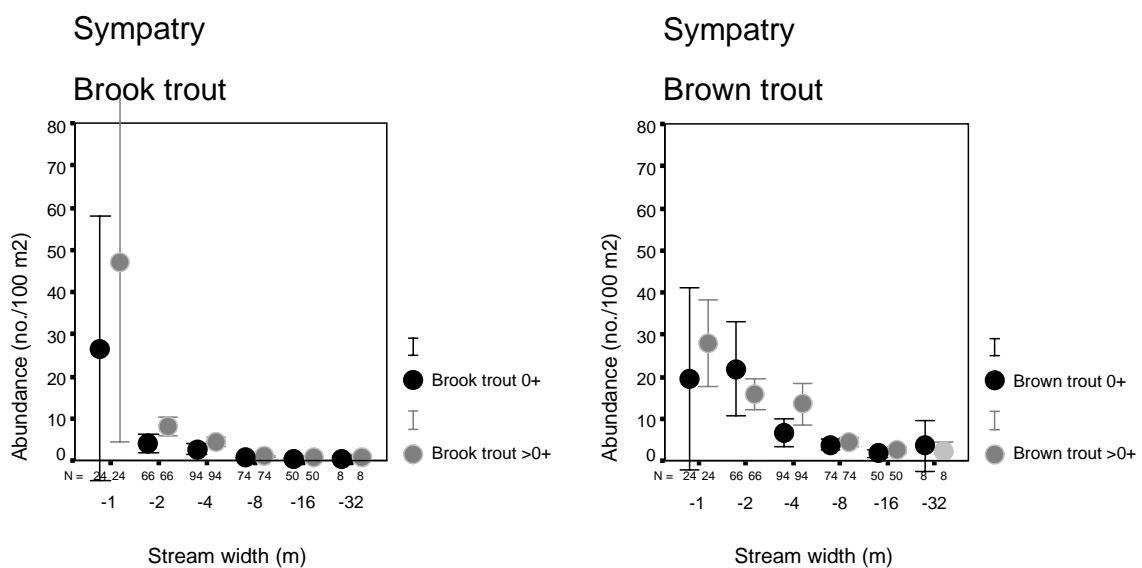


Figure 14. Average abundance of sympatric brook- and brown trout, separated in 0+ and older fish, versus wetted stream width.

Table 7. Average density (number/100 m<sup>2</sup>) of brown trout and brook trout on localities with allopatric brown trout populations and sympatric brown- and brook trout populations.

	Allopatry		Sympatry	
	<10 km <sup>2</sup>	10-100 km <sup>2</sup>	<10 km <sup>2</sup>	10-100 km <sup>2</sup>
Brown trout	42.3 (SE 7.5, n=134)	16.7 (SE 2.6, n=194)	32.3 (SE 4.4, n=125)	12.8 (SE 2.0, n=197)
Brook trout	0	0	25.3 (SE 7.4, n=125)	3.7 (SE 0.6, n=197)
Total	42.3 (SE 7.5, n=134)	16.7 (SE 3.0, n=194)	57.6 (SE 8.7, n=125)	16.5 (SE 2.4, n=197)

On brook trout localities, brown trout was present on 69,9% of fishing occasions, while the number for reference localities was 69.7%, i.e. there were no significant difference. The frequency with which pike, burbot, eurasian perch (*Perca fluviatilis*) and minnow occurred was negatively correlated with brook trout presence (table 8). Bullhead was the only species for which occurrence was positively correlated with brook trout presence.

Table 8. Occurrence (% localities with species present) on localities with brook trout present and absent. Differences in frequency of occurrence were tested with chi-square (Fisher exact test, two-way).

Species	Occurrence (%) at sites		Chi-square
	Brook trout absent	Brook trout present	
Brown trout	69,9	69,7	n.s.
Bullhead	24,3	35,4	p<0.001
Minnow	29,4	24,3	p<0,05
Burbot	16	11,1	p<0,05
Pike	16,8	7,9	p<0.001
Perch	6,2	2,8	p<0,05

## Discussion

### Life history of allopatric and sympatric brown trout populations

#### Growth

Sympatric brown trout generally seemed to grow slower than did allopatric trout. Although streams were chosen with emphasis on physical similarity, the possibility that stream characteristics to some extent were causing the observed differences in growth rate should not be ignored. Still, the most obvious difference between the streams is the presence or absence of brook trout and it therefore seems likely that brook trout had a negative impact on brown trout growth. In Höglundabäcken, the two salmonids were more segregated than in the two other streams with sympatric populations. Therefore, it seems logical that brown trout in Höglundabäcken had the highest growth rate, most resembling the ones of the three allopatric populations. In contrast to these results, the SERS-data revealed no difference between allopatric and sympatric under-yearling brown trout growth. It is however not unlikely that the effects of interspecific competition could vary between age-classes. Several authors have found brook trout to be highly abundant in pools and deeper, slow-flowing habitats (Kenleyside 1962, Griffith 1972, Stichert et al 2001). Kenleyside (1962) found brook trout to have territorial behavior in shallow rapids while congregating in large numbers in pools and backwaters. For 0+ brown trout, it could be of minor importance whether the neighbouring territories are occupied by conspecifics or brook trout. For older brown trout holding territories in pools and deeper habitats, congregations or even school-like formations of brook

trout should have negative effects on energy balance and growth. Näslund et al. (1998) compared habitat use and life history metrics of brown trout in three streams with differing fish communities. They found juvenile brown trout growth rate to be higher in sympatry than in allopatry, a pattern that was confirmed by data from the Swedish Electrofishing Register. However, in their streams sympatric brown trout populations coexisted with several species including both potential competitors and predators. In the streams of this study the sympatric populations of brown- and brook trout are almost solely interacting with each other since other fish species are practically absent. This might result in a more strictly competitive situation compared to streams where predators are present and thus reduce the relative importance of factors that could enhance juvenile growth like predation and the lower densities that might follow. Näslund and his co-authors also argues that larger stream size and higher productivity might partly explain the higher growth rates of sympatric brown trout, since these factors are positively correlated to the number of co-occurring species.

### **Maturation**

In the three sympatric populations, a lower portion of individuals caught was mature females. Long sections of these streams were sampled without a single mature female being caught, and the overall impression was that mature females were fewer and more congregated in sympatry. There seem to exist a pattern for females to mature later in the sympatric populations. Estimates on the age when 50% of females would be mature were higher for all three sympatric populations than for two of the allopatric ones, Slandromsån and Stugubäcken. 95 % confidence limits could not be calculated for Stugubäcken, but the differences were significant for Slandromsån. The estimate for Krokdalsbäcken was, not consistently with this pattern, higher than the ones for Färsån and Gulån. These differences were however not significant and the mature females caught in Krokdalsbäcken were significantly younger than those of Färsån and Gulån. It is in line with literature on life histories of fish, that the low growth rates of brown trout in sympatry should be accompanied by delayed maturation (Alm 1959, Hutchings 1993a).

### **Mortality and migration**

The previously mentioned patterns of growth and maturation should theoretically lead to low mortality rates in the sympatric brown trout populations (Roff 1984). In contrast to such expectations, estimates of mortality rate were higher for all three populations of brown trout coexisting with brook trout, than for the allopatric populations. This observation is to some extent supported by the low frequency with which mature brown trout females were caught in sympatry. However, due to the low number of age classes, the accuracy with which mortality rate could be determined was low and the only population significantly deviating from the others was Färsån. It should also be remembered that distinguishing between mortality and migration is very hard, if not impossible based on just electrofishing data. Still, the former observation is very interesting. Ontogenetic niche-shifts are known to be a key factor influencing growth and survival in size-structured populations (De Roos et al 2002). They are often associated with habitat shifts by which an individual gains access to new resources. These habitat shifts can be strongly effected by biotic interactions such as predation and interspecific competition (Persson and Eklöv 1995). Stream resident brown trout utilizes different parts of a stream during ontogeny. Juveniles dwell in shallow gravelly rapids while larger individuals often migrate to deeper areas like pools and backwaters. Studies on large-scale migration (from stream to larger stream, lake or sea) have emphasized the particular importance of such strategies for females, since their fecundity is directly depending on body size (Jonsson 1985). However, the same principles seem to apply also for small-scale within-stream habitat shifts since females need to reach a larger size than males before first maturation (Näslund et al 1998). In contrast to expectations based on life-history theory,

estimates of apparent mortality (i.e. the combined effect of mortality and migration, see Gowan and Fausch (1996)) tended to be higher in sympatry, while growth rates were lower in two of those streams. This could be explained if higher apparent mortality to a large extent were caused by an increased affinity for migration. This was not the case in the study by Näslund et al (1998), where habitat shifts were more common in allopatric populations, while sympatric populations remained in riffles throughout their life cycle. If this pattern is generally applicable, there could be a tendency for higher actual mortality in brown trout coexisting with brook trout. Again though, the effects of sympatry should depend on which species that are coexisting and on physical stream characteristics. In a low-productive small stream, brown trout females should depend heavily on habitat shifts to be able to reach the minimum size of maturity (as suggested by Näslund et al). In such a scenario, population fecundity can be assumed to depend heavily on physically large habitats like pools and beaver ponds. Intense interspecific competition could add further limitations to the ability of brown trout females to reach the size necessary for maturation, and to allocate the energy needed for reproduction. The logical consequence would then be a more or less obligate migratory behavior among the female population. It should be remembered that there is possibly a causative relationship between mortality and migration. If the necessary size for reproduction cannot be reached in riffles, and pools and deeper areas are few, it could ultimately lead to a high juvenile mortality. Since the streams in this study are characterized by small, physically constrained habitats, it is not unlikely that such combined mechanisms are involved in the observed tendency for higher apparent mortality of sympatric brown trout.

### **Fecundity**

Allopatric brown trout tended to have slightly higher rates of length-related increase in fecundity, compared to brown trout in sympatry. In two of the allopatric populations, fecundity was clearly centered above average fecundity for all six populations. Given high growth rates and early maturation, a high reproductive output is in line with expectations based on life history theory. In Stugubäcken however, fecundity was below average and no difference was found when data was pooled in allopatric and sympatric fecundity. This indicates a more complicated relationship between fecundity and the interspecific competitive situation in a given stream, or simply that other factors might be more important in determining reproductive investment. To be able to understand patterns of fecundity and reproductive investment, egg weight is a necessary metric to include in analyses. Information on egg weight was excluded in this study, mainly because of problems with interpreting egg weight-data collected during a relatively long period of time prior to spawning when egg size is increasing rapidly.

## **Life history of brown trout and brook trout**

### **Growth**

Brook trout had higher growth rates in Gulån and Färsån where the two species were less segregated than in Höglundabäcken and Sångbäcken. In the two later streams, some localities had very high densities of brook trout, which could have effected brook trout growth negatively (see Newman 1993). In Höglundabäcken, the major part of the brook trout sample originated in a locality that is smaller, situated further upstream and probably has lower water temperatures than the other localities of that stream. Still, brook trout growth rate was equal to or higher than brown trout growth rate in the two streams. Hence, it could be stated that brook trout had a potentially higher growth rate in the streams and age-classes studied. This pattern

was confirmed by the SERS-data in which length of longest young-of-year brook trout was on average higher than that of brown trout.

### **Maturation**

Mature females were more frequently caught among brook trout than brown trout. There are two possible reasons for that; either the brook trout populations contain a higher proportion of mature females or brown trout females are under-represented in the total catch due to migration to deeper areas. A combination of these two alternatives is the probable cause of the observed phenomenon. Still, most pools and deeper areas in these small streams are perfectly possible to sample by electrofishing, why the second alternative must be regarded as subordinate.

Brook trout females seem to mature much earlier than brown trout females. Estimates of the age when 50 % of females would mature were substantially lower for brook trout in all three streams where mature females of both species were caught. Due to the earlier mentioned poor sample sizes of brook trout, 95 % confidence limits could only be calculated for Höglundabäcken, where brook trout matured significantly earlier. However, the mature brook trout females caught were significantly younger than the mature brown trout females in all three streams. Further more, the mature females of brook trout were, in spite of higher growth rates, smaller than those of brown trout in both Färsån and Gulån (ANOVA, log-transformed data,  $p < 0.05$ ). This provides indirect evidence for the existence of the previously mentioned pattern also in these two streams.

### **Mortality and migration**

Mortality rates were never estimated for brook trout due to insufficient sample-sizes. However, few individuals above the age of 3+ were caught and only one out of the total catch of 640 individuals in 4 streams reached the age of 5+. Obviously these brook trout populations seem to be constituted by predominately very young individuals, indicating high mortality rates. It is unlikely that this phenomenon is caused by migration since large individuals seemed to be much less congregated in large pools than what was the case for brown trout. High mortality rates are, according to life history theory, logical consequences of the observed high growth rates and early maturation in the brook trout populations.

### **Fecundity**

Length-related rates of increase in fecundity was higher for brook trout in Färsån and Gulån, while they did not differ in Höglundabäcken. Brook trout length-specific fecundity was higher than the fecundity of brown trout in all three streams, with the exception of the lower part of the length-interval of mature females in Gulån. This is logical consequences of early maturation and high mortality. It could also possibly be an adaptation to streams where habitats suitable for female maturation are in short supply and interspecific competition among juveniles is relatively low.

## **Spatial and numerical patterns of brown- and brook trout distribution**

### **Stream characteristics**

When interacting with brown trout, brook trout is reportedly often confined to small streams and headwater reaches of river systems (Vincent and Miller 1969, Gard and Flittner 1974, Fausch and White 1981, Kozel and Hubert 1989, Rahel and Hubert 1991). A pattern where brook trout distribution is limited to headwater reaches of streams was confirmed by the

SERS-data. The negative correlation between frequency of occurrence and catchment size was much stronger for brook trout than for brown trout. It has been argued that distinct features of these small streams like low water temperatures and high proportions of upwelling groundwater are responsible for brook trout preference of small streams. Brook trout localities in the SERS-data were on average lower in water temperature than reference localities. Water temperature was also less effected by air temperature on brook trout localities, indicating a high proportion of ground water. However, according to literature, brook trout has the capacity to tolerate as high water temperatures as brown trout. In a study on microhabitat selection by and behavioral interactions between brook trout and cutthroat trout (*Onchorhynchus clarki*), brook trout showed a clear competitive dominance at 20°C (De Staso and Rahel 1994). At 10°C, the species were nearly equal competitors. Further more, areas of upwelling ground water that reortedly enables brook trout to reproduce successfully should also be available in larger streams. Hence, it seems more likely that conditions created by the above factors in combination with other physical features of these streams, provide the relief in intensity of various interspecific interactions necessary for brook trout to endure.

Localities where brook trout was present had significantly lower proportions of lakes within their catchments than reference localities. Brook trout localities were also situated further away from lakes in both up- and down stream directions. Intensified competition and higher levels of predation due to the presence of lake-bound species are possible factors that can limit the distribution of brook trout. The SERS-data showed that the frequency of brook trout occurrence was negatively correlated to occurrence of such species as burbot, pike and perch. It is also possible that the competitive relationship with brown trout shifts towards a brown trout dominance when close to lakes. This seemed to be the case in Höglundabäcken and Sågbäcken (this study) where outlet localities in both streams were totally dominated by brown trout and not a single brook trout was caught. Brook trout were present in both upstream and downstream direction from the two localities, why it seems reasonable to believe that this pattern was caused by a competitive dominance of brown trout. Stream habitats in lake outlet areas are known to be strongly influenced by the lake environment in means of water chemistry, variability of temperature and stream discharge (Spence and Hynes 1971), and productivity (Giller and Malmqvist 1998). These effects are of a nature that probably promotes brown trout dominance, i.e. higher water temperatures and levels of productivity. Brook trout localities were also situated further away from lakes on upstream locations, where habitats not in any way should be effected by lake environments. In small streams where habitats suitable for large females are in short supply, tarns and lakes can offer possibilities for female migration. Even though brook trout can use the same strategy, the population fecundity of brown trout is probably more heavily depending on the presence of large habitats suitable for female maturation. Hence, demographic advantages resulting from habitats being close to lakes are probably bigger for brown trout.

Structural heterogeneity tended to be lower on brook trout localities. Although average depth was the same, maximum depth was higher and bottom topography more varied on localities without brook trout. Bottom substrate on brook trout localities also seemed to be dominated by finer fractions compared to reference localities. It seems as though brook trout were present primarily in habitats that generally are considered as less suitable for brown trout. In the Swedish Electrofishing Register, there is information about “estimated habitat value for juvenile salmonids” for every locality sampled. This estimate was on average a bit higher for localities where brook trout was absent, but the difference was not significant. However, classing habitat value on three-graded scale is a very subjective and not very precise instrument for judging the quality of a habitat. It should also be remembered that reference localities were not chosen on the basis of brown trout presence, but solely on the absence of



brook trout. This might have the effect that there are localities unsuitable for salmonids among the reference localities, thus leading to an underestimation of the differences in habitat quality. It seems very unlikely that brook trout should actively avoid habitats with a high degree of spatial heterogeneity, why competition or predation appear to be logical reasons for the lower frequency of brook trout presence on such localities. Coarse bottom substrate is often linked to high water velocity. Hence, interactions with stream-dwelling species commonly occurring in small streams, i.e. brown trout and bullheads, seem most likely to increase in intensity in habitats with these characteristics.

### **Distribution and densities**

The importance of interactions with bullheads can be questioned since the frequency of bullhead occurrence was positively correlated with brook trout presence in the SERS-data. On the other hand, no difference was found between the frequency of brown trout occurrence on brook trout- and reference localities, indicating a weak competitive interaction between the two species. However, this pattern should be carefully interpreted. 100% of brook trout localities obviously met the basic environmental demands of salmonids, while this not necessarily was the case for reference localities. It is also possible that the smallest, uppermost headwater reaches of streams where brook trout is most likely to be competitively dominant, are underrepresented in the database due to lower value for recreational fisheries. Still, these findings suggest that brown trout in many cases can withstand competition from brook trout. Even though it is a undisputed fact that brook trout in some areas have spread at the expense of brown trout (Filipsson 1994, Spens unpublished), this indicates that for competitive exclusion of brown trout to occur, certain stream characteristics are required.

Differences in brown trout densities within the SERS-data were more related to altitude, stream width and proportion of lakes than the presence or absence of brook trout. In sympatry, brown trout densities exceeded the densities of brook trout also in streams of the smallest catchment size-class, while brook trout densities were as high or even somewhat higher (not significant) than those of brown trout in small streams and allopatry. This gives the impression of an asymmetric competitive relationship where negative effects of brown trout on brook trout in many cases are stronger than the reversed effects. In a study from 1970, Nyman suggested that a brook trout population, co-occurring with brown trout in a Newfoundland stream, were maintained by stocking from small tributaries that are inaccessible to ascending fish. In streams where brook trout dominates the upper reaches, this phenomenon could possibly promote coexistence in lower reaches with supposedly dominant brown trout. A scenario where such source-sink dynamics prevent total exclusion of brook trout over relatively long stream sections could possibly explain why sympatric localities are often numerically dominated by brown trout. Total sympatric densities of brook- and brown trout were significantly higher than allopatric brown trout densities. High densities may effect growth by increasing costs associated with aggressive interactions among individuals (Marchand and Boisclair 1998). Hence, this could provide some support for the finding of negative effects on brown trout growth from the presence of brook trout.

There was no significant difference between allopatric brown- and brook trout densities in small streams, although the average density of brook trout was slightly higher. However, this comparison could be biased if brook trout to a larger extent than brown trout were present in comparably low-productive small streams, which seems likely to be true. If this was the case, brook trout densities would have been underestimated when compared to densities of brown trout. The reported ability to tolerate high densities of conspecifics (Kenleyside 1962, Fausch 1988), higher growth rates and the apparent ability to reach a comparably large size and mature in a physically constrained habitat (this study), indicate that brook trout populations

under certain conditions potentially have a better capacity to transform low-level resources to fish biomass. This pattern could be related to either physiological or behavioral differences. Headwater reaches of streams where brook trout seem to be most successful are often unproductive due to low water temperatures, poor light conditions and low levels of nutrients. According to Hixon's model (Hixon 1980), theoretical territory size will increase as productivity decreases. At a certain point, resource levels will not be sufficient to compensate for high costs of territorial defense and the strategy of territorial behavior will collapse. Hence, somewhere on a productivity-gradient, there should theoretically exist a point where a highly aggressive and obligately territorial species like brown trout cannot maintain a positive energy balance. Of even greater interest is perhaps the theoretical point where net energy gain is too low to enable brown trout females to reach the minimum size necessary for maturation and to allocate the energy required for reproduction. Since brook trout females potentially have higher growth rates (this study) and can mature at a smaller size (Hutchings 1993, this study), this threshold level of productivity should be substantially lower for brook trout. Hence, in sufficiently low-productive habitats, the reproductive potential of brook trout should far exceed that of brown trout. What behavior that is most suitable under a given set of environmental conditions should also be affected by other factors like the frequency with which competitors are encountered (i.e. the density of fish) and the physical features of a territory. Obviously, a flat territory in a dense population will be much more energetically costly to defend than a territory with a high level of structural heterogeneity, surrounded by few competitors. The SERS-survey indicated that brook trout habitats generally were of low structural heterogeneity. Moreover, there are indications that brook trout might be more tolerant to interactions with territorial competitors (Lindberg 2001). If brook trout as reported by several authors is less rigid in its territoriality, this might lead to a more efficient use of energy and thereby enable brook trout to grow faster and reach maturity in low-productive, physically constrained habitats with comparably low levels of structural heterogeneity. SERS-data indicated that total sympatric densities in small streams were higher than those of allopatric brown trout. Hence, the presence of brook trout should add to the downsides of having strict territorial behaviour in small streams.

It remains to be tested whether or not the level of productivity where optimal behaviors shift, lies anywhere near the productivity-span of small Swedish boreal streams. However, this is not necessary for possible behavioral differences to affect interactions between the two species. Increasing relative costs from a more rigid territoriality might in combination with other factors provide a competitive disadvantage for brown trout and result in the patterns of distribution that are typical when the two species coexist. Such factors may include low amounts of suitable habitats for large fish and obstacles preventing female migration.

## **Concluding remarks**

The comparisons of sympatric and allopatric populations of brown trout indicated that brown trout life history was affected by brook trout presence in terms of lower growth rate, delayed maturation and increased apparent mortality. However, to definitely confirm these effects, more and larger samples are needed. Brook trout populations clearly had shorter life histories than those of brown trout, with higher growth rates, earlier maturation and higher fecundity and mortality. This gives brook trout a higher reproductive potential compared to brown trout, something that could have a high adaptive value in small, low-productive streams where population fecundity is low.

This thesis does not provide indisputable evidence of a strong competitive relationship between brook trout and brown trout, a task that can hardly be accomplished without manipulative experiments. Brook trout is however clearly confined to small cold streams, seemingly with low levels of structural heterogeneity. It appears as very unlikely that this pattern should be caused solely by the habitat preferences of brook trout. Out of the biotic interactions that probably limits the distribution of brook trout, competition with brown trout must be regarded as the one most likely to generate the patterns of distribution commonly observed in small streams. Data from the Swedish Electrofishing Register indicates that brown trout in many cases can withstand competition from brook trout. It should however be remembered that very small streams where brook trout is most likely to be competitively dominant probably are underrepresented in the database. Further more, this electrofishing data represents a snapshot in time with no information of past or future conditions. Still, it seems as though certain stream characteristics are required for competitive exclusion of brown trout to occur. With stream size and productivity as the main features structuring interactions between the two species, combinations of other factors like temperature, level of structural heterogeneity, amount of pools and deeper habitats and possibilities for female migration could be important on a spatially smaller scale. I suggest that behavioral differences in combination with the above factors, might gradually decrease the ability of brown trout to withstand competition from brook trout as stream-size and/or productivity declines.

While providing no definite answers, this thesis has raised some interesting questions concerning possible mechanisms by which different adaptations could lead to varying competitive abilities over a stream-size gradient. In future studies, more precise measurements on life-history metrics, together with well designed experiments, should enable us to more accurately specify environmental and biological factors responsible for the species-specific changes in fitness that obviously occurs in small lotic systems.

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